



UNIVERSIDADE FEDERAL DA BAHIA
INSTITUTO DE BIOLOGIA
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA E
BIOMONITORAMENTO



Wellington Bittencourt dos Santos

Análise de livros didáticos e validação de sequência didática sobre pluralismo de processos e evo-devo no contexto do ensino de Zoologia de Vertebrados.

Salvador, Junho de 2011



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Dissertação apresentada ao Instituto de Biologia da Universidade Federal da Bahia, para a obtenção de Título de Mestre em Ecologia e Biomonitoramento.

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Índice

| | |
|---|----|
| Capítulo 1 – A abordagem do pluralismo de processos e da evo-devo em livros didáticos de Biologia Evolutiva e Zoologia de Vertebrados | 7 |
| Resumo..... | 7 |
| Abstract | 8 |
| 1. Introdução..... | 9 |
| 2. Metodologia..... | 12 |
| 2.1. A constituição do <i>corpus</i> de análise | 12 |
| 2.2. Análise dos livros didáticos | 13 |
| 3. Resultados e discussão | 15 |
| 4. Conclusões..... | 19 |
| Referências | 19 |
| Capítulo 2 – Validação de uma sequência didática que utilizou o Pluralismo de processos e Evo-devo em explicações narrativas da conquista do ambiente terrestre | 22 |
| Resumo..... | 22 |
| Abstract | 23 |
| 1. Introdução..... | 24 |
| 2. O uso de narrativas no ensino de evolução | 29 |
| 3. Metodologia de construção, aplicação e validação da seqüência didática | 30 |
| 4. Resultados e Discussão | 34 |
| 5. Considerações finais..... | 39 |
| Referências | 40 |
| Anexo 1 - Questionário de Avaliação dos estudantes | 42 |
| Anexo 2 - Protocolo de entrevista dos estudantes | 49 |
| Anexo 3 - Sequência didática sobre Conquista do meio terrestre..... | 50 |
| Anexo 4 - Transcrição de parte da entrevista com professor da disciplina..... | 53 |
| Anexo 5 - Ementas de zoologia - Português | 55 |
| Anexo 6 -Ementa de zoologia - Inglês | 92 |

| | |
|--|-----|
| Anexo 7 - Ementa de zoologia - Espanhol | 107 |
| Anexo 8 - Ementa de evolução - Português | 136 |
| Anexo 9 - Ementa de evolução - Inglês | 171 |
| Anexo 10 - Ementa de Evolução Espanhol | 206 |
| Anexo 11 - Livros de Evolução | 233 |
| FUTUYMA | 233 |
| RIDLEY | 311 |
| STEANERS | 409 |
| Anexo 12 - Livros De Zoologia..... | 468 |
| HICKMAN..... | 468 |
| HILDEBRAND..... | 484 |
| POUGH | 492 |
| Anexo 13 – Normas para submissão de trabalhos ao periódico científico: Ciência e Educação | 499 |
| Anexo 14 – Normas para submissão de trabalhos ao periódico científico: IENCI Investigação em Ensino de Ciências..... | 504 |

Índice de Tabelas

| | |
|--|----|
| Tabela 1.1 - Livros didáticos de Biologia Evolutiva mais mencionados em ementas de cursos de nível superior localizadas através de busca no Google®, com palavras-chave em português, inglês e espanhol. ... | 13 |
| Tabela 1.2- Livros didáticos de Zoologia de Vertebrados mais mencionados em ementas de cursos de nível superior localizadas através de busca no Google®, com palavras-chave em português, inglês e espanhol. ... | 13 |
| Tabela 1.3 – Distribuição das categorias nos livros didáticos de Biologia Evolutiva. | 15 |
| Tabela 1.4– Distribuição das categorias nos livros didáticos de Zoologia de Vertebrados. | 16 |
| Tabela 4. Categorização das respostas dos estudantes. | 36 |

Índice de Figuras

| | |
|----------------|----|
| Figura 1 | 26 |
|----------------|----|

Capítulo 1 – A abordagem do pluralismo de processos e da evo-devo em livros didáticos de Biologia Evolutiva e Zoologia de Vertebrados

The treatment of process pluralism and evo-devo in higher education Evolution and Vertebrate Zoology textbooks

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Resumo

Este artigo relata os resultados de uma análise de conteúdo comparativa de três livros didáticos de biologia evolutiva e três livros didáticos de zoologia de vertebrados, muitos adotados em ementas de cursos de formação superior de biologia de diversas universidades de países de línguas latinas e anglo-saxônicas. Através de uma análise documental quali-quantitativa dos livros didáticos, realizada através de metodologia de análise de conteúdo, empreendemos uma investigação sobre a abordagem e recontextualização de conteúdos relativos à biologia evolutiva do desenvolvimento (evo-devo) e ao pluralismo de processos presentes nos livros selecionados. Com base nesta investigação, buscamos responder à seguinte pergunta: em que medida e de que maneira os referidos conteúdos, relacionados a avanços importantes que tiveram lugar na biologia evolutiva das últimas duas décadas, estão sendo recontextualizados em livros didáticos de evolução e nas discussões sobre evolução presentes em livros didáticos de zoologia de vertebrados? Os achados deste estudo indicam que os livros de evolução se encontram ainda em uma fase inicial de recontextualização dos conteúdos relativos ao pluralismo de processos e, assim, ao que tem sido denominada a síntese estendida no campo da biologia evolutiva. Contudo, eles se encontram em um estágio mais avançado de recontextualização que os livros de zoologia de vertebrados analisados, nos quais foi observada uma diversidade substancialmente menor de mecanismos evolutivos, com uma grande ênfase apenas sobre a seleção natural. Estes achados não são surpreendentes, uma vez que a idéia de uma síntese estendida ainda não está bem estabelecida na própria biologia evolutiva. No que diz respeito aos conteúdos relativos à evo-devo, foi constatado um nível mais significativo de recontextualização nos livros didáticos de ambos os campos de estudo, o que mostra que ao menos parte do conteúdo da chamada síntese estendida já alcançou o ensino superior de biologia.

Palavras-chave: Pluralismo de processos. Síntese estendida. Evo-devo. Análise de conteúdo. Livros didáticos.

Abstract

This article reports the results of a comparative content analysis of three evolutionary biology textbooks and three vertebrate zoology textbooks, significantly adopted in the biology higher education syllabuses in several universities of Latin and Anglo-Saxon countries. Through a documental quali-quantitative analysis of the textbooks, performed by using content analysis methodology, we undertook an investigation of the approach and recontextualization of contents related to evolutionary developmental biology (evo-devo) and process pluralism in the selected books. Based on this investigation, we sought to answer the following question: to what extent and in what manner those contents, related to important advances that took place in evolutionary biology in the last two decades, are recontextualized in evolution textbooks and in the discussions on evolution present in vertebrate zoology textbooks? The findings of this study show that evolution textbooks are still at an initial phase of recontextualization of the contents related to process pluralism and, thus, to what has been called the extended synthesis in the field of evolutionary biology. However, they are in a more advanced stage of recontextualization than the analyzed vertebrate zoology textbooks, in which a substantially smaller diversity of evolutionary mechanisms was observed, with a large emphasis only on natural selection. These findings are not surprising, since the idea of an extended synthesis is not well established yet in evolutionary biology itself. With regard to the evo-devo contents, a more significant level of recontextualization was observed in the textbooks of both fields, showing that at least part of the content of the so-called extended synthesis already reached biology higher education.

Keywords: Process pluralism. Extended synthesis. Evo-devo. Content analysis. Textbooks.

1. Introdução

A situação atual da biologia evolutiva é marcada por debates em torno das competências explanatórias e do potencial heurístico da teoria sintética da evolução, que têm mostrado limites importantes no que diz respeito à compreensão de uma série de fenômenos evolutivos. Estes limites têm sido postos em relevo, em particular, pela idéia de que não exclusivamente a seleção natural, mas também diversos outros mecanismos evolutivos têm papel causal e explicativo na evolução dos seres vivos, sendo importante ressaltar, contudo, que todos estes mecanismos estão situados dentro de um quadro naturalista (Sepulveda; El-Hani, 2008; Sepulveda; Meyer; El-Hani 2011). O pensamento evolutivo tem vivenciado, pois, um momento intenso de desenvolvimento e reformulações, passando por novas concepções que têm buscado caracterizar esse novo cenário na biologia evolutiva em termos de um pluralismo de processos (Pigliucci; Kaplan, 2000; Meyer; El-Hani, 2005). De um lado, não temos, em tal contexto histórico, uma revolução kuhniana, na medida em que não há incomensurabilidade entre as novas idéias em construção no cenário contemporâneo e a síntese moderna, construída entre as décadas de 1920e 1950; de outro, também não se tratam de meros ornamentos, na medida em que idéias centrais estão sendo acrescentadas à síntese, estendendo-a desde uma abordagem focada em mudanças de frequências gênicas em populações – como nos modelos da genética de populações – para uma abordagem causal-mecanicista da origem da variação e da inovação fenotípica. Podemos falar, assim, numa síntese estendida ou expandida (e.g., Kutschera; Niklas, 2004; Müller, 2007; Pigliucci; Müller, 2010).

Por pluralismo de processos, entende-se o reconhecimento da contribuição de múltiplos fatores evolutivos, que atuam de modo complementar no processo evolutivo, incluindo seleção natural, deriva gênica, plasticidade fenotípica, mecanismos epigenéticos de herança, distintos modos de especiação, construção de nicho, restrições ao processo evolutivo (sejam históricas ou desenvolvimentais), evolvibilidade, simbiogênese, auto-organização etc. Embora outros fatores evolutivos, complementares ao processo de seleção natural, têm sido propostos e apoiados empiricamente, assim como a sua relevância para a diversificação das espécies tem sido cada vez mais reconhecida, é importante ter clareza de quais, exatamente, são os pontos de debate. A proposta de uma síntese estendida, como deixa clara sua própria denominação, não incorpora uma visão anti-selecionista, dado que o papel da seleção natural continua sendo considerado de fundamental importância para a elucidação dos processos evolutivos, não obstante a efetiva perda de poder explicativo que a afeta, na exata medida em que o papel explicativo de outros fatores passa a ser reconhecido. Dizer que se trata de uma síntese estendida significa afirmar que esta é uma teoria também darwinista, sendo aplicado o adjetivo “darwinista”, como propõe Gould (2002), a teorias que mantêm um reconhecimento do papel da seleção natural no processo evolutivo, atribuindo, ademais, importância a este papel. Contudo, abordar os fenômenos evolutivos dentro de uma perspectiva pluralista requer mais do que fornecer, como numa perspectiva adaptacionista (Sepulveda; El-Hani, 2008; Sepulveda; Meyer; El-Hani, 2011; Caponi, 2011), apenas uma explicação seletional para todas as modificações observadas ao longo da história evolutiva de um clado; torna-se necessário buscar compreender a possível influência de outros mecanismos evolutivos que podem estar atuando de modo antagonístico ou sinérgico à seleção.

Dentro da construção da síntese estendida, um campo que tem merecido destaque é a biologia evolutiva do desenvolvimento, em geral referida como evo-devo, que passou a ter, nas últimas décadas, um papel central na compreensão das dinâmicas evolutivas (e.g. Arthur, 2002; Müller; Newman, 2003; Robert, 2004; Love, 2006; Müller, 2007; Laubichler; Maienschein, 2007; Carroll, 2008). O foco nesse caso recai sobre organismos multicelulares, nos quais a variação e inovação fenotípica decorrem de processos de desenvolvimento e, em particular, de morfogênese, de modo que não se pode pôr de lado a relação entre o desenvolvimento e a seleção natural, na medida em que esta atua sobre o repertório de variantes possíveis produzidas pelo desenvolvimento, a depender de vias desenvolvimentais herdadas na história de um clado.

Um importante avanço para entender a relevância dos estudos sobre o desenvolvimento se deve à compreensão de que, a um mesmo passo em que é através dele que inovações morfológicas

são produzidas e podem ser submetidas à seleção natural, ele também restringe as possibilidades de modificações que podem ser originadas. Ou seja, o desenvolvimento impõe limites para as possibilidades de variação das características que uma população pode expressar, na medida em que não é infinitamente plástico. Os processos de geração da forma no desenvolvimento resultam, pois, em restrições desenvolvimentais, que enviesam a distribuição de variantes na população, uma vez que propriedades entrincheiradas dos sistemas de desenvolvimento, ou seja, que não admitem muita variação, sob pena de o desenvolvimento ser interrompido, tornam certas formas de mudança mais prováveis do que outras. Para usar uma analogia proposta por Goodwin (1986), isso significa que a seleção não pode escolher qualquer “prato” no “restaurante” das formas variantes de vida, mas apenas “pratos” disponíveis no “cardápio” estabelecido pelo desenvolvimento, com seu espaço de possibilidades e restrições.

Uma vez que a seleção natural atua sobre um repertório limitado de possibilidades estabelecidas por restrições decorrentes dos processos desenvolvimentais – entre outras restrições, como as restrições físicas, por exemplo – a evolução e o desenvolvimento se influenciam mutuamente, embora representem processos distintos que atuam em escalas temporais diferentes: o desenvolvimento ao longo da vida do organismo, no tempo ontogenético, e de uma maneira transformacional, e a evolução ao longo das gerações que constituem uma linhagem, no tempo filogenético, e de uma maneira variacional. Compreender adequadamente a relação entre desenvolvimento e evolução, por mais íntima, requer não perder de vista estas diferenças entre os dois processos, que trouxeram, por muito tempo, dificuldades para a formulação de uma teoria evolutiva consistente e empiricamente adequada (e.g., Bowler, 2003).

Não se pode perder de vista, ainda, que o desenvolvimento, como as demais características dos indivíduos em uma população, também é alvo da seleção natural, da deriva e de outros processos, e se modifica no decorrer do processo evolutivo, canalizando caminhos possíveis de serem percorridos na evolução. Uma vez que o desenvolvimento depende, fundamentalmente, de vias desenvolvimentais herdadas de gerações anteriores e a seleção tem papel importante (mas não exclusivamente determinante) na distribuição destas vias que serão herdadas, a seleção influencia o desenvolvimento tanto quanto este a influencia. Os organismos recebem também um legado desenvolvimental por meio da herança, não somente genética, mas também epigenética, desta maneira reproduzindo em parte os padrões de desenvolvimento dos seus ancestrais (Jablonka & Lamb, 2006). Por conseguinte, é esta herança de padrões de desenvolvimento que determina os limites e as possibilidades das inovações morfológicas das futuras gerações. Consequentemente, devemos entender os estudos relativos à restrição desenvolvimental como fundamentais para a elucidação da origem e transformação das estruturas morfológicas, ao longo da história filogenética dos grupos. Estas restrições desenvolvimentais promovem um enviesamento na produção das variantes fenotípicas, dado que limitam a variabilidade em função da estrutura, caráter, composição ou dinâmica do sistema desenvolvimental (Maynard Smith et al., 1985). Contudo, elas não cumprem apenas um papel negativo na evolução, na medida em que podem também canalizar processos de mudança evolutiva, acelerando a transformação da forma orgânica nas linhagens e também estabelecendo direcionalidade no processo evolutivo (Gould, 2002).

A biologia evolutiva do desenvolvimento também desempenha outro papel importante na reestruturação do pensamento evolutivo, na medida em que contribui para a superação do gradualismo estrito que caracterizou a síntese moderna, ao fornecer uma base causal-mecanística que nos permite explicar mudanças na velocidade das taxas evolutivas, decorrentes de uma dinâmica de profusão de inovações morfológicas que podem ser explicadas com base em alterações regulatórias no desenvolvimento. A evo-devo explica como alterações nos padrões de expressão gênica, decorrentes de mudanças nas seqüências regulatórias de genes desenvolvimentais, podem conduzir a mudanças radicais na morfologia, canalizando o surgimento de novidades evolutivas (Wagner, 2000). Nestes casos, podem ser originadas grandes mudanças na morfologia dos organismos a partir de pequenas mudanças nas seqüências de DNA, com certas estruturas morfológicas surgindo através de uma transformação discreta e completa, sem uma série gradual de etapas intermediárias entre uma forma e outra, estendida ao longo de muitas gerações. Essas

mudanças homeóticas contrastam com a ênfase, na teoria sintética da evolução, assim como na teoria darwinista original, sobre o acúmulo lento e gradual de pequenas modificações ao longo de grandes escalas temporais, pela ação exclusiva do mecanismo de seleção natural. Hoje, é possível entender como mudanças no desenvolvimento podem rapidamente dar origem a indivíduos muito diferentes das médias morfológicas das populações às quais pertencem, por meio de mecanismos estudados pela evo-devo. Se, de um lado, estas mudanças morfológicas são demasiadamente rápidas para serem explicadas apenas pelo poder cumulativo da seleção natural, de outro, não podemos perder de vista que elas, como quaisquer inovações morfológicas, são submetidas à peneira da seleção. Portanto, se tiveram conseqüências evolutivas, é porque foram preservadas em determinados regimes seletivos, que favoreceram morfologias muito distanciadas da média de uma população, ou, alternativamente, em circunstâncias ambientais em que a força da seleção natural foi relaxada – por exemplo, em circunstâncias nas quais efeito fundador e deriva se tornam muito freqüentes.

Diante deste quadro de mudanças conceituais na biologia evolutiva, entendemos que emerge, na atualidade, uma necessidade de compreender a evolução em termos de um conhecimento integrado, que dê conta da interconectividade de múltiplos mecanismos evolutivos num contexto de condições históricas, desenvolvimentais e ecológicas. Por conseguinte, ao buscarmos reconstituir as dinâmicas evolutivas dos grupos vivos, devemos procurar, de modo complementar e dentro dos seus contextos ecológicos específicos, fornecer tanto explicações relativas a processos graduais, decorrentes da seleção natural, como explicações relativas a alterações morfológicas substancialmente mais rápidas, decorrentes de alterações na regulação do desenvolvimento – para nos atermos a apenas um entre muitos aspectos da construção de uma síntese estendida.

De uma perspectiva educacional, coloca-se a questão de como trabalhar com um conhecimento integrado e pluralista sobre o processo evolutivo na formação de biólogos, tanto aqueles que se direcionarão para a pesquisa acadêmica e a atuação técnica, quanto àqueles que serão professores de biologia. Temos investigado, assim, o conhecimento escolar de evolução, nos níveis médio e superior, tanto em termos de um diagnóstico de sua situação corrente, quanto em termos da construção de inovações pedagógicas que permitam não somente ensinar sobre idéias fundamentais da biologia evolutiva de modo efetivo, mas também introduzir ao menos alguns elementos dos debates contemporâneos que discutimos acima. O presente artigo está focado num objetivo de diagnóstico e no contexto do ensino superior, dentro deste programa de pesquisa mais amplo. Trata-se de um estudo sobre se e como livros didáticos de ensino superior das áreas de Biologia Evolutiva e Zoologia de Vertebrados têm tratado de conteúdos relativos ao pluralismo de processos e à evo-devo. Estamos interessados, assim, na recontextualização pedagógica dos conhecimentos sobre evo-devo e pluralismo de processos no ensino superior de evolução, uma vez que, caso tenha ocorrido, produz um marco de referência para tal recontextualização em outros campos da biologia, como o ensino de zoologia.

O foco sobre os livros didáticos se explica pelo papel que cumprem na construção da prática pedagógica, tanto na educação básica quanto no ensino superior, influenciando de modo substancial a formação de cientistas e professores de ciências. Livros didáticos influenciam fortemente a prática da maioria dos professores e a aprendizagem dos estudantes, sendo frequentemente um dos principais determinantes do currículo em ação, dado seu papel na seleção e sequenciação de conteúdos, atividades de aprendizagem, abordagens de avaliação etc. (Ball and Feiman-Nemser 1988; Beltrán et al. 2003; Gayán and García 1997). Eles são, pois, mais do que um material de leitura; eles são mediadores do conhecimento presente na ciência escolar e fontes estruturadoras das atividades em sala (DiGisi and Wilett 1995; Moody 2000). A relevância de investigar livros didáticos do ensino superior também decorre de sua influência sobre os livros da educação básica. Afinal, os primeiros desempenham um papel na formação dos próprios autores de livros didáticos voltados para a educação básica, tendo influência significativa sobre a constituição dos discursos sobre evolução presentes nas salas de aula de Biologia e Ciências.

2. Metodologia

2.1. A constituição do *corpus* de análise

Os livros didáticos submetidos à análise foram selecionados pela representatividade de seu uso em cursos de Evolução e Zoologia de Vertebrados de universidades situadas em países de língua latina e anglo-saxônica. O *corpus* de análise foi constituído por três livros didáticos de Biologia Evolutiva e três de Zoologia de Vertebrados. Para realizar tal seleção, fizemos um levantamento de ementas de tais cursos através da ferramenta de buscas Google®, utilizando, em associação com a palavra-chave “ementa”, as seguintes palavras-chave: “biologia evolutiva”, “teoria evolutiva”, “zoologia vertebrados” e “faculdade de biologia”. Os resultados da busca foram examinados na ordem fornecida pelo Google®, que atende ao critério de ordenação decrescente com base no número de acessos efetivados pelos usuários da internet. As buscas foram realizadas em português, inglês e espanhol, a fim de aumentar a representatividade da amostra de obras utilizadas em programas de formação superior de biólogos em diversas universidades do mundo anglo-saxão e latino.

Nos livros de Evolução, nosso foco de análise recaiu sobre o tratamento de diversos mecanismos evolutivos que são mencionados, no contexto contemporâneo, como parte de um pluralismo de processos. No caso dos livros de Zoologia de Vertebrados, focamos nossa atenção sobre as narrativas evolutivas acerca da conquista do ambiente terrestre e da diversificação dos tetrápodes, que têm papel chave na evolução dos vertebrados.

Devido ao fato de muitas mudanças no pensamento evolutivo, assim como novas interpretações e evidências sobre a conquista do ambiente terrestre pelos tetrápodes, terem ocorrido na última década, foram incluídas obras que continham edições nos últimos dez anos, a contar do ano em que foi feito o levantamento (2008). Afinal, tais mudanças, interpretações e evidências só poderiam estar presentes em edições mais recentes. Nossa intenção inicial era analisar 100 ementas em língua portuguesa, 100 ementas em língua inglesa e 50 ementas em língua espanhola. A decisão de realizar maior amostragem nas línguas inglesa e portuguesa foi decorrente dos seguintes pontos: (1) a língua inglesa é a mais utilizada pela comunidade científica, inclusive na literatura de cursos de formação superior em todo o mundo; (2) temos um interesse específico pelos livros didáticos usados na realidade brasileira, em cujo contexto a pesquisa está sendo desenvolvida. As ementas em espanhol foram analisadas com o intuito de verificar se o mesmo padrão encontrado em inglês e português seria repetido num idioma também muito utilizado pela comunidade científica, assim como na literatura de cursos de formação superior, especialmente no contexto ibero-americano. O mesmo padrão foi de fato encontrado nas ementas em língua espanhola, reforçando nossa confiança na seleção dos livros a serem analisados.

Ao fim do nosso esforço amostral, obtivemos valores bastante próximos em relação às cotas pretendidas. Houve, contudo, um pequeno desequilíbrio entre o número de ementas das disciplinas de Biologia Evolutiva e Zoologia de Vertebrados. Foram obtidas, ao fim e ao cabo, 106 ementas em língua portuguesa, sendo 54 de Zoologia de Vertebrados e 52 de Evolução; 94 ementas em língua inglesa, sendo 37 de Zoologia de Vertebrados e 57 de Biologia Evolutiva; e 50 ementas em língua espanhola, sendo 26 de Zoologia de Vertebrados e 24 de Evolução. Com base no número de ocorrências encontradas na busca realizada, as seguintes obras de Zoologia de Vertebrados foram identificadas como as três mais frequentemente usadas: Pough et al. (2008), Hickman et al. (2007) e Hildebrand; Goslow (1998). Entre as três obras de evolução, por sua vez, temos: Ridley (2006), Futuyama (2009) e Stearns; Hoekstra (2005). Nas Tabelas 1 e 2, os resultados dos levantamentos de livros didáticos são apresentados de modo sintético, incluindo alguns outros livros mencionados numa série de ementas. As tabelas completas, incluindo todos os livros encontrados na busca, as ementas integralmente transcritas e os endereços dos websites dos quais estas foram extraídas, podem ser solicitadas aos autores do artigo.

Tabela 1.1 - Livros didáticos de Biologia Evolutiva mais mencionados em ementas de cursos de nível superior localizadas através de busca no Google®, com palavras-chave em português, inglês e espanhol.

| Biologia evolutiva | Inglês | Português | Espanhol | Total |
|--------------------------------------|---------------|------------------|-----------------|--------------|
| Futuyma (2009) | 17 | 34 | 20 | 71 |
| Ridley (2006) | 16 | 15 | 15 | 46 |
| Stearns & Hoekstra (2005) | 15 | 7 | 11 | 33 |
| Freeman & Herron (2007) | 14 | 5 | 9 | 28 |
| Dawkins (2009) | 8 | 4 | 8 | 20 |

Fonte: Bittencourt-dos-Santos. (2011)

Tabela 2.2- Livros didáticos de Zoologia de Vertebrados mais mencionados em ementas de cursos de nível superior localizadas através de busca no Google®, com palavras-chave em português, inglês e espanhol.

| Zoologia de Vertebrados | Inglês | Português | Espanhol | Total |
|---------------------------------------|---------------|------------------|-----------------|--------------|
| Pough et al. (2008) | 12 | 45 | 5 | 62 |
| Hickman et al. (2007) | 9 | 18 | 23 | 50 |
| Hildebrand & Goslow (1998) | 0 | 31 | 4 | 35 |
| Kardong (2008) | 2 | 2 | 0 | 4 |

Fonte: Bittencourt-dos-Santos. (2011)

2.2. Análise dos livros didáticos

Uma vez selecionado o *corpus* da análise, os livros foram submetidos a uma análise de conteúdo (Bardin, 2000), um conjunto de técnicas de análise das comunicações que utiliza procedimentos sistemáticos e objetivos de descrição do conteúdo das mensagens. Através da busca de indicadores, os quais podem ser qualitativos e/ou quantitativos, este método de análise possibilita acessar tendências presentes, muitas vezes de modo implícito, nas mensagens contidas nos textos. Além disso, ele torna possível realizar inferências a respeito das condições de produção/recepção das mensagens encontradas nos livros analisados. Entre as técnicas de análise de conteúdo, utilizamos a análise categorial, que envolve operações de desagregação dos textos em unidades de análise (ou registro), as categorias, construídas através de reagrupamentos analógicos.

Bardin propõe três etapas no método de análise de conteúdo: (I) pré-análise; (II) análise; (III) categorização. Durante a pré-análise, foi realizada uma “leitura flutuante” do material, ou seja, uma primeira leitura, menos sistemática, que permitiu uma familiarização inicial com os livros e, ao mesmo tempo, o reconhecimento e identificação das unidades de registro buscadas. Os reagrupamentos feitos na técnica de análise categorial são obtidos pela busca de características compartilhadas por elementos do texto, o que, por sua vez, pode ser feita mediante critérios semânticos (i.e., busca da presença de um mesmo significado em um determinado contexto) ou sintáticos (como a presença compartilhada de signos lingüísticos precisos). Em nosso trabalho, utilizamos um recorte de ordem sintática, com as unidades de registro sendo localizadas a partir de palavras-chave previamente definidas, que indicavam fatores evolutivos considerados numa visão pluralista da evolução. Tal busca obedeceu aos critérios de exaustividade, segundo o qual se deve esgotar a totalidade da comunicação, não sendo permitidas incompletudes ou omissões; e de representatividade, segundo o qual a amostra deve representar o universo da análise em sua totalidade. No caso específico de nosso estudo, o universo analisado correspondeu aos seis livros selecionados em sua inteireza.

Foram utilizados como indicadores de busca as seguintes palavras-chaves, as quais, quando encontradas nos textos, correspondem às nossas unidades de registro: “seleção” e “seleção natural”, para identificação do mecanismo de seleção natural; “evo-devo”, “genes hox” e “desenvolvimento”, para a biologia evolutiva do desenvolvimento; “deriva” e “deriva gênica”, para deriva gênica; “mecanismos macroevolutivos” e “macroevolução”, para os mecanismos macroevolutivos; “especiação”, para identificar distintos modos de especiação; “auto-organização”, “simbiogênese”, “restrição” e “construção de nicho”, para os respectivos fatores evolutivos.

Como algumas das unidades de registro definidas em nossa busca poderiam também estar

sendo utilizadas fora de um contexto evolutivo propriamente dito, realizamos interpretações do contexto em que os respectivos termos foram encontrados e, deste modo, determinamos a exclusão de casos em que o assunto tratado não era de fato de caráter evolutivo, como no caso dos termos “desenvolvimento” ou “seleção”, que muitas vezes apareceram aplicados em sentido lato, escapando ao escopo de nossos interesses.

Torna-se necessário esclarecer e salientar que a coleta e interpretação de dados foram concebidos como parte de um processo dialógico estruturado pelas intenções e os procedimentos da pesquisa (Martins 2006). Portanto, nunca pensamos nas unidades de registro como "dados brutos", de onde se poderia obter categorias por meio de processo indutivo. As nossas categorias foram previamente estabelecidas mediante uma consideração de critérios de análise estabelecidos a partir dos nossos objetivos: levar a cabo uma investigação sobre a abordagem e recontextualização de conteúdos relativos a desenvolvimentos recentes da Biologia Evolutiva, em particular, o pluralismo de processos e a evo-devo em livros didáticos de Evolução e de Zoologia de Vertebrados. Conseqüentemente, adotamos palavras-chave relacionadas aos próprios mecanismos evolutivos e à evo-devo para compor nossas categorias, visto que, para responder as questões de pesquisa do presente estudo, precisamos verificar nos livros a presença ou ausência de explicações relativas à evolução do desenvolvimento e suas relações com a seleção natural, bem como de múltiplos mecanismos evolutivos. Utilizando tais categorias, foi possível verificar até que ponto as contribuições recentes relativas à evo-devo e ao pluralismo de processos são abordadas, em primeiro lugar, nos livros didáticos de Biologia Evolutiva, nos quais assumimos ser mais provável sua recontextualização didática, e, em segundo lugar, nos livros didáticos de Zoologia de Vertebrados.

A lista de mecanismos que utilizamos foi elaborada com base na literatura sobre evolução utilizada na fundamentação teórica deste projeto, tendo sido, ainda, complementada através da consulta a um pesquisador da área de Biologia Evolutiva, Diogo Meyer (IB-USP). Considerando também a evo-devo, chegamos à seguinte lista de categorias: Seleção natural, Deriva gênica, Efeito fundador, Mecanismos macroevolutivos, Simbiogênese, Especiação, Construção de nicho, Restrições, Auto-organização e Evo-devo. Estas categorias foram utilizadas para examinar os índices remissivos e realizar uma varredura geral de todas as obras visando identificar as unidades de registro.

No caso dos livros de Zoologia de Vertebrados, foram examinados em detalhe conteúdos relativos à diversificação dos tetrápodes durante a conquista do meio terrestre, os quais são contemplados em um capítulo específico dedicado a esta transição. Este capítulo foi analisado integralmente. Foi feita também uma busca de novas unidades de registro por meio dos índices remissivos, utilizando-se as mesmas palavras-chaves acima. Foram localizados tais indicadores em todos os capítulos do livro, além do capítulo específico sobre a conquista do meio terrestre. Deste modo, foi possível identificar a presença de explicações evolutivas abordadas pelo livro dentro e fora do contexto no qual são discutidos conteúdos específicos sobre a diversificação dos tetrápodes após a conquista do ambiente terrestre, o caso escolhido para nossa análise no caso da Zoologia de Vertebrados.

Na fase de análise, realizamos o processo de transcrição das “unidades de contexto”, sendo que estas correspondem aos trechos do texto nos quais estão contidas as unidades de registro encontradas. A partir das unidades de contexto, foi possível analisar de modo mais preciso o significado atribuído ao termo ou conceito de interesse que estava sendo utilizado. Afinal, é à luz de determinado contexto que adquirem significado as unidades de registro.

O uso das técnicas de análise categorial nos possibilitou uma visualização de quais fatores evolutivos e explicações advindas do pluralismo de processos e do campo da evo-devo estavam sendo contemplados ao longo dos livros, tanto de Biologia Evolutiva, quanto de Zoologia de Vertebrados. A quantificação das ocorrências das unidades de registro enquadradas nas categorias foi utilizada para avaliar a concentração e a ênfase concedida pelos livros aos diversos conteúdos contemplados em nossa análise. Os valores de ocorrência das categorias serviram como orientação, então, para uma análise de caráter qualitativo, a qual utilizou a regularidade com que as unidades

de registro apareceram como um parâmetro de interpretação da significância que foi concedida aos referidos conteúdos. Por esta razão, caracterizamos esse estudo como quali-quantitativo.

Para Bardin, a eficiência de um processo de categorização se deve à manutenção de certas propriedades desejadas, por conseguinte, as categorias devem estar subordinadas a parâmetros definidos de (1) exclusão mútua: cada elemento só pode existir em única categoria; (2) homogeneidade: os elementos agrupados em uma mesma categoria devem ser compreendidos enquanto “entes comuns” sob os critérios de análise utilizados; (3) pertinência: as categorias devem corresponder às intenções do investigador, de acordo com os objetivos definidos da pesquisa; (4) fidelidade objetiva: se as categorias forem claramente definidas e se indicadores de busca que determinam a entrada de um elemento numa categoria forem suficientemente explícitos e sem ambiguidades, não deverá haver distorções na interpretação do enquadramento das categorias decorrentes da subjetividade de diferentes analistas; (5) exclusividade de identificação: um elemento não pode ser passível de ser classificado em mais de uma categoria; e (6) produtividade: as categorias serão ditas produtivas se os resultados forem passíveis de gerar inferências férteis, hipóteses novas, assim como permitir segurança na interpretação dos dados. Na categorização das unidades de registro obtidas pelas operações de desmembramento dos textos dos livros de Biologia Evolutiva e Zoologia de Vertebrados, foi possível observar todos estes parâmetros.

3. Resultados e discussão

Nas Tabelas 3 e 4, são apresentadas os números de ocorrência e as frequências total e relativa de cada uma das categorias nos livros didáticos de Biologia Evolutiva e de Zoologia de Vertebrados, respectivamente.

Tabela 3.3 – Distribuição das categorias nos livros didáticos de Biologia Evolutiva.

| Categorias | Livros | | Futuyma | Ridley | Stearns & Hoekstra |
|----------------------------|--------------------------|----------------------------|--------------|--------------|--------------------|
| | N. de ocorrências | Seleção | | | |
| Seleção Natural | N. de ocorrências | Seleção | 722 | 987 | 514 |
| | Frequência total: | | 722 | 987 | 514 |
| | Frequência relativa (%): | | 56,8% | 51,4% | 46,6% |
| Evo-devo | N. de ocorrências | Desenvolvimento* | 162 | 182 | 239 |
| | | Gene Hox | 28 | 55 | 29 |
| | | Evo-devo e EDB** | 1 | 19 | - |
| | Frequência total: | | 191 | 256 | 268 |
| | Frequência relativa (%): | | 15% | 13,3% | 24,3% |
| Especiação | N. de ocorrências | | 172 | 315 | 134 |
| | Frequência total: | | 172 | 315 | 134 |
| | Frequência relativa (%): | | 13,5% | 16,4% | 12,1% |
| Deriva Gênica | N. de ocorrências | Deriva Gênica | - | 47 | 53 |
| | | Deriva | 133 | 214 | 61 |
| | Frequência total: | | 133 | 263 | 114 |
| | Frequência relativa (%): | | 10,4% | 13,7% | 10,3% |
| Mecanismos Macroevolutivos | N. de ocorrências | Mecanismos macroevolutivos | - | - | - |
| | | Macroevolução | 15 | 50 | 38 |
| | Frequência total: | | 14 | 50 | 38 |
| | Frequência relativa (%): | | 1,1% | 2,6% | 3,4% |

| | | | | |
|----------------------------|---------------------------------|-------------|-------------|-------------|
| Restrição | N. de ocorrências | 33 | 43 | 29 |
| | Frequência total: | 33 | 43 | 29 |
| | Frequência relativa (%): | 2,6% | 2,2% | 2,6% |
| Efeito Fundador | N. de ocorrências | 7 | 5 | 6 |
| | Frequência total: | 7 | 5 | 6 |
| | Frequência relativa (%): | 0,6% | 0,4% | 0,5% |
| Construção de Nicho | N. de ocorrências | - | - | - |
| | Frequência total: | - | - | - |
| | Frequência relativa (%): | 0% | 0% | 0% |
| Auto-organização | N. de ocorrências | - | - | - |
| | Frequência total: | - | - | - |
| | Frequência relativa (%): | 0% | 0% | 0% |
| Simbiogênese | N. de ocorrências | - | - | - |
| | Frequência total: | - | - | - |
| | Frequência relativa (%): | 0% | 0% | 0% |

Fonte: Bittencourt-dos-Santos. (2011)

* Só foram consideradas ocorrências do termo ‘desenvolvimento’ que tinham conexão com conteúdos evolutivos

** EDB (Evolutionary Developmental Biology) corresponde à sigla utilizada no livro de Futuyma. Pode ser considerada equivalente à Evo-devo.

Tabela 4.4– Distribuição das categorias nos livros didáticos de Zoologia de Vertebrados.

| | Livros | | Pough et al. | Hickman et al. | Hildebrand & Goslow |
|-----------------------------------|---------------------------------|----------------------------|---------------------|-----------------------|--------------------------------|
| Categorias | | | | | |
| Seleção Natural | N. de ocorrências | Seleção | 31 | 110 | 25 |
| | Frequência total: | | 31 | 110 | 25 |
| | Frequência relativa (%): | | 47,7% | 40,9% | 34,7% |
| Evo-devo | N. de ocorrências | Desenvolvimento | 14 | 73 | 22 |
| | | Gene Hox | 15 | - | 21 |
| | | Evo-devo | 5 | - | - |
| | Frequência total: | | 34 | 73 | 43 |
| | Frequência relativa (%): | | 52,3% | 27,1% | 59,7% |
| Restrição | N. de ocorrências | | 0 | 8 | 4 |
| | Frequência total: | | 0 | 8 | 4 |
| | Frequência relativa (%): | | 0% | 3% | 5,6% |
| Especiação | N. de ocorrências | | - | 49 | - |
| | Frequência total: | | - | 49 | - |
| | Frequência relativa (%): | | | 18,2% | 0% |
| Deriva Gênica | N. de ocorrências | Deriva Gênica | - | 18 | - |
| | | Deriva | - | - | - |
| | Frequência total: | | - | 18 | |
| | Frequência relativa (%): | | | 6,7% | |
| Mecanismos Macroevolutivos | N. de ocorrências | Mecanismos Macroevolutivos | - | - | - |
| | | Macroevolução | - | 11 | - |
| | Frequência total: | | - | 11 | - |
| | Frequência relativa (%): | | | 4,1% | |
| Efeito Fundador | N. de ocorrências | | - | - | - |
| | Frequência total: | | - | - | - |
| | Frequência relativa (%): | | 0% | 0% | 0% |
| Construção de Nicho | N. de ocorrências | | - | - | - |
| | Frequência total: | | - | - | - |

| | | | | |
|-------------------------|---------------------------------|-----------|-----------|-----------|
| | Frequência relativa (%): | 0% | 0% | 0% |
| Auto-organização | N. de ocorrências | - | - | - |
| | Frequência total: | - | - | - |
| | Frequência relativa (%): | 0% | 0% | 0% |
| Simbiogênese | N. de ocorrências | - | - | - |
| | Frequência total: | - | - | - |
| | Frequência relativa (%): | 0% | 0% | 0% |

Fonte: Bittencourt-dos-Santos. (2011)

Como indicam os dados apresentados na Tabela 3, os livros de Biologia Evolutiva analisados já trazem em suas explicações evolutivas uma abordagem de parte dos fatores considerados no pluralismo de processos que tem marcado a biologia evolutiva das duas últimas décadas. As contribuições da evo-devo, os mecanismos de especiação e a deriva gênica recebem atenção nos livros, com alguma atenção – ainda que bastante limitada – sendo dada também aos mecanismos macroevolutivos e às restrições. O efeito fundador merece consideração ainda mais limitada, mas não devemos perder de vista suas relações íntimas com a deriva. Outros mecanismos, como a simbiogênese, a auto-organização e a construção de nicho, não são levados em conta. Podemos concluir, assim, que os livros de Biologia Evolutiva já trazem uma perspectiva pluralista, apresentando múltiplos fatores evolutivos, assim como levam em conta os desenvolvimentos da evo-devo. A maior atenção ainda se dirige, de qualquer modo, à seleção natural, que apareceu com alta frequência relativa nos livros, quando comparada às frequências relativas das demais categorias. Podemos afirmar, contudo, que já está em andamento, no campo da Biologia Evolutiva, uma recontextualização pedagógica do pluralismo de processos, que tem marcado cada vez mais o conhecimento acadêmico sobre evolução. Contudo, esta recontextualização ainda está se iniciando, como mostra a grande ênfase dada à seleção natural, em relação aos outros mecanismos, e o fato de que os demais mecanismos evolutivos ainda não são explorados de modo mais aprofundado. Isso fica claro quando se percebe que boa parte dos conteúdos relativos a mecanismos evolutivos que não sejam a seleção natural aparece em apêndices, notas de rodapé, leituras complementares, ou em capítulos específicos, nos quais são abordados de maneira fragmentada, sem a devida integração aos demais conteúdos abordados pelo livro.

Entendemos, sob uma perspectiva de recontextualização pedagógica dos conteúdos, que os conhecimentos científicos produzidos na ciência naturalmente percorram uma trajetória de reconstrução até se fazerem presentes como parte do conhecimento científico escolar. É esperado, assim, que se passe algum tempo até que determinados desenvolvimentos do conhecimento científico estejam representados na ciência escolar. Além disso, esta recontextualização depende de outros fatores, como a real contribuição que os novos conhecimentos trazem para o ensino em diferentes níveis educacionais. Estamos assumindo, pois, que os desenvolvimentos recentes que conduziram a biologia evolutiva rumo a uma visão mais pluralista são suficientemente importantes para a formação dos biólogos a ponto de deverem estar presentes nos livros didáticos das disciplinas biológicas analisadas. O que estamos detectando nos livros de biologia evolutiva é, pois, que o tempo transcorrido já foi suficiente para que boa parte dos mecanismos considerados numa visão pluralista do processo evolutivo esteja neles representada, com exceção de alguns mecanismos e com manutenção de uma predominância da referência à seleção natural. Ainda resta por ser feita, contudo, uma exploração mais aprofundada de tais mecanismos, o que naturalmente colocará em nova perspectiva o tratamento dado à seleção.

Na Tabela 4, podemos ver que, com exceção da seleção natural, os demais fatores evolutivos estão quase sempre ausentes dos livros didáticos de Zoologia de Vertebrados, sendo para a maioria das categorias impossível a identificação de qualquer unidade de registro pertinente ao longo de toda a obra. Esta observação vale tanto para os capítulos referentes à conquista do ambiente terrestre, como para os capítulos restantes. Contudo, houve grande frequência de ocorrências relacionadas à evo-devo. Podemos concluir, assim, que os livros de Zoologia de Vertebrados não apresentam uma abordagem pluralista do processo evolutivo, com exceção da

atenção dada à relação entre evolução e desenvolvimento, nos marcos da evo-devo. A recontextualização do pluralismo de processos parece ser ainda incipiente na Zoologia de Vertebrados.

De um modo geral, foi possível notar um maior avanço da recontextualização dos conteúdos relativos à evo-devo, em relação a outros fatores considerados numa visão pluralista do processo evolutivo. Tal afirmação é válida tanto para os livros de Biologia Evolutiva como para os de Zoologia de Vertebrados. Em todos os seis livros, é possível identificar o tratamento de assuntos concernentes à biologia evolutiva do desenvolvimento, sendo que, entre todas as categorias consideradas na análise dos livros didáticos de Biologia evolutiva, esta teve a segunda maior frequência relativa, superada apenas pela categoria “seleção natural”. Entre os livros de Zoologia de Vertebrados, os mesmos resultados foram encontrados no livro de Hickman et al. (2007), que se diferenciou por apresentar uma visão mais pluralista. Nos outros dois livros, Pough et al. (2008) e Hildebrand e Goslow (1998), os conteúdos relativos à evo-devo foram os mais frequentes, entre todas as categorias encontradas, superando, inclusive, à seleção natural. Isso mostra a atenção dada à compreensão da evolução do desenvolvimento e de suas conseqüências para a evolução dos grupos na Zoologia de Vertebrados, que é um dos campos em que a pesquisa sobre evo-devo tem dado contribuições mais amplas e fundamentais. A evo-devo tem cumprido, por exemplo, papel central nos avanços dos últimos 20 anos sobre a compreensão dos planos de organização dos corpos de animais (ver, por exemplo, Minelli, 2003; Carroll et al, 2005; Davidson & Erwin, 2006; Swalla, 2006; Carroll, 2008; Kuratani, 2009). Não espanta, assim, a atenção dada a esta nos livros de Zoologia analisados.

No livro de Hickman et al. (2007), temos um padrão diferenciado em relação aos outros dois livros de Zoologia de Vertebrados, com a presença de uma visão pluralista, contemplando, além da evo-devo, modos de especiação, deriva gênica, mecanismos macroevolutivos e restrições. Ainda que a frequência de ocorrências que tratam de evo-devo tenha sido menor neste livro do que nos de Pough et al. (2008) e Hildebrand & Goslow (1998), o destaque dado por Hickman e colaboradores a este campo fica claro na presença de um capítulo exclusivamente direcionado ao tratamento das questões desenvolvimentais, intitulado *Principles of development* e trazendo um enfoque de caráter propriamente evolutivo. A ênfase dada pelo livro do Hickman et al. à biologia evolutiva do desenvolvimento pode ser exemplificada no seguinte trecho: “Durante as duas últimas décadas a combinação da genética com modernas técnicas da biologia molecular e celular produziu uma avalanche de informações que resolveu muitas perguntas. As relações causais entre o desenvolvimento e a evolução se tornaram o grande foco de investigação” (Hickman et al., 2007, p.157).

A diversidade de mecanismos encontrada nos livros foi um dos parâmetros importantes em nossa análise. Para tanto, comparamos em cada livro os números de categorias sem qualquer ocorrência com o número de categorias consideradas. Desse modo, foi possível avaliar em que medida os livros analisados contemplavam a pluralidade de processos que tem sido invocados na explicação do processo evolutivo. Mesmo num livro de Zoologia de Vertebrados mais pluralista, como o de Hickman et al., não houve qualquer ocorrência em quatro categorias: auto-organização, simbiogênese, efeito fundador e construção de nicho. Nos outros dois livros de Zoologia de Vertebrados, por sua vez, sete das nove categorias consideradas não foram encontradas. No caso dos livros de Biologia Evolutiva, não foram observadas quaisquer ocorrências de três categorias, sendo as mesmas nos três livros: auto-organização, construção de nicho e simbiogênese. De modo geral, que estes fatores não foram considerados em qualquer dos seis livros analisados.

Entre os fatores que não estão ainda presentes nos livros, temos duas situações que nos parecem distintas: de um lado, é mais provável que mecanismos como a construção de nicho venham a ser recontextualizados em futuro próximo, dada sua maior aceitação pela comunidade científica da área. A necessidade de reconhecimento da construção de nicho como importante mecanismo evolutivo foi recentemente tema de um livro que teve grande impacto, *Niche construction: the neglected process in evolution*, de Odling-Smee, Laland e Feldman (2003). Em artigos das áreas de Evolução e Ecologia, a construção de nicho também tem merecido

significativa atenção (e.g., Hui; Yue, 2005; Wright et al., 2004). De outro lado, fatores como a auto-organização e a simbiogênese já não têm recebido tanta atenção da comunidade científica, podendo não ser recontextualizados, por esta razão, para o conhecimento escolar de biologia evolutiva, nem mesmo na educação superior.

4. Conclusões

Os achados do presente estudo mostram que livros didáticos de Biologia Evolutiva atualmente em uso incluem em suas explicações evolutivas parte dos fatores considerados em visões pluralistas na biologia evolutiva das duas últimas décadas: principalmente contribuições da evo-devo, mecanismos de especiação e deriva gênica e, com menor proeminência, mecanismos macroevolutivos e restrições. Portanto, uma recontextualização pedagógica do pluralismo de processos já vem ocorrendo no conhecimento escolar de Biologia Evolutiva, no nível superior de ensino. Trata-se, contudo, de uma recontextualização ainda inicial, mantendo-se grande ênfase sobre a seleção natural, em relação aos outros mecanismos, que não são abordados de modo aprofundado.

Nos livros didáticos de Zoologia de Vertebrados, por sua vez, seleção natural e contribuições da evo-devo são tratadas com destaque, enquanto os demais fatores evolutivos estão quase sempre ausentes. Portanto, estes livros não apresentam uma abordagem pluralista do processo evolutivo, com exceção da atenção dada à relação entre evolução e desenvolvimento. Em termos gerais, podemos perceber um maior avanço da recontextualização dos conteúdos relativos à evo-devo, em relação a outros fatores incluídas no pluralismo de processos.

Na medida em que a recontextualização da visão pluralista do processo evolutivo se aprofunde nos livros didáticos de Biologia Evolutiva, exercendo, assim, maior influência sobre a formação de biólogos, é possível que esta visão se dissemine de modo mais amplo por diversos campos das Ciências Biológicas, incluindo a Zoologia de Vertebrados. Como uma contribuição para esta incorporação do pluralismo de processos no conhecimento escolar de Biologia, no ensino superior, temos investigado inovações educacionais tratando desta visão no contexto real de salas de aula de Zoologia, num curso superior de Ciências Biológicas.¹ O presente artigo relata os resultados de nossos primeiros passos nessa direção, que consistiram num estudo sobre se e como livros didáticos de ensino superior das áreas de Biologia Evolutiva e Zoologia de Vertebrados têm tratado de conteúdos relativos ao pluralismo de processos e à evo-devo.

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¹ O nome do curso será incluído após arbitragem.

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Capítulo 2 – Validação de uma sequência didática que utilizou o Pluralismo de processos e Evo-devo em explicações narrativas da conquista do ambiente terrestre

Validation of a teaching sequence that used the pluralism of processes and Evo-devo in narratives explanations of the conquest of the terrestrial environment

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Resumo

Este artigo relata os resultados de um estudo qualitativo realizado com uma turma de Zoologia de Vertebrados do curso de Ciências Biológicas da Universidade Federal da Bahia, com base na construção, aplicação e validação de uma sequência didática. A sequência didática utiliza explicações narrativas para realizar uma abordagem integrada de conteúdos de zoologia, de uma visão pluralista dos processos evolutivos, da biologia evolutiva do desenvolvimento (evo-devo) e da ecologia. Ela foi construída com base em um estudo de caso que teve como objeto a radiação dos tetrápodes durante a conquista do meio terrestre. O estudo buscou realizar uma validação interna da sequência didática, segundo a metodologia proposta por Méheut em seu desenho de pesquisa para o desenvolvimento e a validação de sequências didáticas no ensino de ciências. A sequência foi testada na turma, mediante comparação entre os percursos de aprendizagem esperados, conforme os objetivos pretendidos na intervenção pedagógica, e os percursos de aprendizagem efetivamente realizados pelos estudantes. Foram aplicados questionários em três diferentes etapas do processo, referindo-se a diferentes momentos sociais de mobilização dos conteúdos pelos estudantes; e subsequentemente, ao fim do semestre foram gravadas entrevistas individuais com os estudantes. Uma análise das variações das respostas dos questionários respondidos pelos estudantes serviu de informação para avaliar os avanços e a fixação dos conteúdos abordados. As declarações dos estudantes, coletadas através das entrevistas gravadas, foram categorizadas com base nos estágios de apropriação do discurso científico escolar propostos por Mortimer e Scott, avaliando comparativamente os níveis de mobilização (domínio) da linguagem social da ciência alcançado pelos estudantes da turma analisada. O estudo qualitativo que realizamos nos permitiu concluir que a intervenção pedagógica proposta trouxe resultados satisfatórios, tendo influenciado a aprendizagem dos estudantes na direção pretendida.

Palavras-chave: Pluralismo de processos. Evo-devo. Estudo comparativo, Sequência didática

Abstract

This article reports the results of a qualitative study of one class of Vertebrate Zoology of the course of Biological Sciences, Federal University of Bahia, it was made based on the construction, application and validation of an teaching sequence. The teaching sequence uses narrative explanations for taking an integrated subject of zoology, of a pluralistic view of evolutionary processes in evolutionary developmental biology (evo-devo) and ecology. It was built by a development of a study of case that had as its object the radiation of tetrapods during the conquest of the terrestrial environment. The study tried to conduct an internal validation of the teaching sequence, according to the methodology proposed by Méheut in their research design for the development and validation of teaching sequences in science education. The sequence was tested one class by comparing the expected learning pathways, depending on the intended objectives in the educational intervention, and learning pathways effectively performed by the students. Questionnaires were applied on three different stages of the process, referring to different moments of social mobilization of required knowledge by students, and subsequently at the end of the semester have been recorded individuals interviews with the students. An analysis of variations of the responses from questionnaires answered by students was used like information to assess progress and setting the subjects covered. The statements of students, collected through taped interviews were categorized based on the stages of appropriation of scientific school discourse proposed by Mortimer and Scott, by that way make the comparative evaluations of the levels of mobilization (domain) of the social language of science reached by students from the analyzed class. The statements of students, collected through taped interviews were categorized based on the stages of appropriation of scientific discourse school proposed by Mortimer and Scott, benchmarking levels of mobilization (domain) of the social language of science made by students of the class analyzed. The qualitative study we conducted allowed us to conclude that the educational intervention proposed brought satisfactory results, influencing student learning in the intended direction.

Keywords: Pluralism of process. Evo-devo. Teaching sequence. Comparative study

1. Introdução

Para alguns historiadores da ciência, a revolução darwiniana seria tão relevante, no sentido de uma teoria científica simbolizar uma mudança na visão de mundo e nos valores culturais, quanto à própria revolução copernicana (Bowler 2003). Ainda hoje, algumas das idéias básicas do pensamento darwinista são aceitas como elementos fundamentais na estrutura do pensamento evolutivo, tais como: (i) a idéia de que todos os seres vivos são aparentados entre si, ou seja, de que todas as espécies são interconectadas filogeneticamente através de relações de ancestralidade comum; (ii) que as espécies se transformam ao longo do tempo, pois os indivíduos de uma população ao se reproduzirem dão origem a descendentes com modificações; e (iii) o reconhecimento da importância da seleção natural como mecanismo explicativo da mudança evolutiva ao longo das gerações.

Contudo, desde que foi divulgada pela primeira vez, com a publicação dos textos de Darwin e Wallace em 1858 nos *Proceedings of the Linnean Society*, até os dias atuais, as teorias darwinistas percorreram uma trajetória de muitas mudanças e complementações. De fato, a teoria da seleção natural nem sempre usufruiu do prestígio e da confiança conquistada desde os anos 1930. Tendo ultrapassado a sua maior fase de descrença, durante o chamado “eclipse do darwinismo”, como foi denominado por Julian Huxley (1942), o darwinismo se reergueu, revertendo o momento histórico de descrédito vivenciado durante o período que antecedeu à síntese moderna.

Por volta das décadas de 1930 e 1940, como resultado de uma elaboração coletiva que contou a participação de grandes nomes da ciência da época, como Theodosius Dobzhansky, J.B.S. Haldane, Sewall Wright, Julian Huxley, Ernst Mayr, George Gaylord Simpson, G. Ledyard Stebbins, entre outros, foi realizada a moderna síntese evolutiva. Durante a referida síntese, o darwinismo e a genética (mendeliana e de populações) foram conjuntamente incorporados na confecção de uma teoria amplificada, na qual as complementações advindas destes campos iriam projetar as dimensões de um pensamento adaptacionista, o qual se fixou e se estendeu de forma dominante por quase todo o restante do século XX. Este modo adaptacionista de pensar admite a produção direta de adaptações através da seleção natural como sendo a causa primária da maioria das características biológicas relevantes (Sepulveda & El-Hani, 2008). Podemos entender, deste modo, que uma concepção adaptacionista admite que a presença de uma característica orgânica possa ser sempre compreendida em termos do caráter adaptativo que conferiu ao organismo que a possui; ou seja, o adaptacionismo admite que seja sempre possível, através do entendimento da seleção natural, fornecer todas as explicações que justifiquem o porquê de uma característica específica existir em uma determinada linhagem de organismos.

Contudo, foi somente a partir da década de 1970 que novas questões, capazes de transpor o pensamento puramente adaptacionista e levar a uma melhor compreensão dos limites do papel da seleção natural, emergiram, se instauraram e passaram a se amplificar nos correntes debates travados na comunidade científica ligada ao estudo da evolução. Ainda que muitas das idéias básicas do pensamento darwinista tenham sido mantidas com um papel central no pensamento evolutivo, muitos avanços importantes tiveram lugar, merecendo destaque no contexto contemporâneo. A história da evolução dos seres vivos tem passado a ser compreendida, nas últimas décadas, não apenas como o resultado cumulativo dos efeitos da seleção natural. Hoje, sabemos que nem todas as características presentes nos seres vivos são adaptações, ou seja, nem tudo que reconhecemos expresso em um organismo pode ser entendido como um produto da seleção natural. Entre os recentes avanços alcançados pela biologia evolutiva, podemos destacar a idéia de que outros mecanismos evolutivos, além da seleção natural, têm papel causal e explicativo na evolução dos seres vivos.

Torna-se necessário, assim, investigar e compreender como e em que condições uma série de

outros mecanismos evolutivos pode também estar atuando. Esta nova perspectiva de interpretação dos fenômenos evolutivos pode ser caracterizada como um pluralismo de processos (Pigliucci; Kaplan, 2000, Meyer; El-Hani, 2000). Por pluralismo de processos, entende-se o reconhecimento da contribuição de múltiplos fatores que atuam de modo complementar nos processos evolutivos, incluindo seleção natural, deriva gênica, distintos modos de especiação, restrições ao processo evolutivo (sejam históricas ou desenvolvimentais), construção de nicho, simbiogênese, auto-organização etc.

Os estudos desenvolvidos pela biologia evolutiva do desenvolvimento (evo-devo) têm sido responsáveis por uma parte relevante destes avanços relativos aos limites explicativos da teoria sintética da evolução, principalmente no que se refere à elucidação dos processos de morfogênese e produção de inovações morfológicas em organismos multicelulares. Estes estudos têm permitido a compreensão dos limites plásticos e da conservação dos padrões corporais dos animais, com base no entendimento de que os organismos, ao longo do desenvolvimento, estão submetidos a restrições, as quais determinam possibilidades de expressão das suas características e, assim, o repertório de variantes sobre as quais atuará a seleção natural. Restrições desenvolvimentais promovem um enviesamento na produção das variantes fenotípicas, ao mesmo passo em que limitam a variabilidade fenotípica em função da estrutura, caráter, composição ou dinâmica do sistema desenvolvimental, Maynard Smith J, et al. (1985).

A evo-devo, nas últimas décadas, passou a ter um papel central na compreensão da dinâmica evolutiva, visto o reconhecimento de suas contribuições para a elucidação das dinâmicas regulatórias dos processos desenvolvimentais que produzem as formas dos organismos multicelulares. O desenvolvimento está relacionado a uma gama de processos fundamentais, tais como a regulação gênica, a diferenciação celular e morfogênese (origem das formas). Compreender os processos desenvolvimentais é a base para que possamos entender a produção das inovações morfológicas. Estas mesmas inovações, por sua vez, é que irão enriquecer o repertório de variantes possíveis, sobre as quais a seleção subsequentemente irá atuar. O estudo dos processos desenvolvimentais que determinam tal repertório de variantes possíveis tem permitido uma compreensão mais aprimorada das possibilidades e dos limites da seleção natural.

Um importante avanço para entender a relevância dos estudos sobre o desenvolvimento se deve à compreensão de que, a um mesmo passo em que o desenvolvimento é o processo que produz inovações morfológicas, ele também restringe as possibilidades de modificações que podem ser originadas. Ou seja, o desenvolvimento impõe limites para as possibilidades de variações das características que uma população pode expressar. Tal restrição se dá devido ao fato de que o desenvolvimento não é infinitamente plástico. A complexidade do desenvolvimento em seu ordenamento de etapas sequenciadas orienta os sentidos possíveis para o surgimento de certas inovações morfológicas, enquanto outras mudanças são menos cabíveis de serem originadas.

A evolução e o desenvolvimento se influenciam mutuamente, embora representem processos distintos e atuem em escalas temporais diferentes: o desenvolvimento ao longo da vida do organismo, de um modo transformacional, e a evolução ao longo de várias gerações numa linha, de um modo variacional. O desenvolvimento, assim como as demais características dos indivíduos em uma população, também é alvo da seleção natural e se modifica no decorrer do processo evolutivo, canalizando certos caminhos mais prováveis de serem percorridos pela evolução. Por meio da herança, tanto genética, quanto epigenética, os organismos recebem também um legado desenvolvimental, ou seja, reproduzem os padrões de desenvolvimento dos seus ancestrais. Por conseguinte, é esta herança dos padrões de desenvolvimento que determina os limites e as possibilidades das inovações morfológicas das futuras descendências. Por conseguinte, a biologia evolutiva do desenvolvimento tem nos permitido entender as restrições como um fator evolutivo fundamental para a elucidação dos processos de origem e transformação das estruturas morfológicas, ao longo da história filogenética dos grupos.

Um interessante exemplo de restrição pode ser dado em relação ao ramo dos tetrápodes: neste grupo, podemos notar que não são encontradas, desde os organismos mais plesiomórficos aos mais derivados, uma variação que tenha permitido originar indivíduos com seis ou oito, ou qualquer outro número diferente de quatro patas. Esta constatação de invariância possivelmente poderia ser explicada com base na compreensão de um rigoroso sequenciamento progressivo das etapas durante o desenvolvimento dos tetrápodes, o qual foi herdado de seus ancestrais mais remotos. Tal condição de estabilidade de padrão nos indica que o percurso descrito pelo padrão desenvolvimental desses animais impossibilita uma variação em relação ao número de patas. Este exemplo dado pode nos ajudar a compreender como a seleção natural atua apenas sobre um repertório limitado de possibilidades, as quais são estabelecidas por restrições decorrentes dos processos desenvolvimentais. Entre os tetrápodes, é possível a observação de uma infinidade de formas de patas adaptadas às mais diversas condições, contudo sempre em número de quatro.

A evo-devo também tem explicado como alterações nos padrões de expressão gênica, decorrentes de mudanças nas seqüências regulatórias de genes desenvolvimentais, podem conduzir a mudanças radicais na morfologia, influenciando o surgimento de novidades evolutivas (Wagner, 2007). Essas mudanças no desenvolvimento podem rapidamente dar origem a indivíduos muito diferentes das médias morfológicas das populações às quais pertencem, sendo que este salto na morfologia, inclusive, pode se dar de uma geração para outra. A evo-devo, neste sentido, tem desempenhado um papel importante na reestruturação do pensamento evolutivo, porque nos confere a possibilidade de realizar uma interpretação diferenciada em relação às taxas nas mudanças dos padrões evolutivos. Estamos nos referindo aqui a uma interpretação diferenciada porque segundo o modelo do gradualismo filético, que é admitido pela teoria sintética da evolução, as taxas nas mudanças dos padrões evolutivos ocorre sempre de modo lento e gradual, acumulando pequenas alterações ao longo de grandes escalas temporais. Tal convicção é justificada pela teoria sintética com base no entendimento de que a seleção natural não fornece explicações para os rápidos saltos evolutivos e como esta admite a seleção natural como mecanismo exclusivo, a evolução deveria, por conseguinte, ocorrer de modo gradualista.

Essa controvérsia em relação às velocidades das taxas de mudança evolutiva deu origem a importantes polêmicas em outro momento histórico da biologia evolutiva, no início na década de 1970, quando foi proposto o modelo de equilíbrio pontuado, por Niles Eldredge e Stephen Jay Gould (1972). Este modelo foi desenvolvido de modo a se ajustar a padrões evolutivos frequentemente encontrados nos registros paleoecológicos, que incluem longos períodos de estabilidade, durante os quais as espécies permaneceriam praticamente inalteradas (momentos de estase); estes, por sua vez, seriam intercalados por períodos comparativamente mais curtos nos quais ocorrem rápidas mudanças morfológicas nos organismos, correspondendo aos períodos em que novas espécies têm origem (momentos de pontuação). Na Figura 1, podemos observar uma contraposição entre os padrões filogenéticos propostos pelo gradualismo filético, característico da teoria sintética, e pela teoria do equilíbrio pontuado.



Figura 1 Padrões filogenéticos propostos pelo gradualismo filético (esq) e pelo equilíbrio pontuado (dir) (Ridley, 2005)

Nota-se que, no gradualismo filético, a diversificação morfológica das espécies, que explica os padrões macroevolutivos, se origina por divergência gradual de características ao longo do tempo, em linhagens separadas por processos de especiação, enquanto, no padrão do equilíbrio pontuado, a divergência morfológica ocorre no momento mesmo da especiação, sendo as características das espécies mantidas após sua diversificação, provavelmente com o surgimento de adaptações, via seleção natural, por ajuste mais fino das morfologias aos regimes seletivos.

Gould e Eldredge buscaram explicar os momentos de pontuação com base em na teoria do efeito fundador, proposta por Ernst Mayr De acordo com esta teoria, novas espécies surgem frequentemente quando pequenos conjuntos de indivíduos são isolados do restante de uma população. Estes pequenos grupos carregariam consigo combinações de genes diferentes da população original, de modo que estas devido a tal característica poderiam se diferenciar rapidamente, enquanto a p populações maiores permaneceriam estabilizadas por conta do fluxo gênico entre os indivíduos que as manteria geneticamente coesas. Contudo, além de estudos genéticos comprovarem que a maior parte das diferenças encontradas entre indivíduos de espécies distintas é muito semelhante à diferença encontrada entre indivíduos de uma mesma espécie, ainda que ocorram em número maior; também a idéia de que apenas este mecanismo seria suficiente para explicar a imensa diversidade de formas vivas, em contraposição à idéia de origem das diferenças entre espécies por lento acúmulo de características por seleção natural, não se sustentou perante as muitas críticas da comunidade científica à credibilidade das explicações fornecias para o modelo. Não obstante os processos propostos por Gould e Eldredge não terem sido aceitos, o padrão do equilíbrio pontuado é lagamente aceito, sendo, exatamente por isso, necessário explicá-lo de modo mais consistente.

Hoje, passadas algumas décadas e em decorrência dos progressos alcançados na biologia evolutiva, inclusive na evo-devo, talvez seja possível fornecer explicações mais plausíveis em relação à questão de como, ao longo da história da vida, se dão as rápidas mudanças nos padrões evolutivos que correspondem às pontuações. Estas explicações têm sido marcadas por uma tendência mais pluralista, envolvendo a contribuição coletiva de múltiplos mecanismos, tendo em vista que as mudanças observadas durante as pontuações evolutivas são demasiadamente rápidas para que possam ser explicadas apenas do ponto de vista da seleção natural. O entendimento das rápidas mudanças morfológicas decorrentes de alterações dos processos de regulação gênica durante o desenvolvimento pode contribuir, decerto, para explicar em parte como ocorrem as explosivas diversificações características dos momentos de pontuação evolutiva.

No contexto atual da pesquisa, torna-se necessário o desenvolvimento de um conhecimento integrado que possa, concomitantemente, buscar estabelecer relações entre as condições ecológicas, os possíveis mecanismos que possam estar atuando paralelamente na evolução e as mudanças nas taxas evolutivas. Um caminho interessante a seguir seria buscar estudar e compreender os regimes seletivos que operam durante as condições ecológicas relativas aos fenômenos de explosiva diversificação morfológica, com o surgimento de novas espécies, durante os momentos de pontuação na história evolutiva. Para tal, ainda mantendo como base as questões referentes ao atual panorama de mudança conceitual e da necessidade de integração destes novos conteúdos da biologia evolutiva e do pluralismo de processos aos estudos da ecologia, o presente trabalho procurou abordar também algumas questões relativas os modos através dos quais tais conteúdos podem ser trabalhados na formação de novos biólogos. Deste modo, em uma perspectiva educacional, o presente trabalho buscou desenvolver e validar uma sequência didática construída com base em um estudo de caso, o qual teve como objeto a pontuação evolutiva relativa à radiação dos tetrápodes após a conquista do meio terrestre. Esta sequência buscou reconstituir um dos cenários explicativos possíveis para o regime paleoecológico envolvido nesta mudança, o qual foi modelado sob uma perspectiva pluralista.

Formulamos nossa questão de pesquisa tendo como referência a moldura teórica da *Design Research*, entendida como o estudo sistemático do *design* (ou planejamento), do desenvolvimento e da avaliação de intervenções educacionais, tais como programas, estratégias de ensino e aprendizagem, materiais, produtos e sistemas. Esta investigação sobre intervenções educacionais busca não somente desenvolver soluções para problemas de ensino, mas também avançar o nosso conhecimento sobre as próprias características de intervenções bem sucedidas e de seus processos de *design* e desenvolvimento (Plomp, 2009). O planejamento de um processo de ensino e aprendizagem deve ser feito de forma que se promovam condições para que os estudantes desenvolvam uma visão clara sobre as idéias que se pretende que eles aprendam. Contudo para se alcançar este objetivo, torna-se necessário o desenvolvimento explícito de estratégias específicas, ou seja, um conspicuo tratamento a respeito dos detalhes e da seqüência das atividades de ensino-aprendizagem propostas (Chinn & Malhotra, 2002). Para este desenvolvimento, princípios de *design* devem ser propostos com base no conhecimento acumulado, tanto na didática das ciências, quanto no conteúdo específico, bem como a partir de estudos empíricos da implementação de intervenções educacionais, tal como realizado, por exemplo, no presente estudo. Princípios de *design* podem ser entendidos como orientações heurísticas para a formulação dos componentes de uma estratégia de obtenção de efeitos pedagógicos específicos em contextos específicos encontrados em sala de aula (Van den Akker et al., 2006).

Estudos empíricos sobre seqüências didáticas, sobretudo quando realizados por meio de uma estreita colaboração entre professores-investigadores e pesquisadores educacionais, podem fornecer referências e orientações heurísticas para futuros trabalhos, que buscarão aprimorar o *design* da intervenção educacional alcançado até aquele momento da pesquisa, possibilitando, então, possíveis avanços em um ciclo seguinte da pesquisa. Desse modo, a pesquisa sobre o *design* de intervenções educacionais deve ter uma estrutura iterativa, com ciclos seguidos de testes de seqüências didáticas, visando ao desenvolvimento das mesmas. Após tal desenvolvimento, torna-se possível, então, investigar os efeitos das seqüências didáticas. Os estudos de efeitos ou da eficácia de uma ferramenta pedagógica correspondem a estudos sobre relações de causa e efeito, nos quais abordagens experimentais ou *quasi*-experimentais, com abordagem quali-quantitativa, são necessários. Estudos experimentais ou *quasi*-experimentais requerem, ainda, número suficiente de réplicas, de modo a acomodar as variáveis que interferem em investigações realizadas em sala de aula. Contudo, não parece valer a pena o grande investimento de pesquisa num teste de eficácia de uma seqüência didática antes de tê-la desenvolvida a contento, o que requer estudos de desenvolvimento anteriores, realizados por meio de estudos de caso em pequena escala, nos quais o conjunto configurado pela sala de aula e seu professor se tornam uma unidade de análise (Cobb, Stephan, McClain, & Gravemeijer, 2001). Em tais estudos, o que se busca responder não é uma questão de pesquisa focada na análise dos efeitos de uma seqüência didática em comparação com uma situação de ensino na qual a mesma não tenha sido implementada, mas uma questão focada na comparação entre o que se pretende que os estudantes aprendam com a seqüência didática (vias de aprendizagem esperadas) e o que eles efetivamente aprendem na intervenção feita no estudo (vias de aprendizagem realizadas). Tendo em vista que o presente estudo está dando início à investigação de uma seqüência didática que aborda a radiação dos tetrápodes após a conquista do ambiente terrestre, desde uma perspectiva pluralista, ele se caracteriza como um estudo de *desenvolvimento*, e não de teste de eficácia, enfocando, pois, a comparação entre vias de aprendizagem esperadas e realizadas.

Neste estudo, buscamos responder à seguinte questão de pesquisa, formuladas nos termos da *Design Research*: Quais seriam as características de uma intervenção x visando à obtenção de um dado resultado y num contexto z ? A intervenção desenvolvida (x) consistiu numa seqüência didática na qual se procurou: (i) integrar conteúdos de zoologia, evolução e ecologia, (ii) utilizar explicações narrativas, (iii) abordar vários mecanismos evolutivos e suas interações, e (iv) contemplar contribuições da biologia evolutiva do desenvolvimento (evo-devo). Os resultados de

aprendizagem pretendidos (y) enfocavam conteúdos relativos à radiação adaptativa dos tetrápodes após a conquista do ambiente terrestre, bem como à pluralidade de mecanismos envolvidos no processo evolutivo, em termos mais gerais. O contexto pedagógico em que o estudo teve lugar (z) foi o de uma disciplina de zoologia de vertebrados do ensino superior de biologia, na Universidade Federal da Bahia; não tendo sido possível acompanhar mais do que duas turmas, pela disponibilidade de turmas de zoologia de vertebrados no curso investigado, considerando o número de oferecidas por semestre. No primeiro semestre observamos e no segundo efetivamos a nossa intervenção. Os focos de nossa análise recaíram sobre uma comparação entre vias de aprendizagem esperadas e realizadas com uma turma da disciplina, na qual o ensino foi realizado conforme sequência didática construída em colaboração com o professor, com as características ou princípios de *design* acima.

2. O uso de narrativas no ensino de evolução

A seqüência didática foi construída com base no estudo de caso proposto, tendo se utilizado, ainda, das explicações narrativas como ferramenta, uma vez que consideramos que, através do uso das narrativas, seja possível motivar os estudantes para discutirem os processos evolutivos que deram origem a grupos particulares de organismos. Como bem colocado por Norris *et al.* (2005), as explicações narrativas dos processos evolutivos podem funcionar como ferramentas adequadas para o ensino de biologia evolutiva, porque refletem a natureza histórica das linhagens, que se modificam e se transformam ao longo do tempo. Através das explicações narrativas, um processo pode ser explicado por meio de uma série de eventos inteligíveis interligados. As explicações narrativas também podem ser usadas para introduzir os conteúdos e, simultaneamente, estimular a curiosidade pela investigação científica, na medida em que exploram o potencial narrativo dos acontecimentos, conduzindo o estudante de modo envolvente. As narrativas possuem muitos efeitos positivos na ativação da memória, facilitam a compreensão e aumentam o interesse dos estudantes em acompanhar o encadeamento de idéias, fatos e conceitos que estão imbricados através do método narrativo.

Devido às propriedades de contingência e indeterminação intrínsecas à dinâmica dos processos evolutivos, torna-se necessário citar exemplos únicos como explicação para outros eventos únicos. Ao mesmo passo, é também necessário extrair a partir da explicação de casos particulares conhecimentos úteis para lidar com outros casos, além daqueles que foram examinados. Neste sentido, com base numa distinção entre explicações de processos robustos e explicações de seqüências de acontecimentos reais (Sterelny & Griffiths, 1999), a seqüência didática abordou o estudo de caso sob dois âmbitos de explicação: (1) De um lado, abordou explicações de processos robustos, ou seja, tratou de modelos gerais, identificando uma possível macro-estrutura de processos invariantes em relação às mudanças dos processos dependentes das suas peculiaridades micro-históricas. As explicações de processos robustos caracterizam eventos em termos de sua generalidade, de modo que tal explicação permanece válida quando eventos similares substituem aqueles que orientaram a formulação da explicação realizada, ou seja, é uma explicação passível de ser transposta e aplicada na elucidação de outros casos. Este tipo de explicação, em seu caráter generalizante, pode auxiliar na compreensão de outras pontuações na história da evolução dos seres vivos. (2) De outro lado, a seqüência buscou fornecer explicações das seqüências de acontecimentos reais, ou seja, caracterizou os eventos envolvidos na diversificação dos tetrápodes após a conquista do meio terrestre em seus detalhes particulares, reconstruindo um dos cenários explicativos possíveis para a referida pontuação, sob uma perspectiva pluralista. As explicações de seqüências reais caracterizam os eventos em seus fins detalhes, de modo que, se estes forem substituídos por outros eventos similares, a explicação se tornará inválida.

Problemas na formação dos biólogos podem ser gerados, em parte, pela ausência de um tratamento adequado dos conteúdos em uma abordagem integrada, a qual permita a articulação entre os conhecimentos da biologia evolutiva, os estudos da ecologia e as demais sub-disciplinas da biologia. Pensar biologicamente é pensar evolutivamente (Meyer & El-Hani, 2005). Como foi dito pelo célebre pesquisador ucraniano Dobzhansky, “nada em biologia faz sentido exceto à luz da evolução”. Entendemos que, dentro de uma perspectiva atual, trabalhar com uma concepção evolutiva pluralista no ensino superior de biologia pode ser uma estratégia didática eficiente e também mais abrangente para apresentar os fundamentos necessários para a formação dos futuros biólogos, mantendo em consideração o contemporâneo quadro de mudança conceitual vivenciado em nossa disciplina. Pretendemos através do uso que demos as narrativas no ensino de evolução contribuir para que os estudantes construam uma visão pluralista sobre a evolução, segundo a qual uma pluralidade de mecanismos estariam coletivamente influenciando no curso evolutivo dos organismos.

3. Metodologia de construção, aplicação e validação da seqüência didática

A etapa de construção contou com a participação do professor responsável pela disciplina no curso de graduação. Ao todo, foram três pesquisadores coletivamente envolvidos na construção da seqüência: Prof. Marcelo Napoli, ministrante da disciplina sob intervenção; Thiago de Sá, pesquisador e colaborador que também desenvolveu um projeto de mestrado associado à seqüência construída; e Wellington Bittencourt, autor do presente trabalho. Foram realizados encontros regulares com esta equipe ao longo de todo o primeiro semestre, nas quais realizávamos discussões críticas a respeito das aulas, dos conteúdos abordados e, sobretudo, em relação à metodologia de abordagem dos mesmos. Ao longo destas discussões, os integrantes da equipe traziam contribuições oriundas da análise de livros didáticos de biologia evolutiva e zoologia de vertebrados (ver cap. 1), de modo a aprimorar o tratamento dos conteúdos relativos à evolução dos tetrápodes após a conquista do ambiente terrestre, bem como à pluralidade de mecanismos evolutivos. Foram também realizadas buscas de artigos, em periódicos de zoologia de vertebrados e evolução, que fornecessem apoio à construção da seqüência.

Adotamos o modelo de construção e validação de seqüências didáticas proposto por Martine Méheut (2005) para o desenho de pesquisa qualitativa do presente projeto. O professor, com base na perspectiva adotada, é uma peça fundamental na proposta de intervenção pretendida: (i) porque, na condição de professor-investigador, traz um conhecimento docente que é fundamental para a validação *a priori* da seqüência; (ii) porque é responsável por ministrar a seqüência didática após a elaboração, o que se mostra mais poderoso e pertinente do que se isso fosse feito pelo mestrando, com menor experiência docente, na medida em que não é professor da disciplina; e (iii) porque compreendemos a intervenção como um elemento no processo de desenvolvimento profissional e construção da prática pedagógica do próprio professor. Ou seja, não estamos lidando com uma perspectiva distanciada da prática e do conhecimento do professor e, por conseguinte, não almejamos uma intervenção que seja externa aos propósitos particulares e alheia ao trabalho pedagógico do docente. Ao contrário, entendemos a pretendida intervenção como mais um dos elementos co-substaciativos da própria dinâmica de desenvolvimento das aulas do professor.

Utilizamos durante a elaboração e validação da seqüência didática proposta os critérios de justificação *a priori* e de validação *a posteriori* descritos por Méheut (2005). Os critérios de justificação *a priori* foram utilizados para orientar a construção da seqüência de modo a maximizar a sua inteligibilidade, de acordo as especificidades do seu contexto de aplicação. Estes critérios contemplam três dimensões de análise: i) uma dimensão epistemológica, relacionada à significância dos conteúdos a serem aprendidos, aos problemas que eles podem resolver, e à gênese

histórica destas investigações; ii) uma dimensão psicocognitiva, na qual se tem em vista as características cognitivas dos estudantes para os quais seriam aplicadas a sequência; e iii) uma dimensão didática, na qual se busca compreender as restrições colocadas pelo próprio funcionamento da instituição de ensino na qual será implementada a sequência, no que se refere à adequação aos programas, cronogramas, infra-estrutura básica local, entre outras particularidades.

Num processo de validação *a posteriori* de sequências didáticas, podem ser considerados dois pontos de vista complementares, segundo Mehéut (2005): a validação externa ou comparativa, a fim de comparar efeitos da sequência didática que está sendo investigada com outros modos de ensino já em andamento no mesmo contexto, sendo realizada comumente através de pré-, pós-testes e testes de retenção, dentro de um desenho experimental ou quase-experimental; e a validação interna, realizada através da análise dos efeitos da sequência em relação aos seus objetivos, buscando comparar as vias de aprendizagem realizadas com as vias de aprendizagem esperadas, conforme o planejamento da sequência.

No presente projeto, realizamos um processo de validação interna da sequência construída, envolvendo um estudo qualitativo com uma turma da disciplina em questão que seguiu as aulas do semestre sob nossa intervenção. Tivemos em tal estudo o objetivo de comparar as relações entre vias realizadas e esperadas de aprendizagem. Mais especificamente, realizamos este estudo qualitativo através da comparação da evolução da compreensão dos estudantes em relação aos conteúdos concernentes ao pluralismo de processos e à evo-devo enfocados em nossa sequência. É importante ressaltar que esta comparação não teve – nem poderia ter – a intenção de uma validação externa, que demandaria comparações entre números maiores de turmas, num desenho experimental ou quase-experimental. No entanto, dados relevantes para o desenvolvimento posterior da sequência podem resultar da comparação entre o que teve lugar e o que se planejou em termos de aprendizagem, seja na prática docente pré-intervenção, seja na sequência didática.

Ao fim das aulas da turma na qual realizamos a intervenção, com o objetivo de caracterizar as propostas de ensino que foram implementadas antes e depois da nossa intervenção, foi realizada uma entrevista semi-estruturada com o professor, na qual se buscou caracterizar, desde sua perspectiva, as mudanças efetivamente alcançadas em sua prática docente. Trazemos aqui em destaque as principais diferenças elencadas no depoimento do professor da disciplina e também com base nas observações durante o acompanhamento das aulas. A principal delas esta de fato relacionada ao âmbito de abordagem pluralista focado em nossa proposta de ensino, as aulas pré-intervenção não buscava tratar da ação de múltiplos mecanismos evolutivos, as mudanças sofridas pelo grupo eram discutidas apenas dentro da perspectiva de adaptabilidade. A apresentação das estruturas durante o segundo semestre era quase sempre conjugada com a discussão sobre quais os possíveis processos evolutivos relacionados, estratégia que não era utilizada antes da intervenção. As questões relativas ao estudo da evo-devo eram muito pouco tratadas, ao segundo semestre estes estudos foram prioritariamente enfocados. Nas aulas ministradas pré-intervenção ocorria caracteristicamente também uma grande fragmentação na abordagem no que concerne aos estudos de fisiologia e os estudos ecológicos, ao passo que buscamos trabalhar conciliando ao máximo estes dois campos. Apesar das aulas anteriores a intervenção já possuírem em sua forma originalmente ministrava elementos narrativos, as narrativas não eram utilizadas como um eixo condutor na apresentação dos conteúdos, onde podíamos observar momentos de contar história e outros momentos isolados para se trabalhar os demais conteúdos fora da história. Contudo, em nossa estratégia de abordagem os conteúdos específicos eram encadeados de acordo à sequência da narrativa dos processos evolutivos. Seguirá no anexo 3 a sequência didática que desenvolvemos.

A aprendizagem realizada pelos estudantes foi investigada por meio de questionários aplicados em três etapas: antes da aplicação da sequência, após a aplicação da sequência e três meses depois do final da intervenção, referindo-se a diferentes momentos sociais de mobilização dos conteúdos pelos estudantes. O último dos momentos de aplicação se refere a um teste de

retenção, que nos permite avaliar de modo mais seguro o que foi realmente aprendido, visto que a aprendizagem é um processo associado à memória de longo termo, e não apenas de curto termo. Como a disciplina investigada foi a Zoologia de Vertebrados, o questionário inclui questões tanto de evolução, quanto de zoologia. O questionário foi composto de quinze questões de múltipla escolha, sendo apresentado no Anexo 1. De modo a atender algumas necessidades específicas da análise da nossa sequência didática com base nos efeitos pedagógicos pretendidos, o questionário foi composto por cinco diferentes tipos de abordagem em suas questões: (1) um grupo de questões teóricas, abordando conteúdos relativos aos mecanismos evolutivos, fora do contexto de exemplos ecológicos; (2) um segundo grupo de questões, abordando conteúdos específicos de zoologia de vertebrados, sem tratar dos processos evolutivos envolvidos; (3) um terceiro grupo de questões, também abordando conteúdos específicos de zoologia de vertebrados, mas tratando paralelamente de mecanismos evolutivos, dentro de um cenário da conquista do meio terrestre; (4) um quarto grupo tratando do reconhecimento do cenário evolutivo e da sequência de acontecimentos ocorridos durante a radiação dos tetrápodes após a conquista no meio terrestre; e (5) por último, um grupo de questões abordando os mesmos mecanismos em cenários evolutivos que não dizem respeito ao estudo de caso usado na sequência.

Com estes diferentes tipos de questões, pretendemos responder às seguintes perguntas: (1) os estudantes compreendem melhor os mecanismos evolutivos e os conteúdos específicos dentro ou fora de um contexto ecológico? (2) o uso de narrativas auxilia na apreensão dos conteúdos específicos de zoologia? (3) o uso de narrativas auxilia no entendimento dos mecanismos evolutivos? (4) os alunos que acompanharam a sequência didática, baseada em narrativas de processos evolutivos, são mais competentes no reconhecimento do cenário evolutivo e da sequência de acontecimentos correspondentes ao estudo de caso? (5) o uso de narrativas históricas tem uma influência positiva na habilidade dos estudantes para transpor ou deslocar o conhecimento adquirido para responder a novas questões em que os mesmos mecanismos evolutivos estão envolvidos?

Além dos questionários, foram realizadas e gravadas em vídeo entrevistas semi-estruturadas individuais com os estudantes, estas foram posteriormente transcritas e analisadas, de modo a avaliar o grau de apropriação da linguagem social da ciência com base em nossos objetivos de abordagem. O protocolo de entrevista desenvolvido para a entrevista com os estudantes segue no anexo 2. Através das aplicações dos questionários e das entrevistas, buscamos obter dados que permitissem analisar o modo como os estudantes mobilizam determinadas idéias e conceitos quando colocados em situações de interação social estruturadas pelo contexto da pesquisa. Em particular, a entrevista se mostra mais poderosa para produzir interações discursivas com os estudantes, a partir de situações narrativas, que suscitem dados sobre a mobilização das idéias científicas. Além disso, buscamos estimular os estudantes a exporem também as dúvidas que emergiram ao longo da aplicação dos questionários, bem como a justificarem suas convicções em relação aos itens “corretos” e “incorretos” contidos nas questões.. Do, mesmo modo os estudantes foram requeridos, questão a questão, a explicitarem de que forma as aulas recebidas os influenciaram nas suas mudanças de entendimento. Esperávamos através desta estratégia obtermos dados que permitissem compreender as mudanças de entendimento detectáveis em suas respostas, ao longo das três etapas de aplicação

Ao nos referirmos à *compreensão* de uma visão pluralista da evolução, como objetivo de ensino, entendemos ‘compreensão’ sob o parâmetro dos critérios discutidos por Smith e Siegel (2004). Estes autores entendem a compreensão das idéias científicas dos estudantes (em oposição à crença nestas), como objetivo do ensino de ciências, nos seguintes termos: *conectividade*, i.e., a conexão das novas idéias que estão sendo aprendidas entre si e com os conhecimentos prévios dos estudantes, sendo esta uma condição primordial para a compreensão; *atribuição de significado*, na medida em que a conexão das novas idéias com as idéias prévias conduz a um processo de construção de significado, pelo estudante, para as novas idéias, bem como a um processo de

ressignificação das idéias anteriores, na medida em que elas estabelecem relações com as novas idéias; *aplicação*, que se refere ao potencial de uma pessoa que compreende uma nova idéia de extrapolá-la das situações em que a aprendeu a situações diversas, tornando-se capaz de aplicá-la em situações escolares e não-escolares; e *justificação*, que se refere ao fato de que a compreensão envolve uma apreciação coerente de pelo menos algumas razões que justificam a idéia aprendida, entendendo-se, pois, que compreender uma idéia é compreender um argumento que apresenta a idéia.

Para Bakhtin (1978), a construção de sentido sempre se dá por meio de um dialogismo, ou seja, um enunciado sempre se relaciona com enunciados anteriormente produzidos. Todo e qualquer discurso é constituído ou permeado pelo discurso do outro, sendo que estes discursos não são necessariamente convergentes; podem, inclusive, serem discursos contrários, conflituosos e, deste modo, muitas vezes múltiplos e polifônicos. Isso significa que a apropriação do discurso do outro se dá na medida em que o sujeito recria, reinterpreta, reconstrói a idéia alheia, para torná-la própria e significativa para si mesmo. No presente estudo, buscamos estágios de apropriação gradual e progressiva de significados pelos estudantes, conforme distinguidos por Mortimer & Scott (2003):

Estágio (1) - Os estudantes ainda consideram as idéias científicas como constituintes de um discurso alheio, do outro, estranho às suas próprias visões e experiências, não articulando aquelas idéias de forma fluente e apresentando dificuldades em transpor ou deslocar os conceitos adquiridos para explicar outros fenômenos, externos ao caso trabalhado.

Estágio (2) - Os estudantes começam a conceber as novas idéias como em parte pertencentes ao outro, em parte pertencentes a eles mesmos. Eles começam a usar idéias da ciência escolar, mas ainda de modo incerto e hesitante, o que é um indício de que as idéias ainda não foram completamente apropriadas.

Estágio (3) - Os estudantes desenvolvem o potencial de aplicar a perspectiva da ciência na interpretação de uma diversidade de fenômenos e situações, apropriando-se das novas idéias da ciência escolar para construir seus próprios argumentos, tornando-se capazes de empregá-las com fluência e em situações que ultrapassam aquelas trabalhadas em sala.

Dentro do âmbito desta pesquisa, foram compostas três categorias para classificar os discursos encontrados nos depoimentos dos estudantes, registrados por meio das entrevistas gravadas. Estas categorias correspondem aos três estágios descritos acima e, ao mesmo tempo, são relacionadas aos conteúdos apresentados e aos objetivos pretendidos pela sequência didática aplicada. Analisamos comparativamente os níveis de mobilização (domínio) da linguagem social da ciência entre os estudantes, tendo como base as vias de aprendizagem realizadas em relação às vias de aprendizagem esperadas. Seguem abaixo as categorias construídas:

Categoria (1): os estudantes apresentam pouca ou nenhuma familiaridade com o pluralismo de processos e as contribuições da evo-devo, não manifestando segurança ou coerência ao discorrerem sobre outros mecanismos evolutivos, complementares à seleção natural. Não entendem o que estes mecanismos explicam nem como se processam e, conseqüentemente, não conseguem construir exemplos evolutivos e/ou ecológicos nos quais os diversos mecanismos estivessem atuando. Ao tratarem do tema da conquista do ambiente terrestre e da radiação dos tetrápodes, apresentam grande dificuldade para construir uma narrativa dos processos evolutivos envolvidos. Não incluem outros mecanismos evolutivos além da seleção natural em suas explicações, porque não compreendem a ação coletiva de múltiplos mecanismos. Não recordam as principais modificações sofridas pelos tetrápodes e descrevem o cenário ecológico com pouca riqueza de detalhes.

Categoria (2): os estudantes apresentam relativa familiaridade com o pluralismo de processos e as contribuições da evo-devo, já se arriscam a discorrer sobre mecanismos evolutivos complementares à seleção natural de um modo mais espontâneo que os estudantes da categoria anterior, contudo, demonstram ainda algumas dúvidas conceituais. Apresentaram um relativo domínio dos temas abordados, são capazes de construir exemplos evolutivos e/ou ecológicos nos quais os diversos mecanismos evolutivos estejam atuando, contudo, sendo ainda possível a identificação alguns problemas teóricos na composição. Ao tratarem do tema da conquista do ambiente terrestre e da radiação dos tetrápodes, recompõem uma narrativa buscando tratar coletivamente dos mecanismos evolutivos que eles entendem terem atuado durante os eventos em questão, embora ainda com pequenas incompletudes. Recordam bem das principais modificações sofridas pelo grupo dos tetrápodes e descrevem o cenário ecológico com razoável detalhamento.

Categoria (3): os estudantes apresentam uma boa familiaridade com o pluralismo de processos e as contribuições da evo-devo, manifestando segurança e coerência ao discorrerem sobre mecanismos evolutivos complementares à seleção natural. Entendem de modo significativo o que estes mecanismos explicam e o modo como se processam. Apresentam fluência ao construir exemplos evolutivos e/ou ecológicos em que os diversos mecanismos evolutivos estejam atuando. Ao tratarem do tema da conquista do ambiente terrestre e da radiação dos tetrápodes, os estudantes são capazes de explicar a participação de múltiplos mecanismos dentro de uma narrativa dos processos evolutivos ligados aos eventos em questão. Explicam coerentemente como estes processos se deram dentro das condições ecológicas específicas, descrevendo o cenário ecológico com relativa riqueza de detalhamento e tratando da maioria das principais modificações sofridas pelo grupo dos tetrápodes.

As categorias acima descritas correspondem a categorias compostas *a priori*, mas, durante a análise e categorização dos dados, emergiu uma outra categoria, *a posteriori*. Isso é natural, uma vez que sempre pode ocorrer de serem encontrados discursos de estudantes que não podem ser incluídos nas categorias *a priori*. A referida categoria *a posteriori* é híbrida e mesclando características de uma ou mais das categorias *a priori*. Como esta nova categoria não é compreendida em um ordenamento sequencial em relação aos estágios de apropriação considerados no trabalho, não utilizamos o sequenciamento numérico que ordenava as categorias, mas a nomeamos como (w).

Categoria (w): os estudantes apresentam pouca familiaridade com o pluralismo de processos e as contribuições da evo-devo, apesar de reconhecerem sua existência. Demonstram grande dificuldade ao tentarem discorrer sobre mecanismos evolutivos complementares à seleção natural, por conta de possuírem ainda muitas dúvidas significativas em relação a tais conteúdos. Mostram bastante dificuldade ao construírem exemplos evolutivos e/ou ecológicos nos quais os diversos mecanismos evolutivos estejam atuando. Ao tratarem do tema da conquista do ambiente terrestre e da radiação dos tetrápodes, reconhecem a ação de múltiplos mecanismos, embora quando procurem tratar coletivamente dos mecanismos evolutivos que entendem terem atuado durante os eventos em questão, mostram-se inseguros e confusos na narrativa que compõem. Não recordam das principais modificações sofridas pelo grupo e descrevem o cenário ecológico com pouca riqueza de detalhes.

4. Resultados e Discussão

Em nossa discussão, trataremos inicialmente de alguns resultados relativos aos questionários aplicados. Como não tivemos a pretensão de realizar testes experimentais ou *quase*-experimentais, mediante comparação de escores entre diferentes turmas. Tratamos isoladamente a turma do semestre em que intervimos. Realizamos com os nossos testes: (1) uma análise pareada das notas dos estudantes obtidas no questionário aplicado antes das aulas com as notas do

questionário aplicado logo depois das aulas, onde buscamos verificar se foi significativo o sucesso de notas entre estas duas etapas de aplicação; e (2) testamos as notas obtidas no questionário aplicado logo após das aulas com as notas do teste de retenção, onde buscamos verificar se foi significativa a queda dos escores entre as correspondentes etapas. Ou seja, realizamos uma análise dos dados pareados das notas do Pré-teste X Pós-teste; e depois Pós-teste X teste-retenção, sendo ao fim dois testes pareados para a referida turma. Utilizamos o programa PAST para rodar os testes das nossas análises. O teste de normalidade de Shapiro Wilk foi utilizado nas três distribuições e os dados são normais. Um teste pareado não paramétrico de Mann-Withiney (com nível de significância 5%) foi realizado devido aos dados não serem balanceados.

Corroborando com os resultados da análise qualitativa que discutiremos mais adiante, foi verificado em nossos testes um aumento extremamente significativo das notas quando comparado os momentos anteriores aos logo imediatamente posteriores a aplicação das sequências; sendo encontrado o seguinte grau de significância ($p = 1,512E-06$). Do mesmo, não foram detectadas quedas de escores significativas quando comparamos as notas logo após a aplicação da sequência com as notas obtidas alguns meses à frente (teste de retenção), sendo encontrado o seguinte grau de significância ($p = 0,7276$). Selecionamos também, ainda nesta primeira fase de análises dos questionários, as respostas que mais variaram positivamente entre as primeiras e segundas aplicações do questionário, depois observamos o quanto destas respostas que variaram positivamente entre as duas primeiras etapas mantiveram-se corretas ainda no teste de retenção, sendo assim: verificamos que as questões que mais variaram positivamente entre as duas primeiras etapas foram as de número 2, 7, 8, 11, 12 e 15, correspondentes aos seguintes tópicos: questões 2 e 8 – biologia evolutiva do desenvolvimento; questão 7 – modificações fisiológicas que permitiram a conquista do ambiente terrestre; questão 11 – reconhecimento do cenário ecológico; questão 12 – sequência de acontecimentos ocorridos durante a conquista do meio terrestre; e questão 15 – conexão entre vários mecanismos evolutivo. No teste de retenção, 72% das respostas que variaram positivamente entre as duas primeiras etapas mantiveram-se ainda corretas.

Os temas associados às questões servem de indicação relativa de quais os conteúdos que mais afetaram positivamente os alunos da turma sob análise. Tendo como base as nossas vias de aprendizagem pretendidas, entendemos que a turma na qual teve lugar a intervenção, obteve um significativo sucesso em relação a conteúdos que foram priorizados na sequência, por sua relação com uma visão pluralista do processo evolutivo e com a evo-devo, tendo avançado também em relação a conteúdos específicos da disciplina. A maioria dos avanços observados logo após a intervenção pareceu, além disso, se manter no teste de retenção e, por conseguinte, na memória de longo termo dos estudantes.

Contudo, os questionários serviram, prioritariamente, para a análise como um elemento de estruturação das entrevistas, visto que, durante as mesmas, os estudantes foram conduzidos a exporem as dúvidas que emergiram ao longo da aplicação dos questionários, a justificarem suas convicções em relação aos itens “corretos” e “incorretos” contidos em suas respostas às questões, assim como explicitar de que forma as aulas recebidas os influenciaram nas suas mudanças de entendimento. Ou seja, os resultados relativos à categorização que trazemos aqui são concernentes às análises relativas aos diferentes níveis de compreensão identificados nas falas dos estudantes gravadas nas entrevistas, tendo como base os critérios de compreensão de Smith e Siegel tratados em nossa metodologia e os estágios de apropriação gradual e progressiva da linguagem social da ciência propostos por Mortimer & Scott (2003). Ao todo, foram entrevistados 10 estudantes da turma-1 e 13 estudantes da turma-2. Entre os 10 alunos da primeira turma, 7 estudantes foram classificados na categoria (1), 1 na categoria (2) e 2 na categoria (z). Entre os 13 estudantes da segunda turma, 2 foram classificados na categoria (1), 6 na categoria (2), 3 na categoria (3) e 2 na categoria (w) (Tabela 1).

Tabela 5. **Categorização das respostas dos estudantes.**

| | Categoria (1) | Categoria (2) | Categoria (3) | Categoria (w) |
|----------------------------|----------------------|----------------------|----------------------|----------------------|
| N. de Estudantes da turma. | 2 | 6 | 3 | 2 |

A partir destes resultados, podemos concluir que a sequência foi validada internamente, mediante a comparação das vias de aprendizagem esperadas, à luz dos objetivos pretendidos, com as vias de aprendizagem efetivamente realizadas. Podemos dizer é que a aprendizagem esperada entre os estudantes que participaram das aulas ministradas conforme a sequência didática foi bem sucedida em 3 dos 13 estudantes, os quais atingiram o mais alto grau de apropriação definido em nossas categorias (categoria 3), ou seja, que mostraram domínio da linguagem social da ciência tanto no que diz respeito aos conteúdos relativos aos mecanismos evolutivos quanto no que concerne ao evento da evolução dos tetrápodes considerado. Dois estudantes mostraram compreensão dos mecanismos evolutivos, mas não conseguiram aplicá-los com sucesso ao caso estudado. Um pouco menos da metade dos estudantes da turma, 6 dos 13, apresentou uma compreensão de nível intermediário em relação aos conteúdos pretendidos, quando analisada em termos da apropriação da linguagem social da ciência.

Além disso, os resultados positivos obtidos na turma se mantiveram mesmo três meses após a intervenção, dada a constatação de que a maioria dos estudantes apresentou em suas entrevistas uma relativa compreensão, de intermediária a ótima, dos aspectos teóricos que eram objetivos prioritários de aprendizagem, conforme pretendido em nossa abordagem. Os dados coletados neste momento são particularmente importantes, uma vez que, mais importante do que o efeito que uma sequência didática tem sobre os estudantes logo após a intervenção, são os resultados que se mantêm meses depois, o que sugere que as idéias científicas foram incorporadas à memória de longo termo, e não somente de curto termo. Estas idéias retidas na memória de longo termo mostram uma chance maior de influenciar as concepções e os modos de pensar dos estudantes envolvidos na proposta. Abaixo podemos verificar tal efeito exemplificado:

(ps) – e em relação à biologia evolutiva do desenvolvimento? Você acha que recebeu durante a sequência didática que acompanhou em sala de aula explicações que foram baseadas na evo-devo que te ajudaram a entender o processo?

(a1) – Sim, claro. Uma coisa mesmo que mudou no meu jeito de ver foi essa coisa da evolução como que se dá assim nessa relação com o tempo. Porque antigamente e acho que é uma coisa que muita gente pensa assim, você imaginava que seriam necessários períodos enormes, assim tempos gigantes pra que fosse possível se originar uma estrutura nova. Só que agora a gente sabe que basta assim uma pequena mudançazinha na regulação, não precisa nem ser assim uma grande mudança, mas basta ter uma mutaçõzinha lá de um gene que controle a expressão durante o desenvolvimento pra que surja assim uma estrutura completamente diferente, assim de uma geração pra outra.

(ps) – e você sabe como é que são chamados esses genes que regulam a expressão de outros genes durante o desenvolvimento?

(e1) – sim, acho que sei, são genes hox, né isso?

(ps) – sim, claro, só pra saber. Mas me diga uma coisa, você acha então que compreende como essas explicações trazidas pela evo-devo sobre o surgimento de novidades evolutivas nos ajuda a fundamentar uma contraposição em relação ao modelo do gradualismo filético? Refiro-me à idéia de que as transformações evolutivas ocorrem sempre através de pequenas mudanças que vão paulatinamente se acumulando ao longo de grandes escalas temporais. Você entende como que

estes estudos desenvolvimentais se opõem à noção gradualista?

(e1) – sim, acho que do jeito que eu te falei, agora a gente entende que as transformações podem ser muito mais rápidas por conta dessas mudanças do desenvolvimento, os processos de regulação e tal.

(ps) – mas então me diga como é que indivíduos que expressam características completamente diferentes das médias morfológicas dos outros indivíduos da sua população iriam poder competir com os outros, disputarem os recursos e tudo mais? Visto que essas características que eles expressam não estão exatamente ajustadas ao meio, já que não são adaptações, não foram frutos da seleção natural, você poderia me dar uma explicação, pra isso? Porque, veja bem, a gente deveria imaginar que dentro de um regime de fortes pressões seletivas os indivíduos que não estivessem finamente adaptados deveriam ser rapidamente eliminados, certo? Será que você entende como é que pode se relacionar essa questão das intensidades das pressões seletivas e sucesso destas alterações decorrentes de mudanças desenvolvimentais? Vá com cuidado, de repente é muita coisa pra relacionar, acha que consegue?

(e1) – mais ou menos, acho até que é uma questão até de parcimônia. Porque claro que se a gente imaginar que eles estiverem sob fortes pressões seletivas aí fica realmente difícil. Tipo como o professor descreveu pra gente, no caso dos tetrápodes mais basais que viviam em águas mais profundas e estavam sob intensa pressão predatória, eu lembro que tinham outros peixes mais rápidos e maiores coisa e tal; mas se for pensar depois que eles migraram pro raso e encontraram refúgio, aí quem sabe nesta outra etapa ou depois mesmo da invasão pra terra mesmo. Porque o legal que eu acho que entendi é que não é assim uma coisa ou outra são as duas coisas juntas, então uma novidade que surgir por causa de uma mudança do desenvolvimento, depois também vai ser como é que se diz? Vai ser tipo que polida pela seleção natural também e depois acaba que confere alguma vantagem adaptativa e vai terminar sendo fixada também. O importante que eu acho que entendi é que se devemos pensar as coisas integradas. Aí fica melhor pra gente entender.

Contudo, podemos concluir que a sequência didática logrou um sucesso que poderia ser ainda potencializado em relação às vias de aprendizagem esperadas, o que aponta para a necessidade de aprimorá-la, tendo como base os resultados aqui relatados dando, desse modo, continuidade ao seu desenvolvimento. Alguns resultados obtidos indicam duas necessidades: (i) de trabalhar mais intensamente os mecanismos evolutivos explorados no interior da sequência; e (ii) a necessidade de um tratamento transversal dos diversos conteúdos evolutivos abordados. O aprimoramento relativo a estes tópicos poderia aumentar as chances de os estudantes atingirem uma compreensão mais clara em relação aos passos evolutivos encadeados na narrativa apresentada. Os depoimentos presentes nos trechos a seguir apontam para tal necessidade de aprimoramento que destacamos:

Categoria (3), (e2) – O bom foi que eu tinha acabado de pegar genética, logo no semestre passado e aí tava ainda com tudo isso mais fresco na mente. Por exemplo, quando o professor botou lá aquelas figuras comparando o pulso, o desenvolvimento dos dígitos tal, na hora lembrei logo do professor de genética II mostrando o embrião todo divididinho puxando as setas pra cada gene *hox* e toda aquela coisa da regulação.

Categoria (2), (e3) - sabe o que é? É que a zoo já tem tanto conteúdo, já é um monte de coisa pra gente aprender, e aí vem no meio um monte de coisa de evolução que a gente não sabe direito, não dá tempo pro professor falar todas aquelas coisas dos bichos e ainda ter de explicar outras coisas que a gente já deveria saber, porque eu acho que evolução deveria ser dada ao longo do curso todo, só que não é assim, a gente vê um pouquinho em biozão (biologia geral), depois só volta a falar em genética II e agora em zoo IV, acho talvez também lá em EPC (evolução do pensamento científico), mas não sei porque ainda não fiz, mas no resto do curso todo a gente não vê nem a sombra.

(pesquisador) – e como é que você entende essa influência mútua entre a evolução e o desenvolvimento?

Categoria (3), (e4) – bem, essa distinção e relação de influência entre o desenvolvimento e a evolução é uma coisa que na verdade só se sedimentou agora pra mim que estou fazendo evolução do pensamento científico. Isso de que o desenvolvimento se dá durante a vida do indivíduo e evolução é mais uma questão de variação dentro das populações ao longo do tempo. Eu acho que essas relações da evolução com desenvolvimento são muito importantes, mas o problema é que na verdade a gente escuta falar muito pouco no nosso curso.

Trataremos agora de algumas questões que nos chamaram a atenção nos resultados relativos às categorias (w), os quais indicaram pontos interessantes para nossa análise que se referem ao conhecimento prévio dos estudantes. Apenas 2 estudantes da turma foram classificados na categoria (w). Estes estudantes possuíam, ao fim do semestre, uma compreensão de que não apenas a seleção natural teria atuado na radiação dos tetrápodes após a conquista do ambiente terrestre, ou seja, admitiam o papel de vários mecanismos evolutivos neste evento. Contudo, em relação aos conteúdos específicos da disciplina, fisiologia, classificação taxonômica, caracterização de paleoecossistemas etc., não obtiveram resultados satisfatórios, não compreendendo bem, por exemplo, as relações de ancestralidade e descendência dentro do grupo dos tetrápodes, as principais modificações sofridas pelo grupo e o cenário ecológico em que evoluíram. Em relação aos conteúdos evolutivos, apesar de reconhecerem a ação de múltiplos mecanismos atuando durante o evento estudado, apresentavam pouca familiaridade com o pluralismo de processos. Mostravam grande dificuldade ao tentarem discorrer sobre mecanismos evolutivos complementares à seleção natural, bem como ao construírem exemplos ecológicos nos quais estes mecanismos evolutivos estivessem atuando. Estes alunos não obtiveram, pois, os resultados de aprendizagem esperados, no que diz respeito a uma apropriação satisfatória da linguagem social da ciência escolar no tratamento dos conteúdos abordados.

Ao analisarmos algumas informações extraídas das entrevistadas realizadas com estes estudantes, foi possível perceber que eles não estavam suficientemente preparados para compreenderem satisfatoriamente uma narrativa que envolvesse os conceitos evolutivos explorados na sequência didática. Parte desta dificuldade podia ser explicada em termos de seus conhecimentos prévios. Boa parte dos alunos da turma, os quais já haviam percorrido mais da metade do curso, visto que chegaram à última disciplina oferecida na cadeia das zoologias, não possuíam uma compreensão clara dos mecanismos evolutivos que permitem explicar a diversidade biológica. Os trechos a seguir, extraídos das entrevistas, apontam tais problemas de entendimento:

Categoria (1), (e6) - acho que o meu problema maior pra entender foi que diferente de alguns alunos eu ainda não fiz genética II, pelo que escuto falar dos meus colegas essa coisa dos mecanismos a gente só vê mesmo na genética II e aí como eu ainda não fiz, pra mim fica mais difícil.

(ps) – Em termos simplificados, você poderia tentar definir pra mim o que é que você entende por restrição?

(e7) – ah! Essa parte de evo-devo, eu sempre tive muita dúvida, sei que é um conhecimento novo que tem influenciado muito a biologia nos últimos tempos, mas a gente escuta falar muito pouco em sala de aula [...] e a gente termina ficando sem base pra entender... sabia que você ia vim me perguntar isso, já tava aqui com medo. Acho que esse mecanismo aí de restrição, ainda não tá muito claro assim pra mim, porque de vez em quando a gente escuta um professor falar, mas acho que eu nunca ouvi uma explicação do que é mesmo uma restrição em si. Aí eu meio que acho que tenho uma idéia assim da minha cabeça mesmo, assim do que eu acho que é, entendeu? Também acho que a culpa é minha também, acho que eu sou preguiçosa, porque dos tempos que eu escuto falar disso aí de restrição e ainda não fui procurar saber direito, qualquer coisa se eu falar besteira você me fala, tá? É tipo assim, vamos dizer que você não tem os dedos, tipo assim os dedos da mão, e aí a seleção não vai poder agir em cima de uma coisa que não existe, então a seleção não vai poder trabalhar naquele ponto e aí você vai ficar restrito, vai ter sofrido uma restrição, entendeu? Tipo a seleção não pode atuar no que não existe é assim que eu entendo.

(e8) – veja bem, esse enfoque evolutivo dos mecanismos tem que ser trabalhado no curso com mais atenção, digo assim na faculdade como todo, acho que não tenho uma base boa pra falar direito disso aí.

(ps) – mas você não quer tentar explicar mesmo em termos simplificados como é que você entende a ação dos fatores de restrições?

(e8) – bom, eu entendo como se fosse tipo uma “distorcenciação” (diferenciação?) negativa, como a seleção é positiva, seria restrição um tipo de seleção negativa, o que impediria o individuo de desenvolver uma característica mais adaptada e ele ficaria restringido, enquanto os outros indivíduos que desenvolverem uma adaptação mais favorável, ia poder deixar mais descendentes e não viver uma evolução naquele sentido. Diferente dos que ficaram restritos. É eu entendo mais ou menos assim.

Estas falas dos dois últimos estudantes indicam também outra problemática recorrente nas falas de muitos dos estudantes entrevistados. Por conta de não terem desenvolvido, ao longo do curso, uma base consistente para a compreensão da evolução, têm dificuldade de construir interpretações claras dos conceitos evolutivos. Isso pode acarretar dificuldades em sua formação como futuros biólogos, dado o papel da compreensão dos processos evolutivos na construção do conhecimento biológico. Os achados relativos aos conhecimentos prévios dos estudantes também nos levam a concluir que os efeitos positivos obtidos com a sequência poderiam ser aumentados, caso os alunos estivessem mais consistentemente embasados em relação aos estudos evolutivos. Contudo, foi possível notar que em relação aos aspectos da estrutura narrativa, a qual adotamos como um eixo de encadeamento das explicações de processo robusto e sequência de acontecimentos reais apresentadas, provocaram um efeito positivo em relação a memorização e envolvimento em relação ao conteúdo trabalhado. O trecho transcrito a seguir demonstra que de fato os estudantes foram sensíveis as diferenças de tratamento empregadas na estrutura narrativa que utilizamos em nossa proposta de ensino:

Categoria (3), (e9) – bem, mas eu posso te dizer que a zoo IV foi muito diferente do que a gente tá acostumado a ver nas disciplinas daqui. Porque não foi apenas aquela coisa de classificação de reconhecer os bichos, dizer as sinapomorfias e funcionamento lá dos aparelhos. E não fui só eu que me identifiquei, pô teve vários colegas também que a gente comenta, o pessoal da minha equipe. Porque não foi aquele negócio parado, foi assim uma história mesmo, sabe? Eu lembrando é como se fosse um filme assim passando. Porque o professor vai criando todo aquele teatro e aí a gente vai imaginando e termina que você acaba querendo saber mesmo com é que foi e vai se envolvendo, pra mim foi bem legal. Porque a gente não estudou apenas o grupo, mas a história evolutiva, essa abordagem aí dos mecanismos que a gente começou falando, acaba deixando as coisas mais amarradas e não fica tudo solto, jogado.

5. Considerações finais

Podemos concluir que uma sequência didática que contemple os princípios de *design* adotados na construção da intervenção investigada no presente trabalho poderá, no contexto do ensino superior de zoologia dos vertebrados, obter resultados positivos no que concerne a: (i) integração dos conteúdos de zoologia, evolução e ecologia, (ii) abordagem de vários mecanismos evolutivos e suas interações, e (iii) no entendimento dos contribuições da biologia evolutiva do desenvolvimento. Por conseguinte, possuímos a expectativa de que a utilização de sequências didáticas com tais características possa ser adotada como estratégia educacional em outros cursos de zoologia de vertebrados, podendo contribuir para uma fundamentação mais consistente no ensino da matéria, principalmente no que se refere ao entendimento da biologia evolutiva desenvolvimental destes organismos, assim como dos múltiplos mecanismos envolvidos em sua história evolutiva.

Os achados do presente estudo sugerem que a sequência didática construída pode de fato promover uma aprendizagem bem sucedida dos estudantes, em relação às vias de aprendizagem

pretendidas em seu planejamento. Foi possível também verificar que uso de narrativas auxilia na apreensão dos conteúdos específicos da disciplina, no entendimento dos próprios mecanismos evolutivos, no reconhecimento do cenário evolutivo e das principais modificações sofridas pelo grupo, assim como em relação à sequência de acontecimentos correspondentes ao estudo de caso. Isso nos leva a concluir que a intervenção pedagógica proposta trouxe resultados satisfatórios, tendo influenciado a aprendizagem dos estudantes na direção pretendida.

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Anexo 1 - Questionário de Avaliação dos estudantes

Inventário sobre mecanismos evolutivos pluralistas (IMEP)

A biologia evolutiva tem vivenciado um grande desenvolvimento nos últimos tempos. Uma importante mudança que podemos destacar é o reconhecimento da ação de múltiplos mecanismos evolutivos atuando na história da vida. Estes mecanismos desempenham importantes papéis no processo de diversificação das espécies e são complementares ao processo de seleção natural. Seriam alguns destes mecanismos: deriva gênica, distintos modos de especiação, construção de nicho, auto-organização e restrições ao processo evolutivo. O estudo destes novos mecanismos tem permitido avançar bastante na compreensão de vários fenômenos evolutivos. No entanto, tais estudos não estão fundamentados em uma visão anti-selecionista, pois o papel da seleção natural continua sendo de extrema importância para o estudo da evolução.

1. Em relação aos fundamentos básicos da teoria da seleção natural, escolha a seguir a resposta INCORRETA:

- a) A seleção natural não é o único processo envolvido na evolução das espécies, mas é o único que dá origem a adaptações.
- b) A seleção não atua apenas ao nível do organismo, mas simultaneamente sob diferentes alvos e em distintos níveis de organização.
- c) A seleção natural está relacionada a um modelo gradualista de evolução dos seres vivos, ou seja, que pressupõe que os organismos se modificam por meio de pequenas mudanças acumuladas ao longo de grandes escalas de tempo.
- d) A seleção natural fornece explicação para o surgimento de novas características nas populações, além de explicar por que certas características são fixadas em uma população.

2. Uma nova área da biologia, a biologia evolutiva do desenvolvimento, frequentemente chamada de evo-devo, tem desempenhado, recentemente, um papel importante na reestruturação do pensamento evolutivo. Esta área inclui pesquisas que têm permitindo avançar na compreensão de fenômenos que não podiam ser explicados apenas com base na teoria da seleção natural. Qual dos itens a seguir NÃO está diretamente relacionado com os estudos desenvolvidos pela Evo-devo?

- a) A evo-devo tem buscado explicar como alterações nos padrões de expressão gênica, decorrentes de mudanças nas sequências regulatórias de genes desenvolvimentais, podem conduzir a mudanças na morfologia dos organismos.
- b) Ela tem permitido o entendimento de que a seleção natural opera sobre um repertório limitado de variantes possíveis, porque os organismos estão submetidos a restrições relacionadas ao seu desenvolvimento.
- c) Ela tem investigado a expressão gênica durante a formação dos embriões, buscando elucidar como mudanças aparentemente simples, como inversões temporais ou espaciais na expressão de um gene, podem levar a profundas alterações na morfologia dos organismos.
- d) Ela procura integrar as idéias de Darwin a novos conhecimentos do campo da genética, especialmente da genética de populações. Além da seleção natural, seus estudos reconhecem como principais fatores evolutivos as mutações e a recompilação gênica.

3. Em população com um tamanho reduzido, a deriva genética ocorre mais rapidamente. Por exemplo, diante de um efeito gargalo, no qual uma percentagem significativa da população morre ou é impedida de se reproduzir, a deriva genética pode resultar em rápidas e profundas alterações nas frequências alélicas. Baseando-se nesta afirmativa e nos seus conhecimentos complementares sobre este mecanismo evolutivo (deriva genética), seria INCORRETO afirmar:

- a) Em circunstâncias como as mencionadas acima, alterações nas frequências alélicas ocorreriam de maneira independente da seleção natural, sendo que muitas adaptações benéficas poderiam ser eliminadas da população.

- b) O grau em que cada alelo é afetado pela deriva genética difere em função das circunstâncias ecológicas.
- c) A frequência de um gene pode, por efeito de deriva, aumentar ou diminuir de uma geração para outra. Em uma população pequena, existe a possibilidade de que um gene seja fixado simplesmente ao acaso, mas em uma população de grande tamanho isso não é possível de acontecer, porque o efeito da seleção natural sobrepõe a deriva genética.
- d) Na ausência de novas mutações, uma população pequena tenderia, por efeito de deriva, a torna-se homocigótica, deste modo, comprometendo sua variabilidade genética.

A transição de peixes a tetrápodes: novos fósseis e interpretações

A idéia de que uma criatura provida de nadadeiras deixou a água e conquistou o ambiente terrestre não é controversa para o público que aceita evolução, mas, nos últimos 10 anos, com novas evidências fósseis, a nossa compreensão de como deve ter ocorrido essa transição foi aprimorada, agora com base em uma quantidade muito maior de evidências. A transição do ambiente aquático para o ambiente terrestre se deu entre 385 e 360 milhões de anos atrás, no final do período Devoniano, com o surgimento de animais com 4 membros dotados de articulações e dedos. Estes animais eram os primeiros tetrápodes, que deram origem a um grupo que hoje inclui todos os vertebrados terrestres, mesmo aqueles que perderam dois ou todos os membros (como baleias e cobras, respectivamente).

No passado, as discussões sobre a origem dos tetrápodes a partir dos peixes se valiam de comparações entre o *Eusthenopteron* (um peixe) e o *Ichthyostega* (um tetrápode). Descobertas posteriores mostraram que o *Ichthyostega* não é um exemplar típico de um tetrápode do Devoniano, mas um animal aquático bastante especializado, mostrando características que favoreciam incursões terrestres, o que mostra que já no Devoniano os tetrápodes apresentavam grande diversidade. Um fóssil que apareceu mais tarde neste debate foi o *Achantostega*, um animal do Devoniano superior que apresenta características marcantes de tetrápodes terrestres e uma menor quantidade de características de peixes. Um fóssil bastante recente e que ganhou notoriedade, tanto pelas suas características muito próximas aos tetrápodes quanto pela sua excelente preservação, é o *Tiktaalik*. Este ainda é um peixe, mas apresenta diversas características dos tetrápodes terrestres, notadamente no crânio e nos membros anteriores.

Desde o Devoniano, existiam diversos organismos que apresentavam características cada vez mais adequadas à conquista do ambiente terrestre. Estes organismos, tanto peixes como tetrápodes, apresentam similaridades morfológicas. Eles surgiram na água e suas características estavam inicialmente mais relacionadas ao hábito de viver em águas rasas do que propriamente de viver em terra. Podemos assim concluir que a origem dos tetrápodes não é o mesmo que a conquista do ambiente terrestre.

Texto baseado em: CLACK, J. 2009. The Fish Tetrapod Transition: New Fossils and Interpretations. *Evolution: Education and Outreach* 2:213-223.

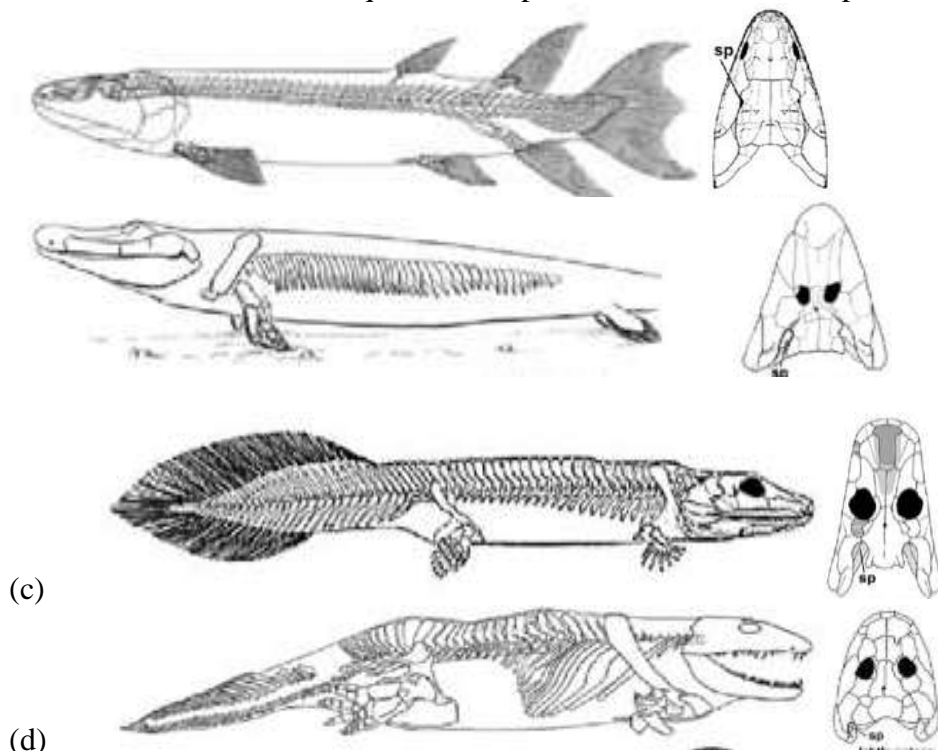
Utilize o texto acima e seus conhecimentos para responder as questões de 4 a 9.

4. Uma série de modificações possibilitou que nossos ancestrais tetrápodes conquistassem o ambiente terrestre. Dentre essas modificações, qual delas NÃO é verdadeira?
- (a) Fusão da cintura pélvica com a coluna.
 - (b) Aquisição de um membro dotado de articulação e dedos.
 - (c) Redução do aparelho hiomandibular e ossos que ligam a cintura escapular à cabeça.
 - (d) Desenvolvimento de um aparelho pulmonar.
5. Embora *Eustheropneustrodon* não pertença à linhagem de tetrápodes e não seja ancestral destes organismos, foram encontrados registros de que ele se locomovia em terra firme. Fósseis de tetrápodes do mesmo período mostram que estes também faziam incursões no meio terrestre, apesar de ainda estarem limitados ao ambiente aquático, graças a outras características. Com base em seus

conhecimentos sobre esta transição na história dos vertebrados, qual proposição explica melhor esta similaridade entre peixe e tetrápodes?

- (a) Semelhanças no desenvolvimento.
- (b) Comportamento altruísta.
- (c) Pressões ecológicas.
- (d) Construção de nicho.

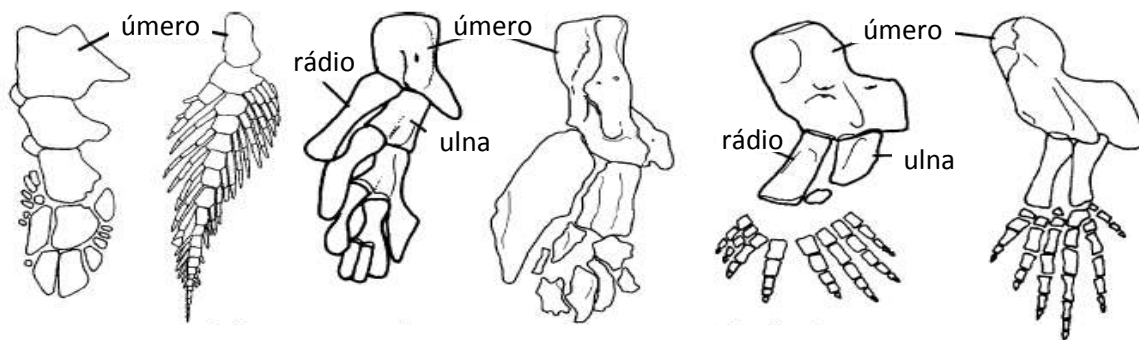
6. As figuras abaixo representam alguns dos animais citados no texto acima. Pelas suas características anatômicas, qual destes apresenta características típicas de um animal terrestre?



7. Sobre as modificações que possibilitaram a conquista do ambiente terrestre pelos tetrápodes e o cenário em que estas ocorreram, identifique a afirmação que NÃO é correta:

- (a) O favorecimento de certas características em populações de tetrápodes ancestrais, bem como de outros grupos, leva em conta fatores ecológicos, como a competição nas águas rasas do Devoniano, onde esses organismos viviam, buscando fugir de predadores de águas profundas.
- (b) Indivíduos que possuíssem características favoráveis tenderiam a deixar mais descendentes.
- (c) Mudanças morfológicas e fisiológicas que acontecem em um organismo não alteram o processo evolutivo, a não ser que essas mudanças cheguem ao nível das populações.
- (d) Dentre os organismos que aparecem na narrativa “A transição de peixes a tetrápodes: novos fósseis e interpretações”, é possível observar grande variabilidade em relação aos tipos de nadadeiras e membros. Essa variedade foi importante para que a seleção natural atuasse de maneira a preservar os indivíduos que viriam a conquistar o ambiente terrestre.

8. Observe a figura abaixo, sobretudo, as homologias entre as partes de cada nadadeira/membro. Usando seus conhecimentos, indique a afirmação que melhor explica o surgimento dessas diferenciações morfológicas.



- (a) Mudanças no padrão de regulação de genes do desenvolvimento, duplicação e cooptação de genes Hox para diferentes funções.
- (b) Mutações em genes específicos que determinam a formação dos fenótipos.
- (c) Auto-organização das estruturas, com fusões de ossos, mudanças na conformação de músculos e tendões.
- (d) Pequenas alterações morfológicas, que ao longo do tempo foram selecionadas, produzindo cada tipo de nadadeira ou membro, adaptado à sua função.

9. Sabe-se que os primeiros tetrápodes tinham um número variável de dedos (7, 8 ou mais), mas todas as linhagens atuais deste grupo descendem de um ancestral comum que tinha 5 dedos. Qual a melhor explicação para o rápido aumento de frequência dessa característica, sabendo que estamos lidando com populações pequenas?

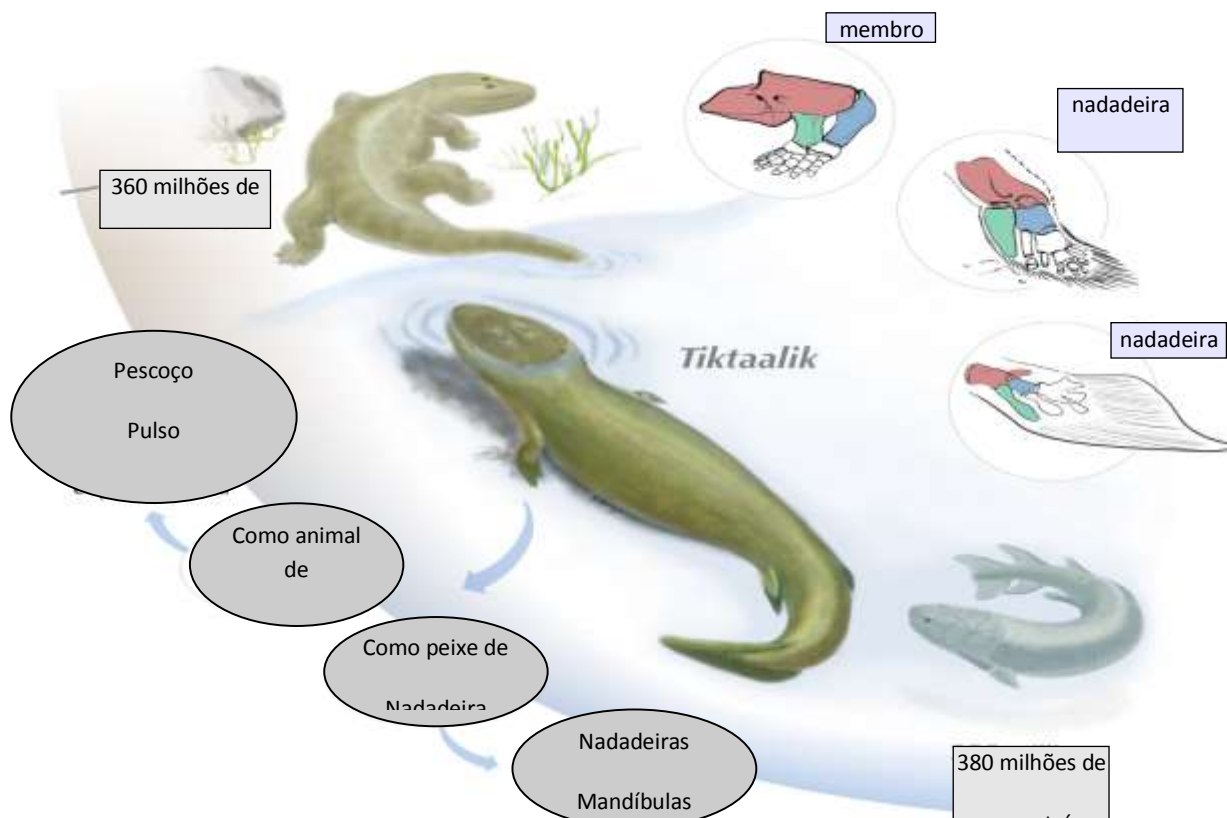
- (a) Seleção Natural.
- (b) Mudanças na regulação do desenvolvimento.
- (c) Deriva genética.
- (d) Mutação.

Os tetrápodes e a transição para vida terrestre

Pelas estimativas atuais, a vida vem evoluindo na Terra há aproximadamente quatro bilhões de anos tendo gerado enorme variedade de formas e muitas adaptações notáveis. A conquista do meio terrestre pelos tetrápodes é uma das mais espetaculares revoluções nas formas de vida. Ela corresponde ao surgimento de criaturas terrestres dotadas de membros e dedos, tendo como ancestrais organismos aquáticos com nadadeiras. Hoje, este grupo é bastante diversificado, incluindo desde as aves e os seus ancestrais dinossauros, até lagartos, serpentes, tartarugas, anfíbios e mamíferos.

A transformação das nadadeiras em membros foi um passo fundamental para essa transição, mas não foi de modo algum a única mudança necessária. Os primeiros ancestrais tetrápodes que se aventuraram em terra firme foram submetidos a desafios que nenhum outro vertebrado havia enfrentado antes. Como a terra era um meio radicalmente diferente da água, durante esta transição os tetrápodes sofreram diversas modificações nas formas de respirar e ouvir. Além disso, surgiram adaptações que respondem aos diferentes efeitos da gravidade, além da temperatura, radiação solar, entre outros problemas.

Vemos abaixo uma figura esquematizando mudanças no desenvolvimento dos membros dos tetrápodes ao longo da transição para o ambiente terrestre. A ilustração utiliza no exemplo o *Tiktaalik*, conhecido e divulgado como fóssil de transição entre peixes e tetrápodes.



Examine o texto e a figura acima e, baseando-se em seus conhecimentos, responda as questões de 10 a 12.

10. Seguem abaixo algumas características que tornaram possível que os tetrápodes tivessem sucesso durante o processo de conquista do meio terrestre, EXCETO:

- Mudanças nos processos fisiológicos envolvidos na regulação térmica dos tetrápodes, que se tornaram endotérmicos, uma condição mais favorável para o seu metabolismo no ambiente terrestre.
- O desenvolvimento de membros a partir de nadadeiras lobadas ancestrais, permitindo locomoção mais eficiente em terra firme.
- Alterações no padrão de captura de luz pelo cristalino, possibilitando melhor percepção visual, diante da diferença de refração entre o ar e a água.
- Modificações em seus tecidos epiteliais, impermeabilizando a superfície corporal, o que permitiu um maior controle do conteúdo hídrico do corpo, por minimizar a perda de água por evaporação.

11. Para você, qual das afirmações apresenta o cenário mais plausível para a transição dos tetrápodes para o meio terrestre?

- O número de continentes no mundo havia se reduzido, com uma aproximação cada vez mais entre eles, num processo que levaria à formação de Pangéia. O clima era quente e o nível dos oceanos, elevado. Isso fez com que muitas terras fossem cobertas por mares rasos, onde proliferavam grandes recifes de corais. Neste período, também surgiram as primeiras florestas. Assim, era possível encontrar muitas formas de vida no ambiente continental, plantas, moluscos e peixes de água doce.
- A fauna marinha não era muito variada, já que 90% das espécies haviam desaparecido na grande extinção do final da Era Paleozóica. As novas espécies, como corais e moluscos bivalves, por exemplo, ainda não tinham proliferado e se diversificado o suficiente para povoar completamente os mares. A flora era relativamente uniforme e consistia, predominantemente, de plantas vascularizadas, semelhantes às samambaias.

c) Neste período, ocorreram inundações constantes dos continentes pelos mares. O clima era ameno, inclusive nos pólos. Os climas tropical e subtropical predominavam. A vegetação era abundante e havia muitas lagoas costeiras e fluviais salobras. Grandes deltas também estavam presentes naquele período. Foi também neste cenário que surgiram as primeiras plantas com flores.

d) Os primeiros tetrápodes evoluíram em habitats de água doce superficiais e pantanosos. As plantas terrestres haviam colonizado alguns habitats de água doce, dando origem a teias alimentares cada vez mais complexas. Estes habitats correspondiam a pântanos rasos, com densa vegetação. Havia também muitos insetos, como moscas, borboletas e libélulas, que serviram de alimento para os primeiros tetrápodes, quando estes conquistaram a terra.

12. Qual dos trechos da narrativa a seguir NÃO lhe parece coerente com a sequência de eventos ocorridos durante o processo de conquista do meio terrestre pelos tetrápodes:

a) Os tetrápodes teriam inicialmente se agrupado em águas rasas, assim como fazem os filhotes de peixes e anfíbios atuais, buscando proteção contra grandes predadores de águas mais profundas. Nesse período, os peixes dominavam os mares e ocupavam o topo da cadeia alimentar...

b) ... devido à insolação direta na massa de água pouco profunda, os tetrápodes estavam submetidos a uma condição bem particular, já que as águas se mantinham quentes e com baixa oxigenação. Possuir pulmão, em tais circunstâncias, lhes conferia uma grande vantagem...

c) ... um tetrápode com respiração aérea poderia utilizar seus membros, desenvolvidos a partir das nadadeiras lobadas de seus ancestrais, de modo a sustentar seus corpos, erguendo-o fora d'água, caso a profundidade não fosse suficiente para a flutuação...

d) ... ao longo de um processo de desenvolvimento gradual, foram originadas formas cada vez mais ágeis, até tornarem-se capazes de explorar o habitat terrestre. Os adultos bem desenvolvidos foram os primeiros a se afirmar como bons predadores terrestres, enquanto os filhotes se mantinham protegidos nas margens de lagos e estuários.

13. Alguns grupos de tetrápodes, que correspondiam a sinapsidas mais derivados, os quais possuíam um uso mais acentuado da articulação mandibular e a necessidade de efetuar mordidas mais fortes, sofreram várias modificações em sua estrutura óssea mandibular. Contudo, tais modificações os tornaram menos eficientes no cumprimento sua função auditiva. Foi sugerido, por exemplo, que na história evolutiva da mandíbula dos cinodontes, um caso bem estudado dentro do grupo, tenha ocorrido um “conflito evolutivo” no desempenho destas duas funções: alimentação e audição. Refletindo sobre esta pequena introdução e utilizando seus conhecimentos sobre seleção natural, identifique a afirmação INCORRETA:

a) No caso abordado acima, podemos afirmar que existem duas pressões seletivas distintas atuando sobre um mesmo conjunto de estruturas e o desequilíbrio destas forças pode levar a um melhor desenvolvimento de apenas uma das funções requeridas, o que comprometeria ou impossibilitaria o desempenho da outra.

b) Dada uma condição ecológica em que a necessidade de morder mais forte é mais importante do que a necessidade de se orientar por meio da audição, podemos esperar que os indivíduos que adquiram uma mordida forte deixem mais descendentes, ainda que escutem com menor eficiência do que seus competidores.

c) Este problema acima poderia ser melhor explicado dentro do ponto de vista de uma restrição desenvolvimental, pois se trata de exemplo onde se expressa uma limitação na variabilidade fenotípica. Isto pode ser causado pela estrutura, caráter, composição ou dinâmica de desenvolvimento da mandíbula.

d) Nem todas as modificações em uma estrutura evoluíram como adaptações, por meio de seleção natural. Alguns efeitos são consequências inevitáveis das leis da física. Muitas “imperfeições” nos seres vivos podem ser causadas por restrições físicas, genéticas, históricas ou desenvolvimentais, assim como pelo efeito da flutuação nas demandas de competição.

14. Os seres humanos são muito diferentes de chimpanzés em uma série de características, mas, apesar deste fato, as duas espécies compartilham cerca de 99% de suas seqüências de DNA. Isso sugere que não é necessária uma mudança muito grande do genoma para dar origem a novas espécies. Reflita sobre esta introdução e, baseando-se no seu conhecimento da biologia evolutiva do desenvolvimento, identifique a afirmativa INCORRETA:

- a) Mudanças na expressão de genes envolvidos na regulação do desenvolvimento resultam, provavelmente, de ganhos, perdas e modificações nos elementos que regulam estes próprios genes.
- b) O surgimento de genes que regulam a expressão de outros genes pode ter tornado a vida mais capaz de evoluir, ou seja, pode ter aumentado a probabilidade de os seres vivos sofrerem mudanças evolutivas.
- c) Os genes regulatórios que controlam outros genes diferem enormemente de uma espécie para outra, o que dificulta bastante as pesquisas. Por exemplo, mesmo com toda similaridade genética entre os humanos e os chimpanzés, é provável que os genes que controlam o desenvolvimento da estrutura ocular de ambos sejam completamente diferentes.
- d) Se uma pequena mudança na regulação gênica pode estar relacionada a um grande efeito fenotípico, é provável que grande parte das mudanças genéticas entre os humanos e os chimpanzés tenha ocorrido em genes reguladores.

15. Acredita-se que o efeito gargalo, no qual uma percentagem significativa da população morre ou é impedida de se reproduzir, já tenha ocorrido em diversas ocasiões na história da evolução humana. Por exemplo, evidências sugerem que as populações humanas sofreram uma redução drástica devido a um grande efeito gargalo, ocorrido há 70.000 anos, devido à maior erupção conhecida do Quaternário, a erupção do vulcão do lago Toba, na Indonésia. Esta erupção vulcânica poderia ter dizimado grande parte das populações humanas, especialmente aquelas que estavam fora de refúgios tropicais isolados. Admitindo-se que Toba possa ter causado tal estrangulamento, sugere-se então que as raças humanas modernas podem ter sido diferenciadas abruptamente há apenas 70 mil anos. Esse evento vulcânico poderia ter reduzido as populações a tamanhos tão pequenos que uma combinação de processos levou a diferenciações rápidas na população global. Qual a SEQUÊNCIA de processos que melhor explicaria a narrativa acima proposta?

- a) Efeito fundador, construção de nicho e mudanças regulatórias em genes envolvidos no desenvolvimento.
- b) Mudanças regulatórias em genes envolvidos no desenvolvimento, deriva genética e efeito fundador.
- c) Deriva genética, efeito fundador e adaptações locais.
- d) Mudanças regulatórias em genes envolvidos no desenvolvimento, adaptações locais e construção de nicho.

Anexo 2 - Protocolo de entrevista dos estudantes

- Primeiro, pedimos que os estudantes que falassem a respeito dos mecanismos evolutivos que conheciam;
- Em seguida, serão foram feitas perguntas sobre o significado de alguns conceitos fundamentais relacionados aos mecanismos mencionados:
 - O que estes mecanismos explicam? Como se processam?
- Depois, pedimos para que os estudantes falarem um pouco sobre a importância do estudo da evolução no aprendizado da zoologia e da ecologia em geral;
- Solicitamos aos estudantes que formulassem alguns exemplos ecológicos com os quais poderiam tratar os mecanismos evolutivos que conhecem;
- Sequencialmente Interrogamos quais eram os mecanismos que eles compreendiam terem participado durante os processos de transição e conquista do ambiente terrestre pelos tetrápodes?
- Por último, pedimos para eles sinteticamente buscassem reconstruir dentro de um cenário ecológico uma pequena narrativa deste processo de transição e conquista, buscando relacionar com os processos evolutivos vivenciados pelos tetrápodes.

Anexo 3 - Sequência didática sobre Conquista do meio terrestre

Aula 1

Objetivo: Abordar a transição dos tetrápodes buscando fornecer explicações do processo robusto, ou seja, procurar extrair generalizações e identificar uma possível macro-estrutura de processos que seja invariante em relação às peculiaridades micro-históricas de diversificação do grupo; de modo que tal explicação possa se compatibilizar e auxiliar na compreensão de outras pontuações na história da evolução dos seres vivos.

1ª Etapa: 60 minutos

- Levantar a discussão sobre os padrões evolutivos, de modo que possa ser possível situar a transição dos tetrápodes enquanto uma pontuação evolutiva,
- Explicar que os padrões evolutivos são frequentemente interpretados pela análise de registros paleontológicos;
- Apresentar a paleontologia enquanto ciência que constrói, através da análise da sucessão cronológica dos fósseis, uma narrativa dos períodos da história da evolução. Depois, acrescentar que nestes registros paleontológicos, por vezes (enquanto generalização), podemos identificar a ocorrência de um padrão intercalado de fases relativamente estáveis, abruptamente entrecortadas por curtos períodos de explosiva diversificação.
- Discutir as bases conceituais da interpretação deste fenômeno, ressaltando o pensamento de alguns biólogos tais como Gould & Eldredge (1997), proponentes da teoria do equilíbrio pontuado.
- Discutir ainda numa perspectiva de generalização o que poderia estar acontecendo nas diversas condições particulares a associadas as pontuações evolutivas, onde explosivas diversificações no surgimento de novos grupos ocorre;.
- Tratando da ação simultânea de múltiplos mecanismos evolutivos, discutir que nesses momentos além da seleção natural, podem estar ocorrendo também efeito de deriva gênica, simbiogênese, distintos modos de especiação, construção de nicho, restrições ao processo evolutivo (sejam históricas ou desenvolvimentais), auto-organização etc.
- Discorrer sobre os acima referidos fenômenos “geologicamente instantâneos” nos rápidos processos de diferenciação morfológica e no surgimento de novos grupos, buscando conduzir a compreensão que se trata de momentos ecológicos específicos em condições particulares. Introduzir a discussão sobre quais seriam estas “condições especiais” da qual emergiram os novos tetrápodes em sua transição?

2ª Etapa: 60 minutos

- Tratar das investigações concernentes ao campo da biologia evolutiva do desenvolvimento (evo-devo), o qual tem desempenhado um papel importante na reestruturação do pensamento evolutivo, fornecendo explicações relativas à profusão de inovações morfológicas e promovendo, por conseguinte, uma possibilidade de entendimento mais completo em relação aos momentos de pontuação evolutiva.
- Discutir sob quais condições ecológicas poderiam organismos muito diferentes das médias morfológicas das suas populações obterem sucesso na competição por recursos e garantir suas possibilidades de sobrevivência e reprodução; visto que estes sob um regime de fortes pressões seletivas, provavelmente seriam rapidamente eliminados. Como elucidar tais “relaxamentos” das pressões seletivas?

- De forma generalizante, discutir quais as condições ecológicas que podem ser associadas a momentos de pontuação? (1) Conquista de novos ambientes; (2) Deriva continental; (3) Interações ecológicas novas; (4) Extinção em massa; (5) Efeito fundador; (6) Quais destas e outras mais condições específicas poderiam estar associadas a radiação dos tetrápodes durante a conquista do meio terrestre?

Aula 2

Objetivo da aula: Fornecer explicações das seqüências de acontecimentos reais, ou seja, buscar caracterizar os eventos em seus detalhes particulares, de modo que tal explicação procure caracterizar as especificidades propriamente relativas à radiação dos tetrápodes na conquista do meio terrestre, reconstruindo um cenário explicativo possível para a referida pontuação, sob uma perspectiva pluralista. Tais explicações das seqüências de acontecimentos reais devem ser apresentadas através da narrativa dos processos evolutivos, introduzindo o conteúdo específico da zoologia durante os passos da narrativa das transformações evolutivas sofridas pelo grupo dentro de seu cenário ecológico específico.

1ª Etapa: 60 minutos

- Caracterizar o paleoecossistema de modo a reconstituir as condições históricas específicas do cenário onde se deram as transformações evolutivas sofridas pelos tetrápodes durante a transição entre os meios terrestres e aquáticos, apresentando e discutindo as seguintes questões: (1) Como era a Geografia Continental? (2) Como era o clima Global? (3) Como eram os dois ecossistemas, aquático (ambientes profundos e rasos) e terrestre? (4) Como era a vegetação do período? (5) Quais as propriedades naturais destes distintos meios? (6) Como eram os organismos desse período? (7) Como se relacionavam ecologicamente? (8) Quais os desafios que precisariam ser transpostos para a conquista do meio terrestre?
- Abordar as questões envolvidas na terrestrialidade. (1) Suporte e locomoção em terra; (2) Sistema axial e costelas; (3) Musculatura axial; (4) Esqueleto apendicular; (5) Locomoção em terra; (6) Alimentação em terra; (7) Reprodução em terra; (8) Respiração do ar em terra; (9) Circulação sanguínea em terra; (10) Sistemas Sensoriais em Terra; (11) Conservação da água em ambiente seco; (12) Controle de temperatura.

2ª Etapa: 150 minutos

4 Caracterizar o devoniano como um período de transição, onde grupos essencialmente aquáticos darão origem a formas que conquistarão o ambiente terrestre. (1) Conformação dos continentes; (2) Paleoclima; (3) Caracterização do ambiente aquático; (4) Caracterizar este período como um período de rápida diversificação dos sarcopterígios e incitar alunos a falar sobre as possíveis causas dessa rápida diversificação.

5 Sarcopterígios basais

5.2 Actinistia

5.2.1 Caracterização ecológica/história natural das formas fósseis;

5.2.2 Caracterização morfológica das formas fósseis;

5.2.3 Comparação do Celacanto com aspectos das formas fósseis.

5.3 Dipnoi

5.3.1 Caracterização ecológica/história natural das formas fósseis;

5.3.2 Caracterização morfológica das formas fósseis;

5.3.3 Comparação dos peixes pulmonados vivos com aspectos das formas fósseis.

6 Discutir sobre o papel das nadadeiras lobadas nos grupos fósseis. Incitar discussão com os

alunos sobre possíveis vantagens. Comentar as hipóteses de secas sazonais e como os dipnoi viventes e a peloecologia ajudam a derrubar esta hipótese e falar da hipótese de predação que hoje é mais aceita.

7 Osteolepiformes

7.2 Pandeirichthys

7.2.1 Aspectos ecológicos/história natural;

7.2.2 Aspectos morfológicos.

7.3 Eusthenopteron

7.3.1 Aspectos ecológicos/história natural;

7.3.2 Aspectos morfológicos.

8 Elpistotegidae

8.2 Tiktaalik

8.2.1 Aspectos ecológicos/história natural;

8.2.2 Aspectos morfológicos.

9 Tetrapoda

9.2 Achanhostega

9.2.1 Aspectos ecológicos/história natural;

9.2.2 Aspectos morfológicos (chamando atenção para as sinapomorfias).

9.3 Ichthyostega

9.3.1 Aspectos ecológicos/história natural;

9.3.2 Aspectos morfológicos.

10 Comentar sobre a rápida diversificação das formas e surgimentos de novas partes da nadadeira lobada para a formação dos membros. Incitar discussão sobre a origem dessa variação de forma tão rápida.

11 Comparar os membros dos grupos apresentados mostrando evidências da origem das partes do membro a partir de mudanças no padrão de regulação no desenvolvimento do embrião (biologia evolutiva do desenvolvimento).

12 Comentar sobre o padrão pentadáctilo que surge em tetrápodos mais derivados e que fica fixado (por efeito fundador) como padrão primitivo para todos os tetrápodes terrestres.

3ª Etapa: 30 minutos - discussão do texto A História de quando éramos peixes, Shubin, Neil (2008, Elsevier Editora.

- Perguntar para os estudantes suas impressões sobre o texto e discutir os tópicos que mais lhes chamaram atenção.
- Explorar aspectos da linguagem em que o conteúdo é apresentado e discutir o método narrativo utilizado.
- Discutir se a narrativa utilizada facilita a apreensão do conteúdo e de que modo se relaciona com o conteúdo previamente exposto.
- Quais as congruências ou possíveis divergências evidenciadas em relação à narrativa apresentada em sala de aula?
- De que maneira essas narrativas se complementam?
- Em relação aos conteúdos de zoologia, evolução e biologia evolutiva do desenvolvimento o que puderam notar?
- Quais as dúvidas conceituais que emergiram durante a leitura.
- Buscar elucidar os problemas teóricos que dificultaram a inteligibilidade do texto.
- Discutir de que forma o texto ajuda a integrar: conteúdo, conhecimento e campos de pesquisa envolvidos na narrativa?

Anexo 4 - Transcrição de parte da entrevista com professor da disciplina

Pesquisador – então Marcelo, a gente poderia começar falando um pouco sobre quais as diferenças significativas que você entende dentro do padrão das duas seqüências como ele era antes demonstrado em sala de aula e como foi agora nessa experiência que a gente teve junto de construção.

Professor da disciplina – eu acho assim, pra ser bem pragmático penso que a principal diferença foi o cuidado que tivemos em tentar incluir nas explicações da matéria que foi lecionada os mecanismos evolutivos, normalmente a gente só comenta seleção e assim mesmo desvinculado do processo. Dentro então daqueles cenários evolutivos que eu trabalhei, na verdade, eu tive mais preocupação de tentar inserir esses mecanismos dentro do cenário e chamar mais atenção para os aspectos ecológicos que já eram chamados, mas que entendo não eram tão vinculados aos mecanismos de evolução como quanto eu estou fazendo agora. Eu trouxe essa influência para esse semestre, tenho feito e chamado mais atenção pra isso. Não só para os mecanismos evolutivos como também para a ecologia e estou inserindo com uma dose maior também questões de biologia evolutiva do desenvolvimento. Venho chamando atenção com as leituras do livro, A História de Quando Éramos Peixes, (Shubin, N, 2008), que tornei obrigatória (livro trabalhado em nossa seqüência didática que envolve uma narrativa da transição combinando aspectos da evo-devo). Do que fazia para o que estou fazendo hoje foi muito positivo, eu acho que a aula ficou mais ligada aos diversos conhecimentos que compõem o conteúdo hoje e eu noto isso nos alunos, tanto é que tem um grupo de alunos estão criando um grupo de estudos que tem como objetivo é criar um conhecimento mais multidisciplinar dentro do instituto, e isso foi iniciativa deles, inclusive me convidaram para participar desse movimento. Eles vêm enfatizando que zoo IV, especificamente ali na minha parte, contribuição de vocês, vem dando um enfoque evolutivo, ecológico integrativo que outras disciplinas não vêm fazendo. Questionaram-me porque, isso esse semestre agora porque dos outros eu não conversei, dessa turma, porque que os outros não fazem assim. Obviamente que eu não respondi absolutamente nada, falei que eu só posso responder pela minha disciplina. Bem é isso, eu achei que foi muito positivo, cresceu muito na minha, em zoologia IV e sem dúvida alguma em futuras disciplinas em que eu venha ministrar também vou utilizar um pouquinho do que a gente conseguiu desenvolver... Acho que o objetivo básico, eu sinto o seguinte, o que eu posso fazer em sala com uma carga horária pífia que você teve a possibilidade de identificar agora, pela quantidade de conteúdo, é tentar despertar coisas esse é o meu objetivo em zoo IV. Eu não tenho sinceramente, eu já refleti muito sobre isso e eu não tenho assim o menor pudor de afirmar e nenhuma ambição de que eles saiam de zoo IV dominado o conteúdo zoológico evolutivo ecológico ou paleontológico, ou qualquer outro “ógico” que você queira profundamente. A minha idéia em zoologia IV é despertar não para a diversidade dos organismos, mas para a integração entre os diversos conhecimentos que permitam que nós entendamos a evolução desses grupos. O que eu sei é mínimo, é uma gota no oceano, literalmente, sem nenhuma demagogia do que existe no conhecimento de morfologia, zoologia, evolução e genética. Eu sou um professor generalista ali. Então, eu sinto como obrigação de juntar essas coisas e dar a eles e incentivá-los a buscar mais informações. Bem, eles usam pelo menos cinco bibliografias grandes ao longo do curso, eles têm muitas horas de teoria e de prática e cabe a eles procurarem essas informações também. Eu acho, eu entendo que o problema deles, quando eles reclamam é que eles não têm tempo em fora de sala pra buscar essas informações de uma maneira mais

integrada. Eu sei que existe uma escola corrente que prega que nos damos as ferramentas para os alunos para eles procurarem as informações. O que eu tenho tentado fazer é dar as ferramentas com um tipo diferente de modelo ou método, apresentar a eles na forma de narrativa como vocês colocaram bem, um pedacinho desse universo pra tentar despertar neles o interesse nesses pedacinhos e que eles passem a ver a zoologia como algo integrado não desvinculado dos outros conteúdos. Em relação à base, eu entendo, eu acho que eles têm bons professores e conteúdos extensos mais a integração ela realmente não acontece de uma maneira uniforme homogênea, enquanto uma perspectiva do curso, digo o curso em si, então a gente fica limitado e eu tenho as minhas próprias limitações, porque é um conteúdo multidisciplinar e nenhum de nós temos domínio sobre tudo que poderia vir a ser trabalhado, daí a importância das integrações, das coisas virem sendo repetidas de disciplina em disciplina de uma maneira cada vez mais integrada...é uma mudança de paradigma do instituto na maneira de trabalhar, eu entendo não seja necessariamente uma mudança de método mais de raciocínio de conceito do que o ensino deve tratar, é diferente, seu método pode ser mais tradicional ou completamente inovador, mais essa visão integradora é o mais importante pra mim... Agora biologia do desenvolvimento é uma coisa muito difícil pra eles eu trabalhei esse semestre, eu trabalhei bem, trabalhei melhor, eu já venho trabalhando isso desde o semestre retrasado com as leituras do Kardong em sala de aula, e ainda assim ao que me parece eles tem muita dificuldade em embriologia especificamente, eles não conseguem associar, não significa que o conteúdo de “embrião” deles é mal dado, isso eu não posso afirmar, mas ao que me parece esta desconectada, então ao que me parece os estudantes tem dificuldade de caminhar enquanto a isso.

Anexo 5 - Ementas de zoologia - Português

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| <p>39.</p> | <p>http://docs.google.com/viewer?a=v&q=cache:1FQb_3LjAGYJ:www1.capes.gov.br/DistribuicaoArquivos/CursoNovo/Arquivos/2002/divulga/25001019/006/2002_006_250010192141_ementas.pdf+EMENTAS+E+REFERENC%8ANCIAS+BIBLIOGR%C3%81FICAS+PARA+MESTRADO+EM+ZOOLOGIA&hl=pt-BR&gl=br&pid=bl&srcid=ADGEESiT7NC2_I tqfFYvcZNAw0IDFMBOfMoxKjLXHosxDzI4IMtNHbPHILOhZfkMyUi2s2RS894SL5YcGZ3XfPFGD8siyWnU5GGkazRFWFSJ2Aj_IxMaYikFp--Zb2usN_XbV2Ry1BHw&sig=AHIEtbRL9iLxFfQIMQd3q3QspRC8xHwFag</p> | <p>UNIVERSIDADE ESTADUAL DE PERNAMBUCO</p> <p>DISCIPLINA: BIOLOGIA ANIMAL</p> | <ul style="list-style-type: none"> • AVISE, J. 1994. Molecular markers, natural history and evolution. Chapman & Hall. • BROOKS, D. R. & MCLENNAHN, D. A. 1991. Phylogeny, Ecology and Behavior. Chicago University Press. • ELDREDGE, N. & CRACRAFT, J. 1980. Phylogenetic patterns and the evolutionary process. Columbia University Press. • ESPINOSA, D. E. & J. LLORENTE B. 1993. Fundamentos de Biogeografias Filogenéticas. Universidade Nacional Autonoma do Mexico. • LI, W. H. & GRAUR, D. 1991. Fundamentals of Molecular Evolution. Sinauer Associates. • MAYR, E. 1977. Populações, espécies e evolução. EDUSP. • SCHOCH, R. M. 1986. Phylogeny reconstruction in Paleontology. Van Nostrand Reinhold. • SMITH, A.B. 1994. Systemics and the fossil record : documenting evolutionary natterns. Blackwell Scientifc Publications. • GITTIEMAN, J. L. 1996. Carnivore Behaviour, Ecology and Evolution. Gittleman (ed.). Cornell University Press, Ithaca. • PRIMACK, R. 1995. A Primer of Conservation Biology. Sinauer Associates Ine., Sunderiands. • LAURANCE, W. F. & BIERREGAARD, R. O. 1997. Tropical Forest Remnants: Ecology, Management and Conservation of Fragmented Communities. Laurance & Bierregaard (eds.). The University of Chicago Press, Chicago. • SCHELHAS, J. & GREENBERG, R. 1996. Forest Patches in Tropical Landscapes. Schelhas & Greembergeds.). Island Press, Washington, D.C. |
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Anexo 6 -Ementa de zoologia - Inglês

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Anexo 7 - Ementa de zoología - Español

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Anexo 8 - Ementa de evolução - Português

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Anexo 9 - Ementa de evolução - Inglês

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Anexo 10 - Ementa de Evolução Espanhol

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Anexo 11 - Livros de Evolução

FUTUYMA

SELEÇÃO

This was the inspiration for Darwin's great idea, one of the most important ideas in the history of thought: natural selection. Pag.6

He wrote a private essay in 1844, and in 1856 he finally began a book he intended to call Natural Selection. He never completed it, for in July 1858 he received a manuscript from a young naturalist, Alfred Russel Wallace (1823-1913). Wallace, who was collecting specimens in the Malay Archipelago, had independently conceived of natural selection. Darwin had extracts from his 1844 essay presented orally, along with Wallace's manuscript, at a meeting of the major scientific society in London, and set about writing an "abstract" of the book he had intended. The 490-page "abstract," titled "The Origin of Species by Means of Natural Selection, or The Preservation of Favoured Races in the Struggle for Life," was published on November 24, 1859; it instantly made Darwin both a celebrity and a figure of controversy. Pag.6

TIU's book lacks an explicit chapter on human evolution because most of the topics it would contain are distributed throughout. Instead, the final chapter treats what I think are increasingly important, indeed indispensable, topics in an undergraduate course on evolution: the evidence for evolution, the nature of science, and the failings of creationism, these themes recur throughout the book, implicitly and occasionally explicitly, but believe it will be useful to treat them as a coherent whole. The final chapter ends on a positive note with a brief survey of some of the social applications of evolutionary biology.

No more dramatic example of evolution by natural selection can be imagined than that of today's crisis in antibiotic resistance. Before the 1940s, most people in hospital wards did not have cancer or heart disease. pag2

This was the inspiration for Darwin's great idea, one of the most important ideas in the history of thought: natural selection. Pág 6

This was the inspiration for Darwin's great idea, one of the most important ideas in the history of thought: natural selection. Pág6

Wallace, who was collecting specimens in the Malay Archipelago, had independently conceived of natural selection. Pág 6

The 490-page "abstract," titled "The Origin of Species by Means of Natural Selection, or The Preservation of Favoured Races in the Struggle for Life," was published on November 24, 1859; it instantly made Darwin both a celebrity and a figure of controversy. Pág 6

This was his theory of natural selection: "if variations useful to any organic being ever occur, assuredly individuals thus characterised will have the best chance of being preserved in the struggle

for the; and from the strong principle of inheritance, these will tend to produce offspring similarly characterised. This principle of preservation, or the survival of the fittest, I have called natural selection." This theory is a VARIATIONAL THEORY of change, differing profoundly from Lamarck's TRANSFORMATIONAL THEORY, in which individual organisms change (Figure 1.4). Pág 7

Natural Selection was Darwin's brilliant hypothesis, independently conceived by Wallace, that changes in the proportions of different types of individuals are caused by differences in their ability to survive and reproduce—and that such changes result in the evolution of adaptations, features that appear "designed" to fit organisms to their environment. The concept of natural selection revolutionized not only biology, but Western thought as a whole. Pág 8

But this consensus did not extend to Darwin's theory of the cause of evolution, natural selection. For about 60 years after the publication of *The Origin of Species*, all but a few faithful Darwinians rejected natural selection, and numerous theories were proposed in its stead. These theories included neo-Lamarckian, orthogenetic, and mutationist theories (Bowler 1989). Pág 8-9

They supposed that such mutant forms constituted new species, and thus believed that natural selection was not necessary to account for the origin of species. Pág 8

Haldane in England and Sewall Wright in the United States developed a mathematical theory of population genetics, which showed that mutation and natural selection together cause adaptive evolution: mutation is not an alternative to natural selection! but is rather its raw material. Pág 9

These authors argued persuasively that mutation, recombination, natural selection, and other processes operating within species (which Dobzhansky termed microevolution) account for the origin of new species and for the major, long-term features of evolution (termed macroevolution). Pág 9

The rate of mutation is too low for mutation by itself to shift a population from one genotype to another. Instead, the change in genotype proportions within a population can occur by either of two principal processes: random fluctuations in proportions (genetic drift), or nonrandom changes due to the superior survival and/or reproduction of some genotypes compared with others (i.e., natural selection). Natural selection and random genetic drift can operate simultaneously. Pág 10

The rate of mutation is too low for mutation by itself to shift a population from one genotype to another. Instead, the change in genotype proportions within a population can occur by either of two principal processes: random fluctuations in proportions (genetic drift), or nonrandom changes due to the superior survival and/or reproduction of some genotypes compared with others (i.e., natural selection). Natural selection and random genetic drift can operate simultaneously. Pág 10

Even a slight intensity of natural selection can (under certain circumstances) bring about substantial evolutionary change in a realistic amount of time. Natural selection explains the origin of both slight and great differences among species, as well as for the earliest stages of evolution of new traits. Adaptations are traits that have been shaped by natural selection. Pág 10

Natural selection can alter populations beyond the original range of variation by increasing the frequency of alleles that, by recombination with other genes that affect the same trait, give rise to new phenotypes. Pág 10

Differences among geographic populations of a species are often adaptive, and thus are the consequence of natural selection. Pág 11

This hypothesis, developed especially by Motoo Kimura (1924--1994), holds that most of the evolution of DNA sequences occurs by genetic drift rather than by natural selection. Pág11

Above all, Darwin's theory of random, purposeless variation acted on by blind, purposeless natural selection provided a revolutionary new kind of answer to almost all questions that begin with "Why?" Before Darwin, both philosophers and people in general answered "Why?" questions by citing purpose. Pág12

This kind of explanation was made completely superfluous by Darwin's theory of natural selection. Pág12

Opponents of evolution have charged that evolution by natural selection justifies the principle that "might makes right," and certainly more than one dictator or imperialist has invoked the "law" of natural selection to justify atrocities. But evolutionary theory cannot provide any such precept for behavior. Like any other science, it describes how the world is, not how it should be. Pág13

The natural world is amoral—it lacks morality altogether. Despite this, the concepts of natural selection and evolutionary progress were taken as a "law of nature" by which Marx justified class struggle, by which the Social Darwinists of the late eighteenth and early nineteenth centuries justified economic competition and imperialism, and by which the biologist Julian Huxley justified humanitarianism (Hofstadter 1955; Paradis and Williams 1989). Pág13

In *The Origin of Species*, Darwin propounded two major hypotheses: that organisms have descended, with modification, from common ancestors; and that the chief cause of modification is natural selection acting on hereditary variation. Pág14

We now know that Darwin's hypothesis of natural selection on hereditary variation is correct, but we also know that there are far more causes of evolution than Darwin realized, and that natural selection and hereditary variation themselves are more complex than he imagined. A body of ideas about the causes of evolution, including mutation, recombination, gene flow, isolation, random genetic drift, the many forms of natural selection, and other factors, constitute our current theory of evolution, or "evolutionary theory." Pág13-14

Several molar characters of these rodents changed directionally throughout Europe, indicating that gene flow among populations enabled the entire species to respond as a whole to selection for increased tooth height (Chaline and Laurin 1986). Pág86

Natural selection in evolution can occur in nonliving systems of replicating molecules. When Sol Spiegelman (1970) placed RNAs, RNA polymerase (isolated from a virus, phage Q-), and nucleotide bases in a cell-free medium, different RNA sequences were replicated by the polymerase at different rates, so that their proportions changed. Pág93

Evolutionary theory does not necessarily predict this, however, because natural selection, having no foresight, cannot prepare species for changes in the environment. If the environmental changes that threaten extinction are numerous in kind, we should not expect much carryover of "extinction resistance" from one change to the next. Pág146

The second tier is "species selection," the differential proliferation and extinction of species during "normal" geological times, which affects the relative diversity of lineages with different characteristics (see Chapter 11). Pág150

They used crosses (see Figure 9.7) in which copies of the wild-type chromosome 2 were carried in a heterozygous condition so that deleterious recessive mutations could persist 'without being eliminated by natural selection. pag173

They may therefore have more harmful collective effects on a population than do strongly deleterious mutations, which are more rapidly expunged by natural selection. pag176

The three mutations together restored the metabolic capacities that had been lost by the deletion of the original IneZ gene. Thus mutation and selection in concert can give rise to complex adaptations Pag177-178

Such "neo Lamarckian" ideas were expunged in the 1940s and 1950s by experiments with bacteria in which spontaneous, random mutation followed by natural selection, rather than mutation directed by the environment, explained adaptation. pag179

Recombination, therefore, has complicated effects on variation: it both retards adaptation by breaking down favorable gene combinations and enhances adaptation by providing natural selection with multitudinous combinations of alleles that have arisen by mutation. pag181

As we will encounter it in the theory of natural selection and other causes of evolution. It has two important implications: First, genotype frequencies attain their H-W values after a single generation of random mating. pag196

Thus the Hardy-Weinberg principle assumes that there is no natural selection affecting the locus. pag196

If the assumptions we have listed hold true for a particular locus, that locus will display Hardy-Weinberg genotype frequencies. But if we observe that a locus fits the Hardy-Weinberg frequency distribution, we cannot conclude that the assumptions hold. For example, mutation or selection may be occurring, but at such a low rate that we cannot detect a deviation of the genotype frequencies from the expected values. Or, under some forms of natural selection, we might observe deviations from Hardy-Weinberg equilibrium if we measure genotype frequencies one stage in the life history, but not at other stages. pag197

The central question was, "Do forces of natural selection maintain this variation, or is it neutral, subject only to the operation of random genetic drift?" pag204

These polymorphisms could be studied in their own right (e.g., to study natural selection), or they could be used simply as genetic markers to determine, for example, which individuals mate with each other. pag204

RESPONSES TO ARTIFICIAL SELECTION. Because a character can be altered by selection only if it is genetically variable, artificial selection can be used to detect genetic variation in a character. To do this, an investigator (or a plant or animal breeder) breeds only those individuals that possess a particular trait (or combination of traits) of interest. Artificial selection may grade into natural selection, but the conceptual difference is that under artificial selection, the reproductive success of individuals is determined largely by a single characteristic chosen by the investigator, rather than by their overall capacity (based on all characteristics) for survival and reproduction. pag211

Artificial selection has been the major tool of breeders who have produced agricultural varieties of corn, tomatoes, pigs, chickens, and every other domesticated species, which often differ extremely in numerous characteristics. pag212

The most likely cause of character displacement is natural **selection** for features that reduce ecological competition between the species, or which reduce the chance that they will hybridize (see Chapters 16 and 18).pag216

So it is with evolution. As we will see in the next chapter, natural **selection** is a deterministic, nonrandom process. But at the same time, there are important random processes in evolution, including mutation (as discussed in Chapter 8) and random fluctuations in the frequencies of alleles or haplotypes: the process of random genetic drift.pag226

Genetic drift and natural **selection** are the two most important causes of allele substitution- that is, of evolutionary change-in populations.pag226

That is, "while natural **selection** results in adaptation, genetic drift does not-so this process is not responsible for those anatomical, physiological, and behavioral features of organisms that equip them for reproduction and survival.pag226

Because all populations are finite, alleles at all loci are potentially subject to random genetic drift- but all are not necessarily subject to natural **selection**pag226

For this reason, and because the expected effects of genetic drift can be mathematically described with some precision, some evolutionary geneticists hold the opinion that genetic drift should be the "null hypothesis" used to explain an evolutionary observation unless there is positive evidence of natural **selection** or some other factor. This perspective is analogous to the "null hypothesis" in statistics: the hypothesis that the data do not depart from those expected on the basis of chance alone." According to this view, we should not assume that a characteristic, or a difference between populations or species, is adaptive or has evolved by natural **selection** unless there is evidence for this conclusion.pag226

Bear in mind that this model, as developed so far, includes only the effects of random genetic drift. It assumes that other evolutionary processes-namely; mutation, gene flow and natural **selection**-do not operatepag228

Natural **selection** can lower N_e by increasing variation in progeny number; for instance, if larger individuals have more offspring than smaller ones, the rate of genetic drift may be increased at all neutral loci because small individuals contribute fewer gene copies to subsequent generationspag232

When we describe the genetic features of natural populations, the data usually are not based on experimental manipulations, nor do we usually have detailed information on the populations' histories. We therefore attempt to infer causes of evolution (such as genetic drift or natural **selection**) by interpreting patterns. Such inferences are possible only on the basis of theories that tell us what pattern to expect if one or another cause has been most important.pag234

From the evolutionary synthesis of the late 1930s until the mid-1960s, most evolutionary biologists believed that almost all alleles differed in their effects on organisms' fitness, so that their frequencies were affected chiefly by natural **selection**. pag236

They argued that natural **selection** could not actively maintain so much genetic variation, and suggested that much of it might be selectively neutral. Atpag236

He concluded that a given protein evolved at a similar rate in different lineages. He argued that such constancy would not be expected to result from natural selection, but would be expected if most evolutionary changes at the molecular level are caused by mutation and genetic drift. These authors and others (King and Jukes 1969) initiated a controversy about molecular polymorphism and evolution, known as the "neutralist-selectionist debate," that is still not entirely resolved. Although everyone now agrees that some molecular variation and evolution is neutral (i.e., a result of genetic drift), "selectionists" think a larger fraction of molecular evolutionary changes are due to natural selection than "neutralists" do. pag236

The neutral theory of molecular evolution holds that although a small minority of mutations if DNA or protein sequences are advantageous and are fixed by natural selection, and although many mutations are disadvantageous and are eliminated by natural selection, the great majority of those mutations that are fixed are effectively neutral with respect to fitness and are fixed by genetic drift. pag236

Many-perhaps most-such features may evolve chiefly by natural selection, and they are based on base pair substitutions that (according to the neutralists) constitute a very small fraction of DNA sequence changes. pag236

Furthermore, the neutral theory acknowledges that many mutations are deleterious and are eliminated by natural selection, so that they contribute little to the variation we observe. Thus the neutral theory does not deny the operation of natural selection on some base pair or amino acid differences. pag236

By effectively neutral, we mean that the mutant allele is so similar to other alleles in its effect on survival and reproduction (i.e., fitness) that changes in its frequency are governed by genetic drift alone, not by natural selection. pag236

Then natural selection and genetic drift operate simultaneously, but because genetic drift is stronger in small than in large populations, the changes in the mutant allele's frequency will be governed almost entirely by genetic drift if the population is small enough. pag236

We must assume that the alleles for which we calculate F_{ST} are selectively neutral (F_{ST} would underestimate gene flow if natural selection favored different alleles in different areas, and it would overestimate gene flow if selection favored the same allele everywhere.) pag241

We must assume that the alleles for which we calculate F_{ST} are selectively neutral (F_{ST} would underestimate gene flow if natural selection favored different alleles in different areas, and it would overestimate gene flow if selection favored the same allele everywhere.) pag241

This assumption can be evaluated by the degree of consistency among different loci for which F_{ST} is estimated. Genetic drift and gene flow affect all loci the same way, whereas natural selection affects different loci more or less independently. pag241

Therefore, if each of a number of polymorphic loci yields about the same value of F_{ST} it is likely that selection is not strong. pag241

The theory of natural selection is the centerpiece of The Origin of Species and of evolutionary theory. pag247

Natural **selection** is a simple concept, but it nevertheless works in many and sometimes subtle ways. pag247

Although it is merely a statement about rates of reproduction and mortality, the theory of natural **selection** is perhaps the most important idea in biology. pag247

Natural **selection** is the only mechanism known to cause the evolution of adaptations, so many biologists would simply define an adaptation as a characteristic that has evolved by natural **selection**. Pag247-248

His alternative to intelligent design was design by the completely mindless process of natural **selection**, according to which organisms possessing variations that enhance survival or reproduction replace those less suitably endowed, which therefore survive or reproduce in lesser degree. pag250

A program like 'wise resides in a computer chip, but whereas that program has been shaped by an intelligent designer, the information in DNA has been shaped by a historical process of natural **selection**. pag250

Many definitions of natural **selection** have been proposed (Endler 1986). For our purposes, we will define natural **selection** as (1) consistent difference in fitness among phenotypically different classes of biological entities. Let us explore this definition in more detail. pag251

When we speak of natural **selection** among genotypes or organisms, the components of fitness generally consist of (1) the probability of survival to the various reproductive ages, (2) the average number of offspring (e.g., eggs, seeds) produced via female function, and (3) the average number of offspring produced via male function. "Reproductive success" has the same components, since survival is a prerequisite for reproduction. pag251

Variation in the number of offspring produced as a consequence of competition for mates is often referred to as sexual **selection**, which some authors distinguish from natural **selection**. We will follow the more common practice of regarding sexual **selection** as a kind of natural **selection**. pag251

That is, natural **selection** exists if there is an average (i.e., statistically consistent) difference in reproductive success. It is not meaningful to refer to the fitness of a single individual, since its history of reproduction and survival may have been affected by chance to an unknown degree, as we will see shortly. pag251

In other words, different kinds of biological entities may vary in fitness, resulting in different levels of **selection**. pag251

The most commonly discussed levels of **selection** are genes, individual organisms that differ in genotype or phenotype, populations within species, and species. Of these, **selection** among individual organisms (individual **selection**) and among genes (genic **selection**) are by far the most important. pag251

Natural **selection** can exist only if different classes of entities differ in one or more features, or traits, that affect the components of fitness. Evolutionary biologists differ on whether or not the definition of natural **selection** should require that these differences be inherited (i.e., have a genetic basis). We will adopt the position taken by those (e.g., Lande and Arnold 1983) who define **selection** among individual organisms as a consistent difference in fitness among phenotypes. Whether or not this variation in fitness alters the frequencies of genotypes in subsequent generations

depends on whether and how the phenotypes are inherited-but that determines the response to selection, not the process of selection itself. Although we adopt the phenotypic perspective, we will almost always discuss natural selection among heritable phenotypes because selection seldom has a lasting evolutionary effect unless there is inheritance. pag251

Notice, finally, that according to our definition, natural selection exists whenever there is variation in fitness. Natural selection is not an external force or agent, and certainly not a purposeful one. It is a name for statistical differences in reproductive success among genes, organisms, or populations, and nothing more. pag251

However, natural selection has not occurred, because the genotypes do not differ consistently in fitness: the alternative allele could just as well have increased. pag251

But natural selection resides in the difference in rates of increase among biological entities that is not due to chance. Natural selection is the antithesis of chance. pag252

If fitness and natural selection are defined by consistent, or average, differences, then we cannot tell whether a difference in reproductive success between two individuals is due to chance or to a difference in fitness. pag252

We can ascribe genetic changes to natural selection rather than random genetic drift only if we observe consistent, nonrandom changes in replicate populations, or measure numerous individuals of each phenotype and find an average difference in reproductive success. pag252

In the child's "selection toy" pictured in Figure 11.5, balls of several sizes, when placed in the top compartment, fall through holes in partitions, the holes in each partition being smaller than in the one above. pag252

Thus we must distinguish selection of objects from selection for properties (Sober 1984). Balls are selected for the property of small size-that is, because of their small size. pag252

They are not selected for their color, or because of their color; nonetheless, here there is selection of red balls. Natural selection may similarly be considered a sieve that selects for a certain body size, mating behavior, or other feature. There may be incidental selection of other features that are correlated with those features. pag252

The importance of this semantic point is that when we speak of the function of a feature, we imply that there has been natural selection of organisms with that feature and of genes that program it, but not for the feature itself. We suppose that the feature caused its bearers to have higher fitness. The feature may, however, have other effects, or consequences, that have nothing to do with its function, and for which there was no selection. For instance, there was selection for an opposable thumb and digital dexterity in early hominins, with the incidental effect, millions of years later, that we can play the piano. pag252

We can illustrate the foregoing rather abstract points by presenting several studies of natural selection. These examples also show how natural selection can be studied by controlled experiments. pag252

experiment conveys the essence of natural selection: it is a completely mindless process without forethought or goal. Adaptation---evolution of a bacterial population with a higher average ability to

metabolize lactose—resulted from a difference in the rates of reproduction of different genotypes caused by a phenotypic difference (enzyme activity)
pag253

Another experiment with bacteria illustrates the distinction between "selection of" and "selection for." In *E. coli*, the wild-type allele *his+* codes for an enzyme that synthesizes histidine, an essential amino acid, whereas *his-* alleles are nonfunctional
pag253

Subsequently, the alternative allele (*his+*) might increase because of linkage to a new advantageous mutation at another locus all together. Thus there was selection for the advantageous mutations in these bacterial populations, and selection of neutral alleles at the linked *his* locus.
pag253

Thus there was selection for the advantageous mutations in these bacterial populations, and selection of neutral alleles at the linked *his* locus.
pag253

Moreover, natural selection must be acting in such a way as to maintain variation (polymorphism); it does not necessarily cause fixation of a single best genotype. When the genotype frequency reach equilibrium, natural selection continues to occur, but evolutionary change does not.

These experiments show that natural selection may sometimes lie only in differences in reproductive rate, not survival. Differences in mating success, which Darwin called sexual selection, result in adaptations for obtaining mates, rather than adaptations for survival.
pag254

The net reproductive rate also declined. In treatment C, these declines must have been due to evolution within each population, due to natural selection among the genotypes of individual beetles within each population.
pag256

But in treatments A and B, Wade imposed another level of selection by allowing some populations, or groups, but not others, to persist based on a phenotypic characteristic of each group—namely, its size. This process, called group selection or interdemic selection, operates in addition to individual selection among genotypes within populations.
Pag255-256

We must distinguish selection within populations from selection among populations
pag256

By selecting groups for low population size (treatment B), Wade reinforced these same tendencies. In treatment A, on the other hand, selection at the group level for large population size opposed the consequences of individual selection within populations. Compared with the C populations, beetles from treatment A had higher fecundity in the presence of other beetles and they were less likely to cannibalize eggs and pupae. Thus selection among groups had affected the course of evolution.
pag256

This experiment shows that the size or growth rate of a population may decline due to natural selection even as individual organisms become fitter. It also illustrates that selection might operate at two levels: among individuals and among populations.
pag256

Selfish genetic elements forcefully illustrate the nature of natural selection: it is nothing more than differential reproductive success (of genes in this case), which need not result in adaptation or improvement in any sense. These elements also exemplify different levels of selection: in these

cases, genic **selection** acts in opposition to individual **selection**. **Selection** among genes may not only be harmful to individual organisms, but might also cause the extinction of populations or species. pag257

It is common to read statements to the effect that oysters have a high reproductive rate "to ensure the survival of the species," or that antelopes with sharp horns refrain from physical combat because combat would lead to the species' extinction. These naive statements betray a misunderstanding of natural **selection**. If traits evolve by individual **selection**- by the replacement of less fit by more fit individuals, generation by generation then the possibility of future extinction cannot possibly affect the course of evolution. Moreover, an altruistic trait-a feature that reduces the fitness of an individual that bears. pag257

Delve into the genetical theory of natural **selection**; we should keep the following important points about natural **selection** in mind: pag270

Natural **selection** is not the same as evolution. Evolution is a multi-step process: the origin of genetic variation by mutation or recombination, followed by changes in the frequencies of alleles and genotypes, caused chiefly by genetic drift or natural **selection**. Neither natural **selection** nor genetic drift accounts for the origin of variation, pag270

Natural selection is different from stabilizing selection. In some instances, **selection** occurs-that is, in each generation, genotypes differ in survival or fecundity-yet the proportions of genotypes and alleles stay the same from one generation to another. pag270

Moreover, an altruistic trait-a feature that reduces the fitness of an individual that bears it for the benefit of the population or species-cannot evolve by individual **selection** pag257

There is a way, however, in which traits that benefit the population at a cost to the individual might evolve: by group **selection**. Populations made up of selfish genotypes, such as those with high reproductive rates that exhaust their food supply, might have a higher extinction rate than populations made up of altruistic genotypes. If so, then the species as a whole might evolve altruism through the greater survival of groups of altruistic individuals, even though individual **selection** within each group would act in the opposite direction (Figure 11.13A) pag257

The hypothesis of group **selection** was criticized by George Williams (1966) in his influential book, *Adaptation and Natural Selection*. Williams argued that supposed adaptations that benefit the population or species, rather than the individual, do not exist: either the feature in question is not an adaptation at all, or it can be plausibly explained by benefit to the individual or the individual's genes. Pag257-258

William S based his opposition to group **selection** on a simple argument. Individual organisms are much more numerous than the populations into which they are aggregated and they turn over-are born and die-much more rapidly than populations, which are born (formed by colonization) and die (become extinct) at relatively low rates. **Selection** at either level requires differences-among individuals or among populations-in rates of birth or death. Thus the rate of replacement of less fit by more fit individuals is potentially much greater than the rate of replacement of less fit by more fit populations, so individual **selection** will generally prevail over group **selection** (Figure 11.13B). Although some evolutionary biologists have argued that group **selection** is important in evolution (e.g., Wilson 1983), the majority view is that few characteristics have evolved because they benefit the population or species. pag258

We may therefore define kin **selection** as a form of **selection** in which alleles differ in fitness by influencing the effect of their bearers on the reproductive success of individuals (kin) who carry the same allele by common descent. pag258

Selection among groups of organisms is called species **selection** or taxon selection when the groups involved are species or higher taxa (Stanley 1979; Williams 1992b). pag258

In the orchid/iris example, there is species **selection**/or specialized pollination (i.e., specialized pollination causes a higher speciation rate). Because of the correlation between petiole structure and mode of pollination, there has also been **selection** of (but not **selection** for) twisted petioles. The increasing incidence of twisted petioles among these plant species is an effect of a fortuitous association with speciation rate. pag260

An exaptation may be further modified by **selection** so that the modifications are adaptations for the feature's new function: the wings of penguins have been modified into flippers and cannot support flight in air (Figure 11.17B). pag261

Second, Ule hait may have evolved by random genetic drift rather than by natural **selection**. pag262

We conclude this discussion of the general properties of natural **selection** and adaptation by considering a few common misconceptions of, and misguided inferences from, the theory of adaptive evolution. pag264

It is naive to think that if a species' environment changes, the species must adapt or else become extinct. Not all environmental changes reduce population size. Nonetheless, an environmental change that does not threaten extinction may set up **selection** for change in some characteristics. Thus white fur in polar bears may be advantageous, but not necessary for survival (William 1966). Just as a changed environment need not set in motion **selection** for new adaptations, new adaptations may evolve in an unchanging environment if new mutations arise that are superior to any pre-existing genetic variations. We have already stressed that the probability of extinction of a population or species does not in itself constitute **selection** on individual organisms, and so cannot cause the evolution of adaptations. pag264

Darwin noted that "natural **selection** will not produce absolute perfection, nor do we always meet, as far as we can judge, with this high standard in nature" (The Origin of Species, chapter 6). **Selection** may fix only those genetic variants with a higher fitness than other genetic variants in that population at that time. pag264

As we have seen, **selection** at the level of genes and individual organisms is inherently "selfish": the gene or genotype with the highest rate of increase increases at the expense of other individuals. pag265

This is an example of kin **selection**, an important basis for the evolution of cooperation within. pag265

Natural **selection** is just a name for differences among organisms or genes in reproductive success. Therefore, it cannot be described as moral or immoral, just or unjust, kind or cruel, any more than wind, erosion, or entropy can be. pag265

Herbert Spencer, considered natural **selection** to be a beneficent law of nature that would produce social progress as a result of untrammelled struggle among individuals, races, and nations. pag265

Natural **selection** is the most important concept in the theory of evolutionary processes
pag269

In its elementary form, natural **selection**-differential reproductive success-is a very simple concept.pag269

Modern evolutionary theory started to develop as the growing understanding of Mendelian genetics was synthesized with Darwin's theory of **selection**.pag270

Although natural **selection** may be said to exist whenever different phenotypes vary in average reproductive success, natural selection can have NO evolutionary effect unless phenotypes differ in genotype. For instance, **selection** among genetically identical members of a clone, even though they differ in phenotype, can have no evolutionary consequences. Therefore, it is useful to describe the reproductive success, or fitness, of genotypes, even though genotypes differ in fitness only because of differences in phenotype.pag270

Because natural **selection** is variation in average reproductive success (which includes survival), a feature cannot evolve by natural **selection** unless it makes a positive contribution to the reproduction or survival of individuals that bear it.. pag270

Unless otherwise specified, the subsequent discussion of natural **selection** concerns **selection** at the level of individual organisms within populations. The consequences of natural **selection** depend on (1) the relationship between phenotype and fitness, and (2) the relationship between phenotype and genotype. These relationships, then, yield (3) a relationship between fitness and genotype, which determines (4) whether or not evolutionary change occurs. pag270

The relationship between phenotype and fitness can often be described as one of three **MODES OF SELECTION** (Figure 12.1). For a quantitative (continuously varying) trait, such as size, **selection** is directional if one extreme phenotype is fittest, stabilizing (NORMALIZING) if an intermediate phenotype is fittest, or diversifying (disruptive) if two or more phenotypes are fitter than the intermediates between them, which genotype has the highest fitness under a given **selection** regime depends on the relationship between phenotype and genotype. For example, under directional **selection** for large size, genotype A,A, would be most fit if it were largest, but A,Az would be favored if it were larger than either homozygote. pag270

Thus, if the mean body size is below the optimum, it will be directionally selected until it corresponds to the optimum (at least approximately); after that, it is subject to stabilizing **selection**. pag271

Because we are concerned with only those effects of **selection** that depend on inheritance, we will use models in which an average fitness value is assigned to each genotype. pag271

Another important term is the coefficient of **selection**, usually denoted s , which is the amount by which the fitness of one genotype is reduced relative to the reference genotype. In our example, $1 - 0.25 = 0.75$, so $s = 0.25$. The coefficient of **selection** measures the selective advantage of the fitter genotype, or the intensity of **selection** against the less fit genotype. It is easy to show mathematically that the rate of genetic change under **selection** depends on the relative, not the absolute, fitnesses of genotypes. pag271

These allele frequencies are affected by several components of **selection** at the "zygotic" (organismal) stage, and sometimes by **selection** at the gametic stage as well (Figure 12,3;

Christiansen 1984), Table 12.1 summarizes the components of **selection** in a sexual species. pag273

These allele frequencies are affected by several components of **selection** at the "zygotic" (organismal) stage, and sometimes by **selection** at the gametic stage as well (Figure 12, 3; Christiansen 1984), Table 12.1 summarizes the components of **selection** in a sexual species. pag273

Evolution by natural **selection** depends on the way in which changes in allele frequencies are determined by the components of fitness of each zygotic and each gametic genotype, pag273

In that example, one genotype had superior fecundity and the other had superior survival: a genotype may be superior to another in certain components of fitness and inferior in others, but its overall fitness determines the outcome of **selection**, pag273

In the following discussion, we make the simplifying assumptions that the population is very large, so genetic drift may be ignored; that mating occurs at random; that mutation and gene flow do not occur; and that **selection** at other loci does not affect the locus we are considering. We will later consider the consequences of relaxing these unrealistic assumptions. We also assume, for the sake of simplicity, that **selection** acts through differential survival among genotypes in a species with discrete generations. The principles are much the same for other components of **selection** and for species with overlapping generations, although these factors introduce complications when data from real populations are analyzed pag273

In any model of **selection**, the change in allele frequencies depends on the relative fitnesses of the different genotypes and on the allele frequencies themselves. Box A provides a mathematical framework for several models of **selection**. pag273

An advantageous allele may initially be fairly common if under previous environmental circumstances it was selectively neutral or, was maintained by one of several forms of balancing **selection** (see page 280). However, an advantageous allele is likely to be initially very rare if it is a newly arisen mutation or if it was disadvantageous before an environmental change made it advantageous. pag274

A simple example of directional **selection** occurs if the fitness of the heterozygote is precisely intermediate between that of the two homozygotes (i.e., neither allele is dominant with respect to fitness). pag275

Equation 12.1 tells us that Δp is positive whenever p and q are greater than zero. Therefore allele A_1 increases to fixation ($p = 1$), and $p = 1$ is a stable equilibrium. The rate of increase (the magnitude of Δp) is proportional to both the coefficient of **selection** s and the allele frequencies p and q , which appear in the numerator. Therefore the rate of evolutionary change increases as the variation at the locus increases. (It is approximately proportional to $2pq$, the frequency of heterozygotes, when **selection** is weak.) Another important aspect of Equation 12.1 is that Δp is positive as long as s is greater than zero, even if it is very small. Therefore, as long as no other evolutionary factors intervene, a character state with even a slight advantage will be fixed by natural selection pag275

One might suppose that a less detailed resemblance would provide sufficient protection against predators, and some species are indeed less elaborately cryptic; but if all extra blotch increases the

likelihood of survival by even the slightest amount, it may be fixed by **selection** (providing, we repeat, that no other factors intervene). pag276

Selection that reduces the frequency of a deleterious mutation or eliminates it is referred to as purifying **selection**, which is simply directional **selection** in favor of the prevalent, advantageous homozygous genotype pag276

The number of generations required for an advantageous allele to replace one that is disadvantageous depends on the initial allele frequencies, the **selection** coefficient, and the degree of dominance (Figure 12.6). pag276

After a dominant advantageous allele attains high frequency, the deleterious recessive allele is eliminated very slowly, because a rare recessive allele occurs mostly in heterozygous form, and is thus shielded from **selection**. pag276

The mean fitness therefore increases as natural **selection** proceeds. In a graphical representation of this relationship (Figure 12.7A), we may think of the population as climbing up a "hillside" of increasing mean fitness until it arrives at the summit pag276

This is one of estimating the strength of natural **selection**. Several other methods are used to estimate **selection** coefficients pag276

If a locus has experienced consistent directional **selection** for a long time, the advantageous allele should be near equilibrium—that is, near fixation. Thus the dynamics of directional **selection** are best studied in recently altered environments, such as those altered by human activities. Many examples of rapid evolution under such circumstances have been observed. Many are changes in polygenic traits, described in the next chapter. pag277

Although the most advantageous allele at a locus should in theory be fixed by directional **selection** if deleterious alleles often persist because they are repeatedly reintroduced, either by recurrent mutation or by gene flow from other populations in which they are favored by a different environment. pag278

Until the 1940s, the prevalent, or classic, view had been that at each locus, a best allele (the "wild type") should be nearly fixed by natural **selection**, so that the only variation should consist of rare deleterious alleles, recently arisen by mutation and fated to be eliminated by purifying **selection**. pag278

the factors that might be responsible for this variation are: (1) recurrent mutation producing deleterious alleles, subject to only weak **selection**; (2) gene flow of locally deleterious alleles from other populations in which they are favored by **selection**; (3) selective neutrality (i.e., genetic drift); and (4) maintenance of polymorphism by natural **selection**. The last of these hypotheses was championed by British ecological geneticists led by E. B. Ford and American population geneticists influenced by Theodosius Dobzhansky. They represented the BALANCE SCHOOL, holding that a great deal of genetic variation is maintained by balancing **selection** (which is simply **selection** that maintains polymorphism). pag278

Several models of natural **selection** can account for persistent, stable polymorphism, but we do not know, the extent to which they actually account for the observed genetic variation within populations. pag280

The heterozygote advantage therefore arises from a balance of OPPOSING SELECTIVE FACTORS: anemia and malaria. In the absence of malaria, balancing selection gives way to directional selection, because then the AA genotype has the highest fitness, the African-American population, which is not subject to malaria, the frequency of S is about 0.05, and is presumably declining due to mortality. pag281

James Maljean and Nicholas Barton (1989) showed that within *Heliconius erato*, gene flow from one geographic race to another is countered by positive frequency-dependent selection: immigrant butterflies that deviate from the locally prevalent color pattern are selected against because predators have not learned to avoid attacking butterflies with unusual color patterns. pag286

From bill marks left on the wings of butterflies that had escaped from birds, the authors concluded that the missing butterflies were lost to bird predation, and calculated an average selection coefficient of 0.52 against the "wrong" color pattern in either population. This amounts to a selection coefficient of about $s = 0.17$ at each of the three major loci that control the differences in color pattern between the races. Very strong selection indeed. pag286

Recall that we can calculate the mean fitness (\bar{W}) of individuals in a population with any conceivable allele frequency (p) and plot a curve showing it as a function of p (see Figure 12.7A, B). When fitnesses are constant, natural selection changes allele frequencies in such a way that mean fitness (\bar{W}) increases, so that the population moves up the slope of this curve. The current location of the population on this slope is then a simple guide to how allele frequencies will change under selection: simply see which direction of allele frequency change will increase \bar{W} . For an underdominant locus, the curve dips in the middle and slopes upward to $p = 0$ and $p = 1$ (see Figure 12.7D). Thus natural selection decreases or increases p depending on whether a population begins to the left or the right of the minimum of the curve. pag287

In developing the theory of selection so far, we have assumed an effectively infinite population size. However, in a finite population, allele frequencies are simultaneously affected by both selection and drift. As the movement of an airborne dust particle is affected both by the deterministic force of gravity and by random collisions with gas molecules (Brownian movement), so the effective size (N_e) of a population and the strength of selection (s) both affect changes in allele frequencies. The effect of random genetic drift is negligible if selection on a locus is strong relative to the population size—that is, if s is much greater than $1/(4N_e)$. Conversely, if s is less than $1/(4N_e)$, selection is so weak that the allele frequencies change mostly by genetic drift: the alleles are nearly neutral. pag287

The effect of population size on the efficacy of selection has several important consequences. First, a population may not attain exactly the equilibrium allele frequency predicted from its genotypes' fitnesses; instead, it is likely to wander by genetic drift in the vicinity of the equilibrium frequency. Second, a slightly advantageous mutation is less likely to be fixed by selection if the population is small than if it is large, because it is more likely to be lost simply by chance. Conversely, deleterious mutations can become fixed by genetic drift, especially if selection is weak and the population is small. pag287

The principle that genetic drift could prevail over selection might be especially important if heterozygotes are inferior in fitness, so that the adaptive landscape has two peaks (see Figure 12.70). pag288

But during episodes of very low population size, allele frequencies may fluctuate so far by genetic drift that they cross the adaptive valley after which selection can move the population "uphill" to the other peak (Figure 12.20B). pag288

Thus, when there are multiple stable equilibria, genetic drift and **selection** may act in concert to accomplish what **selection** alone cannot, moving a population from one adaptive peak to another. pag288

Any subchromosome, introduced by gene flow into a population that is adapted for a different arrangement, is reduced in frequency by natural **selection**, so no two "chromosome races" sympatric; instead, they meet in "tension zones" only 200-300 meters wide (White 1978). pag288

Variation in DNA sequences can provide evidence of the action of natural **selection** if the pattern of variation differs from patterns expected under the neutral theory of molecular evolution. pag288

Selection should eventually lead to linkage equilibrium (see Chapter 9). Now suppose that natural **selection** acts at a particular base pair site within a gene, and consider the effects of this selection on sites that are closely linked to the selected site. POSITIVE DIRECTIONAL SELECTION (directional **selection** for an advantageous mutation) reduces variation at closely linked sites. If an advantageous mutation occurs in a gene for which neutral variation exists in the population, and if this mutation is fixed by **selection**, then all the copies of the gene in the population will be descended from the single copy in which the mutation occurred. pag289

Compared with the neutrally evolving gene, the copies of the gene that was fixed by **selection** are descended from a more recent common ancestor (the one in which the favorable mutation occurred); they have had less time to accumulate different neutral mutations, and so are more similar in sequence. pag290

The effects of balancing **selection** (e.g., heterozygote advantage or frequency-dependent **selection**) are opposite to those of positive directional **selection**. Assume that two variants are maintained at a polymorphic site, and again, assume that recombination is low in the vicinity of that site. pag290

Thus, compared with a gene with solely neutral variation, a gene subjected to balancing **selection** will display elevated variation in the vicinity of the selected site (Strobeck 1983). In a genealogy of sequences sampled from a population, the common ancestor of all the sequences may be older than if they had been evolving solely by genetic drift because **selection** has maintained two gene lineages longer. [In fact, the polymorphism may have been maintained by **selection** for so long that speciation has occurred in the interim. pag290

Purifying **selection** against deleterious mutations reduces neutral polymorphism at closely linked sites. Brian Charlesworth and colleagues (Charlesworth et al. 1993; Charlesworth 1994a), who have termed this effect background **selection**, pointed out that when a copy of a deleterious mutation is eliminated from a population, selectively neutral mutations linked to it are eliminated as well (Figure 12.210). pag290

Theoretical analyses indicate that this pattern is more consistent with positive **selection** for advantageous mutations (selective sweeps) than with background **selection** against deleterious mutations (Andersson and Przeworski 2001). pag290

Clinal patterns of geographic variation (see Figure 9.25) show that some kind of balancing **selection** maintains the polymorphism for "fast" and "slow" allozymes of alcohol dehydrogenase (Adh) in *Drosophila melanogaster*, which is due to a single mutation at position 1490 (Figure 9.14). The level of synonymous polymorphism at sites closely linked to position 1490 is much higher than

elsewhere in the *Adh* gene region, supporting the hypothesis of balancing selection (Figure 12.22).pag290

Gene genealogies have also provided evidence for balancing selection. Frequency-dependent selection often maintains polymorphism in the self-incompatibility alleles of plants, as we saw above. In the family Solanaceae, selection has maintained such a polymorphism for so long that many of the alleles in different genera of plants that diverged more than 30 My ago (e.g., petunia and tobacco) are genealogically more closely related.pag290

The human G6PD (glucose-6-phosphate dehydrogenase) locus, located on the X chromosome, shows evidence of strong selection and recent changes in allele frequencies.pag292

The greatly reduced variation and high linkage disequilibrium are consistent with the hypothesis that the A- and Med mutations have increased rapidly and recently due to natural selection. If the increase in allele frequency had happened long ago, new microsatellite mutations would have replenished variation; moreover, recombination would have pag292

However most observed instances of rapid evolution by natural selection involve quantitative characters that have (or probably have) a polygenic basis. Rapid adaptation, at rates far greater than the average evolutionary rates documented in the fossil record, is most often seen when a species is introduced into a new region or when humans alter features of its environment (Endler 1986; Taylor et al. 1991).pag298

The additive genetic variance plays a key role in evolutionary theory because the additive effects of alleles are responsible for the degree of similarity between parents and offspring and therefore are the basis for response to selection within populations. When alleles have additive effects, the expected average phenotype of a brood of offspring equals the average of their parents' phenotypes. Evolution by natural selection requires that selection among phenotypically different parents be selected in the mean phenotype of the next generation. Therefore, V_A enables a response to selection—a change in the mean character state of one generation as a result of selection in the previous generation.pag300

The variation at these loci is therefore not due to mutation-selection balance, but is either selectively neutral or is maintained by balancing selection (Chapter 12).pag303

In the simplest model of the effect of selection on a quantitative trait, such as the tail length of rats, we assume that it has a normal frequency distribution in a population. (A roughly normal distribution is expected if a large number of loci, all with relatively small effects on the character, freely recombine.) Suppose an experimenter imposes selection for greater tail length by breeding only those rats in a captive population with tails longer than a certain value. This form of selection is called truncation selection. The mean tail length of the selected parents differs from that of the population from which they were taken (\bar{z}) by an amount S , the selection differential (Figure 13.8A). The average tail length (\bar{z}') among the offspring of the selected parents differs from that of the parental generation as a whole (\bar{z}) by an amount R , the response to selection (Figure 13.8A, right-hand graph). The pag305

Since this equation can be rearranged as $h^2 N = R/S$, heritability can be estimated from a selection experiment in which S (which is under the experimenter's control) and R are measured. pag306

As **selection** proceeds, it increases the frequencies of those alleles that produce phenotypes closer to the optimum value. As those frequencies increase, multilocus genotypes (combinations of alleles at different loci) that had been extremely rare become more common, so phenotypes arise that had been effectively absent before. Thus the mean of a polygenic character shifts beyond the original range of variation as **selection** proceeds, even if no further mutations occur. pag306

If alleles at different loci differ in the magnitude of their effects on the phenotype, those with the largest favorable effects are likely to be fixed first (Orr 1998). In the absence of complicating factors, prolonged directional **selection** should ultimately fix all favored alleles, eliminating genetic variation. Further response to **selection** would then require new variation, arising from mutation. pag306

Animal and plant breeders have used artificial **selection** to alter domesticated species in extraordinary ways (Figure 13.9). Darwin opened the Origin of Species with an analysis of such changes, and evolutionary biologists have drawn useful inferences about evolution from artificial **selection** ever since then. Artificial **selection** differs from natural **selection** because the human experimenter focuses on one trait rather than on the organism's overall fitness. Nevertheless, natural **selection** often operates much like artificial selection. pag306

Nevertheless, natural **selection** often operates much like artificial **selection**. Responses to artificial **selection** over just a few generations generally are rather close to those predicted from estimates of heritability based on correlations among relatives such as parents and offspring. These heritability estimates seldom predict accurately the change in a trait over many generations of artificial **selection**, however, because of changes in linkage disequilibrium and genetic variance, input of new genetic variation by mutation, and the action of natural **selection**, which often opposes artificial **selection** (Hill and Caballero 1992). pag306

For 86 generations, Yoo scored bristle numbers on 250 flies, and bred the next generation from the top 50 flies, of each sex. In the base population from which the **selection** flies were drawn, the mean bristle number was 9.35 in females, and more than 99 percent of females had fewer than 14 bristles (i.e., three standard deviations above the mean). pag306

In a very short time, **selection** had accomplished an enormous evolutionary change, at a rate higher than is usually observed in the fossil record. pag307

Several populations eventually stopped responding: they reached a **selection** plateau. This cessation of response to **selection** was not caused by loss of genetic variation, because when Yoo terminated ("relaxed") **selection** after 86 generations, mean bristle number declined, proving that genetic variation was still present. pag308

A **selection** plateau and a decline when **selection** is relaxed are commonly observed in **selection** experiments. These patterns are caused by natural **selection**, which opposes artificial **selection**: genotypes with extreme values of the selected trait have low fitness. pag308

This is because more genetic variation is introduced by mutation in large than in small populations, large populations lose variation by genetic drift more slowly, and **selection** is more efficient in large populations. (Recall from Chapter 12 that whether allele frequency changes are affected more by **selection** or by genetic drift depends on the relationship between the coefficient of **selection** and the population size. pag308

In studies of natural populations, several measures of the strength of natural selection on quantitative traits have been used. The simplest indices of selection can be used if the mean (\bar{z}) and variance (V) of a trait are measured within a single generation before (\bar{z}_b , V_b) and then again after (\bar{z}_a , V_a) selection has occurred. (For instance, these measurements may be made on juveniles and then on those individuals that successfully survive to adulthood and reproduce. pag308)

From the differences in morphology between the survivors (\bar{z}_a) and the pre-drought population (\bar{z}_b) the intensity of selection i and the selection gradient b were calculated for three characters: pag309

Selection strongly favored birds that were larger and had deeper bills because they could more effectively feed on large, hard seeds, virtually the only available food. The negative b values show that selection favored shorter bills. Nevertheless, bill length increased, in opposition to the direction of selection, because bill length is correlated with bill depth. Thus a feature can evolve in a direction opposite to the direction of selection if it is strongly correlated with another trait that is more strongly selected. (We will soon return to this theme. pag309)

Thus conflicting selection pressures create stabilizing selection that, on average, favors an intermediate bill size. pag309

EVIDENCE OF STABILIZING SELECTION. Many traits are subject to stabilizing selection, so the mean changes little, if at all. For example, human infants have lower rates of mortality if they are near the population mean for birth weight than if they are lighter or heavier (Figure 13.12; Karn and Penrose 1951). pag309

Stabilizing selection often occurs because of trade-offs, antagonistic agents of selection (Travis 1989). Arthur Weis and colleagues (1992) found that different natural enemies impose conflicting selection on the size of galls induced by the goldenrod gall fly (*Eriosoma solidaginis*). The larva of this fly induces a globular growth (gall) on the stem of its host plant. ... pag309

Taken together, these enemies imposed rather strong stabilizing selection ($j = -0.30$), but because selection by parasitoids was weaker than selection by birds, a directional component ($i = 0.34$) was detected as well (Figure 13.13). pag310

Neo-Darwinian theory offers two possible explanations: either mutations that cause degeneration of an unused character become fixed by genetic drift because variations in the character are selectively neutral, or there is selection against an unused organ, perhaps because it interferes with some important function or requires energy and materials that could better be used for other purposes. In addition, selection could indirectly reduce an unused organ if, due to pleiotropy, it were negatively correlated with another feature that increased due to selection (Fong et al. 1995). pag310

The investigators estimated that the selection gradient (b) was about -0.30 , indicating that selection for small eyes was quite strong. Why amphipods with reduced eyes should have higher mating success is not clear, but the authors speculated, based on neurobiological studies by other researchers, that reduction of the unused visual system might free more of the central nervous system to process nonvisual sensory input. pag310

THE STRENGTH OF NATURAL SELECTION. The strength of selection has been estimated in many studies of quantitative traits in natural populations (Kingsolver et al. 2001). The strength of selection is commonly quite modest, although strong selection (b greater than, say, 0.25) has often been recorded (Figure 13.14A). Stabilizing selection and diversifying selection (i.e., selection on variance) appear to be about equally common (Figure 13.14B). There is a tendency for the strength

of **selection** due to variation in mating success and female fecundity to be greater, all average, than that of **selection** due to differences in survival.pag310

Such constancy is expected only if **selection** does not affect the character.pag311

The very low rate at which most characters seem to have evolved suggests that stabilizing **selection** has maintained them at roughly constant values for long periods.

pag311

As we have seen, many quantitative characters are subject to fairly intense **selection**. Moreover genes contributing to quantitative traits have pleiotropic effects on survival and other fitness components, as we know from studies of *Drosophila* bristles. Thus even characters that might in themselves be selectively "trivial" are probably subject to indirect **selection** because of the pleiotropic effects of the underlying genes (Dobzhansky 1956).pag312

Of the several hypotheses that have been advanced to account for quantitative genetic variation, the most likely may be VARIABLE **SELECTION** and MUTATION-**SELECTION** BALANCE.

pag312

Moreover populations in which stabilizing **selection** favors the same phenotype can diverge in genetic composition as mutation and genetic drift create turnover in alleles at the contributing loci. Gene flow among such populations can help to maintain genetic variation (Goldstein and Holsinger 1992).pag312

However, laboratory populations, maintained under rather uniform conditions and isolated from gene flow, do not differ substantially in heritable variation from natural populations, casting doubt on the importance of variable **selection** and gene flow (Burger et al. 1989).pag312

A currently favored hypothesis is that levels of polygenic variation reflect a balance between the erosion of variation by stabilizing **selection** and the input of new variation by mutation (V_m) (Lande 1976b; Houle et al. 1996). There is some doubt that V_m is high enough to counter the strong stabilizing **selection** that acts on many traits, a point against this hypothesis (Turelli 1984). Moreover, some of the alleles that contribute substantially to the variance in traits such as bristle number have higher frequencies than predicted from a balance between mutation and purifying **selection** (Lai et al. 1994). On the other hand, far more loci contribute to a fitness-related trait than to a single morphological trait, so V_m should be higher for fitness-related traits, and should maintain higher genetic variance (V_g). In fact, V_A is considerably greater for fitness-related traits than for morphological traits, as predicted by the mutation-**selection** balance hypothesis (Houle et al. 1996).pag312

Evolutionary change in one character is often correlated with change in other features. For example, species of animals that differ in body size differ predictably in many individual features, such as the length of their legs or intestines. Correlated evolution can have two causes: correlated **selection** and genetic correlation.pag312

Correlated **selection** in correlated **selection**, there is independent genetic variation in two or more characters, but **selection** favors some combination of character states over others, usually because the characters are functionally related.pag312

Edmund Brodie (1992) found evidence of correlated **selection** on color pattern and escape behavior in the garter snake *Thamnophis ordinoides* (Figure 13.15).pag312

Thus there was correlated **selection** on color pattern and escape behavior in the direction that had been predicted from comparisons among species of snakes and from the theory of visual perception. pag313

A genetic correlation caused by linkage disequilibrium, such as the correlation between pistil length and stamen height in the primrose *Prunella* (see Figure 9.16), will decline due to recombination unless **selection** for the adaptive gene combinations maintains it. pag313

Another cause of change in genetic correlation is natural **selection**, which may favor MODIFIER ALLELES that alter the pleiotropic effects of other loci. pag313

Stamen and corolla tube lengths, which are under correlational **selection** in wild populations, showed some of the strongest correlations (Figure 13.16). In this case, the genetic correlations are probably caused by pleiotropy, because they were not diminished by nine generations of recombination. pag314

A conflict may therefore exist between the genetic correlation of characters and directional **selection** on those characters. When such a conflict exists, the two characters may evolve to their optimal states only slowly, and may even evolve temporarily in a maladaptive direction. (You have already seen that **selection** for a deeper bill in the Galapagos finch *Ceospiza fortis* caused average bill length to increase, even though **selection** favored a shorter bill.) In some cases, a genetic correlation may be so strong that one or both traits cannot reach their optimal states. For example, there is a necessary trade-off between the number and the size of eggs (or seeds) that an organism can produce because the resources that it can allocate to reproduction are limited. pag315

Body size would evolve much more slowly in response to **selection** if every organ had to undergo independent genetic change than if there were coordinated increases or decreases in the sizes of the various organs. pag316

If the response to **selection** in natural populations were never limited by the availability of genetic variation in single characters or combinations of characters, the rate and direction of adaptive evolution would depend only on the strength and direction of natural **selection**. pag316

But after further **selection**, a considerable portion of the population was crossveinless even without heat shock, and the crossveinless condition was heritable. A character state that initially developed in response to the environment had become genetically determined, a phenomenon that Waddington called genetic assimilation. pag319

Selection for this pattern favors alleles that canalize development into the newly favored pathway. As such alleles accumulate, less environmental stimulus is required to produce the new phenotype. The finding that genetic assimilation does not occur in inbred populations that lack genetic variation supports this interpretation (Scharloo 1999). pag319

Does variability depend solely on immutable "laws" of development, or does it evolve by natural **selection**? This question applies to both variability in individual characters and correlations among characters. pag319

Can natural **selection** produce the same result? Wagner et al. (1997) and Kawecki (2000) have explored the evolution of canalization mathematically. According to their studies, alleles for environmental canalization should increase if there is prolonged stabilizing **selection** against

deviations from an optimal phenotype. The evolution of genetic canalization, however, would be expected only under rather restricted conditions. If directional selection fluctuates rapidly in direction, canalization of the phenotype may be advantageous because it prevents a response to selection in one generation that is maladaptive a few generations later. pag320

Under consistent, long-term stabilizing selection, canalization evolves only if selection is neither too weak nor too strong. If stabilizing selection is weak, alleles that prevent the phenotypic expression of mutations have too slight a selective advantage to increase. If stabilizing selection is strong, it eliminates new mutations so fast that few individuals deviate from the optimum, and so there is little selection for alleles that prevent the phenotypic expression of the mutations. pag320

Wagner and Lee Altenberg (1996) have shown theoretically that prolonged directional selection favors modifier alleles that entrance a pleiotropic correlation between functionally related traits along an axis pointing toward the optimum for the characters (marked with an asterisk in Figure 13.8A). For example, if it were functionally important for the upper and lower mandibles of a bird's bill to be the same length, then selection for a longer bill would include selection for alleles that coordinate the development of the two mandibles, creating a pleiotropic correlation between them.

pag321

On the whole, however, the evidence that genetic correlations reflect selection for proper function, rather than developmental pathways that may or may not be adapted to the species' special ecological situation, is equivocal (Armbruster et al. 1999; Herrera et al. 2002). Just how prevalent adaptive phenotypic integration is remains to be seen

pag321

Darwin first conceived of natural selection when he read the economist Thomas Malthus's theory that population growth must inevitably cause competition for food and other resources. pag325

Thus conflict has been inherent in the idea of natural selection from the start. Darwin soon realized however, that not all of natural selection stems from overt struggle among members of a species.

pag325

Characteristics that benefit the population or species, but not the individual, can evolve only by group selection, as we saw in Chapter 11. Because group selection is generally a weak agent of evolutionary change, most evolutionary biologists seek explanations of the evolution of cooperation and conflict based on selection at the level of the individual organism or the gene. pag326

At this level, selection based on inclusive fitness is called kin selection because these other individuals are the bearer's relatives, or kin. pag326

Kin selection is one of the most important explanations for cooperation (Hamilton 1964; Michod 1982). Let us suppose that an individual performs an act that benefits another individual, but incurs a cost to itself: a reduction in its own (direct) fitness. pag326

It is often useful in this context to think of selection at the level of the gene. Bear in mind, then, that one allele replaces another in a population if it leaves more copies of itself in successive generations by whatever effect it may have. pag326

The fundamental principle of kin selection is that an allele for such an ALTRUISTIC trait can increase in frequency only if the number of extra copies of the allele passed on by the altruist's

beneficiary (or beneficiaries) to the next generation as a result of the altruistic interaction is greater on average, than the number of allele copies lost by the altruist Pag326-327

The simplest example of a trait that has evolved by kin **selection** is parental care. If females with allele A enhance the survival of their offspring by caring for them, whereas females lacking this allele do not, then if parental care results in more than two extra surviving offspring, pag327

Parental care illustrates why indiscriminate altruism cannot evolve by individual **selection**. If allele A caused a female to dispense care to young individuals in the population at random, it could not increase in frequency because, on average, the fitness of all genotypes in the population, whether they carried A or not, would be equally enhanced. pag327

Characters such as the toad's croak might be HONEST SIGNALS of the individual's fighting ability or resource-holding potential, or they might be deceptive signals, indicating greater fighting ability than the individual actually has. Theoretically, deceptive signals should be unstable in evolutionary time because **selection** would favor genotypes that ignored the signals, which, having then lost their utility would be lost in subsequent evolution.pag329

Darwin introduced the concept of sexual **selection** to describe differences among individuals of a sex in the number or reproductive capacity of mates they obtain. pag329

Sexual **selection** was Darwin's solution to the problem of why conspicuous traits such as the bright. pag329

He proposed two forms of sexual **selection**: contests between males for access to females and female choice (or "preference") of some male phenotypes over others. Several other bases for sexual **selection** have been recognized (Table 14.1).pag330

Sexual **selection** exists because females produce relatively few, large gametes (eggs) and males produce many small gametes (sperm).pag330

Thus the intensity of male mating success is generally greater among males than among females (Figure 14.4), and indeed, is a measure of the intensity of sexual **selection** (Wade and Arnold 1980). In some species, however, the tables are turned.pag330

In sexual **selection** by male contest, directional **selection** for greater size, weaponry, or display features can cause an "arms race" that results in evolution of ever more extreme traits. Such "escalation" becomes limited by opposing ecological **selection** (i.e., **selection** imposed by ecological factors) if the cost of larger size or weaponry becomes sufficiently great (West-Eberhard 1983). The equilibrium value of the trait is likely to be greater than it would be if only ecological **selection** were operating. As Darwin noted, the duller coloration and lack of exaggerated display features in females and nonbreeding males of many species implies that these features of breeding males are ecologically disadvantageous.pag331

In some species of *Drosophila*, snakes, and other animals with internal fertilization, the seminal fluid of a mating male reduces the sexual attractiveness of the female to other males, reduces her receptivity to further mating, or forms a copulatory plug in the vagina (Partridge and Roff 1998; see the discussion below on "chase-away" sexual **selection**).pag332

Closely related species of hummingbirds, birds of paradise, cichlid fishes, and many other groups show astonishing differences in colors, ornaments, and displays that are thought to have evolved by sexual **selection** (see Figure 15.6).pag332

Subject to limits imposed by ecological **selection**, male traits will obviously evolve to exaggerated states if they enhance mating success. pag332

Under these circumstances there is **selection** pressure on females to recognize males that are superior providers by some feature that is correlated with their ability to provide.

pag333

The female preference evidently evolved in the common ancestor of these genera, and thus provided **selection** for a male sword when the mutations for this feature arose.

pag333

The two prevalent models of such indirect benefits are runaway sexual **selection** (sometimes called the "sexy son" hypothesis), in which the sons of females that choose a male trait have improved mating success because they inherit the trait that made their fathers appealing to their mothers, and good genes models, in which the preferred male trait indicates high viability, which is inherited by the offspring of females who choose such males. pag334

RUNAWAY SEXUAL SELECTION. In runaway sexual **selection**, as proposed by R. A. Fisher (1930), the evolution of a male trait and a female preference, once initiated, becomes a self-reinforcing, snowballing or "runaway" process (Lande 1981; Kirkpatrick 1982; Pomiankowski and Iwasa 1998). This process is often referred to as the "Fisherian model" of sexual **selection** (even though Fisher discussed both kinds of indirect benefits). pag334

If females have genetically variable responses to each of several or many male traits, different traits or combinations of traits may evolve depending on initial genetic conditions (Pomiankowski and Iwasa 1998). Thus runaway sexual **selection** can occur. Different paths in different populations, so that populations may diverge in mate choice and become reproductively isolated. Sexual **selection** is therefore a powerful potential cause of speciation (see Chapter 16). Runaway sexual **selection** of this kind could explain the extraordinary variety of male ornaments among different species of hummingbirds and many other kinds of animals. pag335

Any male trait that is correlated with genetic quality--any INDICATOR of "good genes"--could be used by females as a guide to advantageous matings, so **selection** would favor a genetic propensity in females to choose mates on this basis. pag335

In this model, the strength of indirect **selection** on female preference is proportional to the genetic variance in fitness in the population. However, natural **selection** should reduce variance in fitness. pag335

Large gastropods, *Haliotis*). Sperm compete to fertilize eggs, so **selection** on sperm always favors a greater ability to penetrate eggs rapidly. But **selection** on eggs should favor features that slow sperm entry, or else POLYSPERMY (entry by multiple sperm) may result. pag337

Nonsynonymous differences between the *lys* genes of different species of abalones have evolved much faster than synonymous differences, a sure sign of natural **selection** (Vacquier 1998; see also Palumbi 1998 and Chapter 19) pag337

Thus females evolve resistance to males' inducements to mate, and their resistance selects for features that enable males to overcome the females' reluctance--a dynamic that has been termed CHASE-AWAY SEXUAL **SELECTION** (Holland and Rice 1998). pag338

Under chase-away **selection** males may evolve increasingly strong stimuli, such as brighter colors or more elaborate song, to induce reluctant females to mate
pag338

Darwin's theory of natural **selection**, as we have seen, is based on individual advantage: traits that enhance an individual's fitness relative to that of other members of the population—"selfish" traits—increase in frequency if they are heritable. Thus cooperative interactions seem antithetical to evolution by natural **selection** and require explanation. Until the 1960s, it was common for biologists to assume that cooperation—especially altruism—had evolved because it benefited the population or species—that is, by group **selection**. The modern study of cooperation, which for the most part rejects group **selection**, issues largely from William Hamilton's (1964) theory of kin **selection** and from the realization, articulated most forcefully by George Williams (1966), that group **selection** is a weaker process than individual **selection** (see Chapter 11).pag339

Traits that appear harmful to the possessor but beneficial to other individuals have been explained by four major classes of individual **selection** hypotheses: Hamilton's rule, individual advantage, reciprocity, and kin selection. pag339

If the cell dies, so do all the included genes; if the organism dies, so do its cells. **Selection** at the higher level—cell or organism—thus eliminates outliving genes or renegade cells that selfishly diminish the survival of the group. pag340

At the start of this chapter we introduced the concept of kin **selection**, which is one of the most important explanations of cooperation among conspecific individuals. For kin **selection** to operate, individuals must dispense benefits more often to kin than to nonkin. pag341

Several factors may explain cooperative breeding (Emlen 1997; Cockburn 1998), including kin **selection**, since in many species, the helpers aid their parents in rearing their siblings. pag341

These insects have been especially important in studies of social interactions and the role of kin **selection** because they are HAPLODIPLOID: females develop from fertilized eggs and are diploid, but males develop from unfertilized eggs and are haploid. Thus kin **selection** is thought to have shaped the interactions among members of a hymenopteran colony, and it has been hypothesized that. pag341

The role of kin **selection** has been tested by a theory of conflict between queens and workers, proposed by Trivers and Hare (1976). The queen's fitness would be maximized by investing equally in reproductive daughters and sons, because she is equally related ($r = 0.5$) to both (see Chapter 12 on the evolution of the sex ratio).pag342

If kin **selection** has shaped the behavior of workers, we would expect the sex ratio of reproductive offspring to be biased toward 0.75 (3:1 female: male) in colonies with a single queen. In colonies with multiple queens, workers would have a coefficient of relationship over 0.75 to many of the offspring they rear (since they are not full sisters), so the sex ratio should be closer to 0.5 (1:1).pag342

Moreover, there is direct evidence in the wood ant (*Formica exsecta*) that workers manipulate the sex ratio as kin **selection** theory predicts (Swldstrom et al. 1996). Although all colonies have about the same sex ratio among eggs, the sex ratio among pupae becomes shifted toward females in single-queen colonies, but toward males in multiple-queen colonies, which would be advantageous

for the queens (Figure 14.17). In **selection** may not be the only possible explanation of these patterns (Mehdiabadi et al. 2003), but so far it seems the most likely. pag342

However~ evolutionary biologists have had to understand that these interactions are pervaded with potential conflict, and that much of the diversity of reproductive behavior and life histories among organisms stems from the balance between conflict and cooperation. (Incidentally, the way in which some animal species behave toward family members starkly show that natural **selection** utterly lacks morality, as we pointed out in Chapter 11.) pag343

if offspring survival were almost as great with uniparental care as with biparental care, **selection** would favor females that defected, abandoning the brood to the care of the male-or vice versa (Figure 14.18). pag343

Thus a conflict between mates arises as to which will evolve a promiscuous habit and which will care for the eggs or young. **Selection** favors defection more strongly in the sex for which parental care is more costly (in terms of lost opportunities for further reproduction). pag343

All else being equal, the strength of natural **selection** for parental care is proportional to the probability that individuals are actually caring for their own offspring (carrying their genes). pag344

The answer appears to be that there exist conflicts between different genes as an outcome of **selection** at the gene level. Such conflicts can arise whenever a gene has a transmission advantage over other genes, perhaps by a segregation advantage during meiosis or perhaps by not following the rules of meiosis at all. pag346

Such "outlaw genes," which promote their own spread at a faster rate than other parts of the genome, can create a context in which there is **selection** for genes at other loci to suppress their effects. When this is the case, a genetic conflict is said to exist (Hurst et al. 1996). pag346

The Seychelles and other areas where the disorder gene has increased in frequency, there has been **selection** for autosomal suppression of its effects (Atlan et al. 1997). pag347

Terms of **selection** at the level of genes, the fitness of paternally inherited genes will be greatest if the embryo survives, since copies of those genes will not be carried by the mother's subsequent offspring if she mates with a different male. pag348

Consider~ for example, a genetic element-a gene or set of genes-that can replicate faster than the rest of the genome with which it is associated. It might be, for example, a bacterium that lives within a host organism's cells. (Such an organism is called an ENDOSYMBIONT.) If the population of endosymbionts within a single host is genetically variable, **selection** within that population favors (by definition) the genotype that increases numbers faster than others pag348

Therefore, **selection** favors symbiont genotypes with a high reproductive rate, even if they kill the host. In other words, **selection** favors evolution of a PARASITE that may be highly virulent. pag349

Selection for high proliferation within the symbiont populations occupying each host is opposed by **selection** among the populations of symbionts that occupy different hosts. On balance, **selection** at the group level favors genotypes with restrained reproduction-those that do not extract so many

reSOLU"CeS from the host as to calise its death before it can transmit the endosymbionts to its progeny.pag349

Selection may even favor alleles in the symbiont that enhance the host's fitness, since that also enhances the fitness of the symbionts carried by that host. Furthermore, **selection** favors host alleles that control or inhibit the symbiont (an instance of genetic conflict). Evolution in both the symbiont and its host may therefore result in mutualism (an interaction in which two genetic entities enhance each other's fitness). (We return to the evolution of parasitism and mutualism in Chapter 18.)pag349

The fundamental answer is kin **selection**: if the cell lineages in a multicellular organism arise by mitosis from a single-celled egg or zygote, the genes of cooperative cells that sacrifice reproduction for the good of the cell "colony" are propagated by closely related reproductive cells.pag350

Selection at the level of whole colonies of cells-organisms-therefore opposes **selection** among cells 'within colonies. It has favored mechanisms of "policing" that regulate cell division and prevent renegade cell genotypes from disrupting the integrated function of the organism. In animals, it has resulted in the evolution of a germ line that is segregated early in development from the soma thereby excluding most disruptive mutations from the gametes and reducing their possible fitness advantage.pag350

Selection for organismal integration may be responsible for the familiar but remarkable fact that almost all organisms begin life as a single cell, rather than as a group of cells. This feature increases the kinship among all the cells of the developing organism, reducing genetic variation and competition within the organism and increasing the heritability of fitness. The result, then, has been the emergence of the "individual," and with it, the level of organization at which much of natural **selection** and evolution take place.pag350

Furthermore, two or more loci should be nearly at linkage equilibrium, unless very strong **selection** or suppression of recombination exists. If these loci affect a more or less additively inherited character, its variation will have a single-peaked, more or less normal distribution.pag363

This result sheds some light on the more rapid evolution of sterility in male than in female *Drosophila* hybrids, an instance of Haldane's rule. It has been proposed that X-linked genes diverge faster than autosomal genes because favorable X-linked recessive alleles are most exposed to natural **selection** (since males carry only one X). In addition, autosomal genes affecting male sterility have diverged faster than those affecting female sterility, possibly because of sexual **selection**. pag368

Presgraves found that in both species lineages, amino acid-replacing nucleotide substitutions have occurred in the N1p96 gene at a high rate relative to synonymous substitutions, a clear indication that natural **selection**, rather than genetic drift, has driven divergence (Figure 15.15). Why **selection** favored changes in this protein is not yet known.Pag368-369

This pattern is expected if chromosomal heterozygotes have lower fitness than homozygotes (are UNDERDOMINANT), perhaps due to reduced fertility caused by aneuploidy. If so, a chromosome introduced by gene flow from one population into another would seldom increase in frequency; because its initial frequency would be low, it would occur mostly in heterozygous condition, and it would probably be eliminated by **selection** (see Chapter 11).pag370

According to the COALESCENT THEORY described in Chapter 10, genetic drift in each species eventually results in the loss of all the ancestral lineages of DNA sequence variants except one; that is, coalescence to a common ancestral gene copy occurs in each species. (This process can also be caused by directional **selection** for a favorable mutation.)pag372

However, shared polymorphisms can persist for a long time if natural **selection** maintains the variation in both species. For example, humans and chimpanzees are each other's closest relatives, sharing several gene lineages at two loci in the major histocompatibility complex (MHC), retained from their common ancestor since divergence occurred about 5 million years ago.pag373

Hybrid zones are thought to be caused by two processes. PRIMARY HYBRID ZONES originate in situ as natural **selection** alters allele frequencies in a series of more or less continuously distributed populationspag374

However, we might expect that in a primary hybrid zone, natural **selection** on different loci or characters would result in clines with different geographic positions, and that selectively neutral variation would not display a clinal pattern (Figure 15.20A).pag373

Dispersal, **selection**, and linkage also affect the distribution of alleles and phenotypic characters in hybrid zones. Let us consider how these factors affect clines in tension zones, in which hybrids have low fitness due to epistatic incompatibility or heterozygote disadvantage at certain loci (Barton and Gale 1993).pag374

Thus **selection** against hybrids acts as a barrier to gene flow, and the steepness of the cline at the A locus depends on the strength of **selection** against hybrids relative to the magnitude of dispersal. Unless the rate of dispersal or interbreeding changes, this cline persists indefinitely.pag375

A hybrid zone may persist indefinitely, with **selection** maintaining steep clines at some loci even while the clines in neutral alleles dissipate due to introgression. If the hybrid zone is a tension zone, it may movepag375

Natural **selection** may favor alleles that enhance prezygotic isolation, resulting ultimately in full reproductive isolationpag376

If we considered species to be merely populations with distinguishing characteristics, the question of how they originate would be easily answered: natural **selection** or genetic drift can fix novel alleles or characteristics (see Chapters 10-13).pag379

The causes of evolution of reproductive barriers, as of any characters, are genetic drift and natural **selection** of genetic alterations that have arisen by mutation. Peripatric speciation, a hypothetical form of speciation that is also referred to as TRANSIENT SILENCE or SPECIATION BY PEAK SHIFT, requires both genetic drift and natural **selection**. Both sexual **selection** and ecological causes of natural **selection** may result in speciation. In some cases, there may be **selection** for reproductive isolation—that is, to prevent hybridization. (Recall the distinction between selection for and **selection** of characters, discussed in Chapter 11.)pag381

Because both natural **selection** and genetic drift cause populations to diverge in genetic composition, it is probably inevitable that if separated long enough, geographically separated populations will become different species.pag381

Models of vicariant allopatric speciation have been proposed based on genetic drift, natural selection, and a combination of these two factors. The combination of genetic drift and selection is discussed later, in relation to peripatric speciation. pag383

Such an increase to fixation, of course, would be counter to natural selection. Dobzhansky (1936) and Muller (1940) provided a theoretical solution to this problem that does not envision increasing an allele's frequency in opposition to selection. It requires that the reproductive barrier be based on differences at two or more loci that have complementary effects on fitness. (That is, fitness depends on the combined action of the "right" alleles at both loci.) pag383

Therefore these allele substitutions can occur by natural selection (if the fitnesses differ) or by genetic drift (if they do not). However, an epistatic interaction between A1 and B1 causes incompatibility, so that either the hybrid A,A,B,B, has lowered viability or fertility, or A,A,B,B, and A,A,B,B, are isolated by a prezygotic barrier, such as different sexual behavior. pag384

This model is supported by genetic data showing that reproductive isolation is based on epistatic interactions (called Dobzhansky-Muller incompatibilities) among several or many loci (see Chapter 15). The allele substitutions could be caused by either genetic drift or natural selection. For the moment, we will leave open the possibility of speciation through random fixation of alleles, and consider the ways in which natural selection may contribute to the origin of species. pag384

Thus speciation is usually an effect—a by-product—of the divergent selection that occurred in allopatry. The divergent selection may be ecological selection or sexual selection. pag384

A contrasting possibility is that natural selection favors prezygotic (e.g., sexual) reproductive barriers because of their isolating function—because they prevent their bearers from having unfit hybrid progeny. Selection would then result in reinforcement of reproductive isolation. pag384

The most direct evidence comes from laboratory studies of *Drosophila* and houseflies, in which investigators have tested for reproductive isolation among subpopulations drawn from a single base population and subjected to divergent selection for various morphological, behavioral, or physiological characteristics (Rice and Hostert 1994). pag384-385

In many of these studies, partial sexual isolation or postzygotic isolation developed, demonstrating that substantial progress toward speciation can be observed in the laboratory, and that it can arise as a correlated response to divergent selection. pag385

Parallel ecological divergence implies that ecological selection has shaped the differences between the ecomorphs. In laboratory trials, fish of the same ecomorph from different lakes mate almost as readily as those from the same lake, but different ecomorphs mate much less frequently (Figure 16.86). pag385

Molecular data also are beginning to provide evidence of a role for natural selection in speciation. The few genes that contribute to reproductive isolation and that have been sequenced, such as *Nlp96* in *Drosophila* (see Figure 15.15), show the high rate of amino acid-replacing substitutions that indicates directional selection. pag386

Models of sexual selection of male traits by female choice show that divergent traits and preferences can evolve in different populations of an ancestral species, resulting in speciation (Lande 1981; Pomiankowski and Turelli 1998; Turelli et al. 2001). The expected result would be the diversity of different male traits that distinguish species of hummingbirds (see Figure 15.6) and many other groups of animals. pag386

It is very likely that sexual **selection** has been an important cause of speciation, especially in highly diverse groups, such as African lake cichlids, Hawaiian *Drosophila*, pheasants, and birds of paradise, in which males are commonly highly (and diversely) colored or ornamented (Panhuis et al. 2001).pag386

Comparisons of the species diversity of sister groups of birds suggest that sexual **selection** has enhanced diversity (Figure 16.9). Groups of birds with promiscuous mating systems have higher diversity than sister clades in which pair bonds are formed and the variance in male mating success is presumably lower—resulting in weaker sexual **selection** (Mitra et al. 1996). Because sister clades, by definition, are equal in age, the difference in diversity implies a higher rate of speciation (or possibly a lower extinction rate) in clades that experience strong sexual **selection**.pag386

Sexual **selection** in these cichlids has probably contributed to their extraordinarily high rate of speciation.pag387

Michael Ritchie (2000) has provided explicit evidence that sexual **selection** within population results in reproductive isolation. The male song of Mediterranean populations of the bushcricket *Ephippiger ephippiger* has a single syllable, whereas males from the Pyrenees produce polysyllabic songs.pag387

Mediterranean females showed increasing preference, the lower the syllable number, and should therefore exert directional **selection** on males for monosyllabic songs (Figure 16.10). In contrast, Pyrenees females responded most to songs with five syllables, which is actually more than most males in this polysyllabic population emit. Thus females exert directional sexual **selection** for greater syllable number in this population. Why don't Pyrenees males match the females' preference? Possibly females have evolved to resist male stimulation, as the "chase-away" model of sexual **selection** posits (Holland and Rice 1998; see Chapter 14).pag387

We have seen that reproductive isolation can arise as a side effect of genetic divergence due to natural **selection**. However, many persons have supposed that reproductive isolation evolves, at least in part, as an adaptation to prevent the production of unfit hybrids.pag387

Consequently, natural **selection** will favor the spread and establishment of the mutant condition.(Dobzhansky 1951,208)pag387

It is now generally agreed that natural **selection** can enhance prezygotic reproductive isolation between hybridizing populations, but how often this process plays a role in speciation is not known (Howard 1993; Noor 1999; Turelli et al. 2001).pag387

In most organisms, natural **selection** cannot strengthen postzygotic isolation between hybridizing populations because such a process would require that alleles that reduce fertility or survival increase in frequency, which would be precisely antithetical to the meaning of natural **selection**! (See Grant 1966 and Coyne 1974 for possible exceptions.) Postzygoticpag387

However, we have assumed that mutation 82 has no other effect on fitness. It might have disadvantageous pleiotropic effects, or sexual **selection** might disfavor it outside the hybrid zone. If so, B2 might increase in frequency in and near the hybrid zone, but would be selected against elsewhere. Moreover, gene flow into the hybrid zone would increase the frequency of B1, counteracting the increase of B2 by **selection**.pag388

Then divergent sexual **selection** for different mate preference alleles (P1, P2) in the two populations may be reinforced by the low fitness of hybrids. Because sexual **selection** generally creates an association (linkage disequilibrium) between P-locus and T-locus alleles (see Chapter 15), and because the populations are assumed to differ already in the frequencies of the male trait alleles T1 and T2, associations between genes reducing hybrid fitness and genes affecting the mating system are less likely to be broken down by recombination than in the Previous model.pag389

Hence **selection** would alter allele frequencies at these loci, and this in turn might select for changes at still other epistatically interacting loci. The "snowballing" genetic change that might result would incidentally yield reproductive isolation.pag389

Selection might then alter polygenic modifier loci to bring about a new coadapted state of the character.pag390

This stage cannot be accomplished by natural **selection**, since **selection** cannot reduce mean fitness. However, **selection** can move the allele frequencies up the slope away from the valley toward the new peak. pag390

If the adaptive valley is very deep (i.e., if there is strong **selection** against heterozygotes), genetic drift is unlikely to move allele frequencies across the valley from one peak to another, unless the founder population is very small.pag390

Thus, if the adaptive valley is shallow enough for a peak shift to be likely, the genetic difference between the populations will cause little reproductive isolation; if **selection** is strong and the valley is deep, the populations will be reproductively well isolated, but the shift to the new genetic composition is unlikely to occur.pag390

Thus peripheral populations (as in the example above) often diverge simply because of natural **selection**, not because of founder effects. The hypothesis that a species arose from a population that was not only peripheral, but also small, would be supported by evidence that the population had lost most of the genetic variation present in its more populous ancestor. pag391

So far, there is little evidence that this divergence is frequently due to peak shifts initiated by genetic drift and completed by **selection**, rather than natural **selection** alone. pag392

Even in allopatric speciation, there may be some gene flow between populations, but it is very low compared with the divergent action of natural **selection** and/or genetic drift. Parapatric speciation is the same process, but since the rate of gene flow is higher, the force of **selection** must be correspondingly stronger to engender genetic differences that create reproductive isolation.pag392

Parapatric speciation can theoretically occur if gene flow between populations that occupy adjacent regions with different selective pressures is much weaker than divergent **selection** for different gene combinations (Endler 1977). Strong **selection** at sharp border between different habitats poses a barrier to gene exchange, caused by the reproductive failure of individuals with the "wrong" genotype or phenotype that migrate across the border.Pag392-393

Russell Lande (1982) has theorized that prezygotic isolation could arise in this way due to divergent sexual **selection**.pag393

Possibly the best-documented example of the parapatric origin of reproductive isolation is attributable not to these theories, but to **selection** for isolation—i.e., reinforcement. pag393

Several populations, under very strong **selection** for heavy metal tolerance, have diverged from neighboring non-tolerant populations (on uncontaminated soil) not only in tolerance, but in flowering time; moreover, they self-pollinate more frequently, having become more self-compatible (Figure 16.15). pag393

Divergent adaptation to the resources might be based on one or on several loci. **Selection** might then favor alleles at one or more other loci that cause nonrandom mating, reducing the frequency of unfit heterozygous offspring. Thus the incipient species would come to differ at several loci, governing both mating behavior and adaptation to different resources. pag393

Thus, just as recombination can prevent reinforcement of sexual isolation in a hybrid zone, as we saw earlier in this chapter; it makes the sympatric evolution of assortative mating unlikely, unless **selection** against heterozygotes is very strong (Felsenstein 1981). The same principle makes it even more unlikely that additional alleles at other loci that would further enhance assortative mating could increase in frequency. pag394

Thus **selection** favors the divergent gene combinations and promotes linkage disequilibrium, so that the antagonism between **selection** and recombination is lower than in the model described previously. pag394

However, if host preference is a continuous, polygenic trait, reproductive isolation will not evolve unless **selection** is strong (Figure 16.16B). Somewhat similar models describe sympatric speciation by adaptation to a continuously distributed resource, such as prey size (Dieckmann and Doebeli 1999; Kondrashov and Kondrashov 1999). Some authors have questioned how realistic these models are (Gavrilets 2004; Coyne and Orr 2004). pag394

Many experiments have been done in which laboratory populations of *Drosophila* have been subjected to disruptive **selection** and then tested for prezygotic isolation (Rice and Hostert 1993). In most, no sexual isolation developed. pag394

However, there are many intermediate cases between auto- and allopolyploids. Moreover, chromosomes of autopolyploids may form bivalents because of natural **selection** for genes that enable the chromosomes to pair normally. pag396-397

Thus hybridization, by generating diverse gene combinations on which **selection** can act, can be a source of new species with novel morphological and ecological features. pag399

We expect the process of speciation (TFS) to be excruciatingly slow if it proceeds by mutation and drift of neutral alleles; we expect it to be faster if it is driven by ecological or sexual **selection**, and to be accelerated if reinforcement plays a role. pag401

Among characteristics studied so far, those that seem most likely to have increased speciation rate as such seem to be animal (rather than wind) pollination in plants and features that indicate intense sexual **selection** in animals (Coyne and Orr 2004). These observations suggest the intriguing possibility that diversification in some groups of animals owes more to the simple evolution of reproductive isolation (due to sexual **selection**) than to ecological diversification. pag401

Although different local populations may diverge rapidly due to **selection**, local populations are ephemeral: as climate and other ecological circumstances change, divergent populations move about and come into contact sooner or later. pag402

Even some professional biologists have been known to answer "yes" to these questions. But either they have assumed that these characteristics did not evolve by Darwinian natural **selection** (**selection** among individuals), or they have not realized that the good of the species does not affect the course of **selection** among individuals—they have not fully understood the meaning of natural **selection**. pag406

Because they are components of fitness, differences in fecundity and life span must have evolved at least partly by natural **selection**. **Selection** among populations—the only possible cause of evolution of a trait that is harmful to the individual but beneficial to the population or species—is generally a weaker force than **selection** among individuals, as we saw in Chapter 11. This must be especially true for life history traits, which are components of individuals' fitness. pag407

The possibility of future extinction due to excessive population growth or inadequate reproduction is irrelevant to, and cannot affect, the course of natural **selection** among individuals. A mutation that increased the fecundity of humans (or any other species), for example, would increase individual fitness (if it had no other effects) and would therefore become fixed—even if overpopulation and mass starvation should ensue. pag407

Correlated responses to artificial or natural **selection** provide some of the most consistent evidence of trade-offs (Reznick 1985; Stearns 1992). Linda Partridge and colleagues (1999) set up ten **selection** lines of *Drosophila melanogaster* from the same base population. pag410

Experimental manipulation of one trait and observation of the effect on other traits often reveals trade-off. For instance, Sgro and Partridge (1999) followed the **selection** experiment on *Drosophila* longevity by experimentally sterilizing females from both "young" and "old" populations, either by gamma radiation or by inheritance of a dominant allele that causes female sterility. pag410

Peter Medawar (1952) proposed that deleterious mutations that affect later age classes accumulate in populations at a higher frequency than those that affect earlier age classes because **selection** against them is weak. pag412

On the other hand, Williams's hypothesis of antagonistic pleiotropy is supported by **selection** experiments like those by Linda Partridge's group (see Figure 7.7), which provide evidence of a negative relationship between early reproduction and both longevity and later reproduction. These experiments are among the most striking confirmations of evolutionary hypotheses that had been posed long before. pag412

Much of the theory of life history evolution described for females applies to males as well. A substantial cost of reproduction, for example, may impose **selection** for delayed maturation and iteroparous reproduction. Competition for mates—the basis of sexual **selection** (see Chapter 14)—is often very costly (Andersson 1994). pag415

This fact has been cited for more than a century as the reason for the existence of recombination and sexual reproduction. But, as we have seen, arguments that invoke benefits to the species are suspect because they rely on group **selection**—which is ordinarily a weak agent of evolution. The

question, then, is whether or not natural **selection** within populations can account for features of the genetic system. pag416

Group **selection** would favor an optimal (greater than zero) mutation rate because genetically invariant species would become extinct, leaving only species that experience mutation. We do not know how fast this process would occur because the faster the environment changes, the higher the mutation rate must be to avert extinction (Lynch and Lande 1993). pag417

In some taxa, recombination and the mode of reproduction can evolve rather rapidly. Using artificial **selection** in laboratory populations of *Drosophila*, investigators have altered the rate of crossing over between particular pairs of loci, and have even developed parthenogenetic strains from sexual ancestors (Carson 1967; Brooks 1988). pag418

The recency of most parthenogenetic lineages suggests that sex reduces the risk of extinction. If this were the reason for its prevalence, sex might be one of the few characteristics of organisms that has evolved by group **selection**. pag418

However, this hypothesis fails to explain the elaborate mechanisms of meiosis and syngamy, so most evolutionary biologists believe that the maintenance of sex in most species must be attributed to other causes involving variation and **selection** (Maynard Smith 1988; Barton and Charlesworth 1998). pag419

ADAPTATION TO FLUCTUATING ENVIRONMENTS. Suppose a polygenic character is subject to stabilizing **selection**, but the optimum character state fluctuates due to a fluctuating environment (Maynard Smith 1980). Let us assume that alleles A, B, C, D ... additively increase a trait such as body size, and alleles a, b, c, d ... decrease it. Stabilizing **selection** for intermediate size reduces the variance and creates negative linkage disequilibrium, so that combinations such as AbCd and aBeD are present in excess (see Chapter 13). If **selection** changes so that larger size is favored, combinations such as ABCD may not exist in an asexual population, but they can arise rapidly in a sexual population. pag420

For this hypothesis to work, the **selection** regime must fluctuate rather frequently, and some factor must maintain genetic variation, because a long-term regime of stabilizing **selection** for a constant optimal phenotype would fix a homozygous genotype (such as AABBccdd) (see Chapter 13). pag421

The Red Queen hypothesis for the advantage of sex may hold true only under special conditions, such as very strong **selection** by parasites (Otto and Nuismer 2004), but it has some evidence in its favor (Jokela and Lively 1995; Lively and Dybdahl 2000). pag421

In small populations, mutations are so few that the first (A) is likely to be fixed by **selection** before the second (B) arises, whether the population is asexual or sexual. Thus recombination may or may not speed up adaptive evolution. pag421-422

Slower adaptation by asexual populations is likely to be a major reason for their high rate of extinction, as documented by the recent origin of most asexual eukaryotes. But directional **selection** is unlikely to be frequent enough to provide the short-term advantage needed to counter the cost of sex. pag422

Answering the question of sex may require both better genetic data (e.g., on mutation rates) and more studies of **selection** in natural populations. pag422

That a polymorphism should have been retained for such a long time is explicable only by balancing **selection** (Clark 1993; see Chapter 12). In contrast, many plants, such as wheat, have evolved a strong tendency toward self-fertilization within flmverpag424

Thus the **selection** that species may exert on each other may differ among populations, resulting in a "geographic mosaic" of coevolution that differs from one place to another (1110mpson 1999). pag430

The possibility that an evolutionary change in one species may evoke a reciprocal change in another species distinguishes **selection** in interspecific interactions from **selection** stemming from conditions in the physical environment. Reciprocal genetic change in interacting species, owing to natural selection imposed by each on the other, is coevolution in the narrow sense. pag430

For example, Darwin envisioned predatory mammals, such as wolves, and their prey, such as deer, evolving ever greater fleetness, each improvement in one causing **selection** for compensating improvement in the other, in an "evolutionary arms race" between prey and predator (Figure 1S.2A). pag430

According to computer simulations, such frequency-dependent **selection** can cause cycles or irregular fluctuations in allele frequencies (Figure 18.6). In wild populations of Australian flax, the frequencies of different rust genotypes fluctuated from year to year (Figure 18.7). pag434

Parasites that kill their host before transmission contribute less to the total parasite population than more benign parasites, so interdemic **selection** (group **selection**) favors low virulence. If a host typically becomes infected by only one individual parasite, or by closely related individuals, the demes are kin groups, so interdemic **selection** is then tantamount to kin **selection** and low virulence may evolve. If, however, each host is infected by multiple, unrelated genotypes of parasites, **selection** within demes favors genotypes with high reproductive rates which will be transmitted in greater numbers. pag438

Second, if hosts rapidly become immune to the parasite (i.e., if r in the above equation is large), **selection** favors rapid reproduction—that is, outwitting the host's immune system—by the parasite. Because this may entail greater virulence, an effective immune system (or a drug that rapidly kills the parasite) may sometimes induce the evolution of higher virulence. pag438

In *The Origin of Species*, Darwin challenged his readers to find an instance of a species' having been modified solely for the benefit of another species, "for such could not have been produced through natural **selection**." No one has met Darwin's challenge. pag439

Thus **selection** will always favor protective mechanisms in one or both species to prevent overexploitation (Bull and Rice 1991). Moreover, **selection** will favor "honest" genotypes if the individual's genetic self-interest depends on the fitness of its host or partner (Herre et al. 1999) pag440

Fruit abortion imposes strong **selection** on moths that lay too many eggs in a flower because the larvae in an aborted flower or fruit perish. Thus the moth has evolved restraint by individual **selection** and self-interest. pag441

Darwin postulated that competition would impose **selection** for divergence in resource use and viewed it as a major reason for the origin and divergence of species. There is now a good deal of evidence that evolution in response to competition is one of the major causes of adaptive radiation (Schluter 2000). pag441

Therefore, the most extreme genotypes will have higher fitness. Such density-dependent diversifying **selection** can result in the two species' evolving less overlap in their use of resources and in a shift of their phenotype distributions away from each other (Slatkin 1980; Taper and Case 1992) pag442

Selection may be stronger in some places than in others, or even favor different characteristics, and gene flow among such populations may result in locally inadequate adaptation. pag444

Throughout much of the distribution of the pine in the northern Rocky Mountains, squirrels harvest and store great numbers of cones and are the primary consumers of pine seeds. Benkman et al. have found that squirrels prefer cones that have a high ratio of seed kernel to cone mass, and so impose **selection** for larger cones with fewer seeds. pag444

Selection on a mimetic phenotype can depend on both its density, relative to that of a model species and the degree of unpalatability of the model. pag446

Mimetic polymorphism in Batesian mimics such as *Papilio dardanus* can therefore evolve by frequency-dependent **selection**: a rare novel phenotype that mimics a different model species will have higher fitness than a common mimetic phenotype, simply because it is less common and predators will not have had an opportunity to learn that butterflies with that phenotype are palatable rather than unpalatable.. pag446

Since Müllerian mimics jointly reinforce aversion learning by predators, there is likely to be strong stabilizing **selection** for a common color pattern in all sympatric unpalatable species (Figure 18.25B).. pag446

The neutral theory states that the vast majority of evolutionary change in genes and chromosomes occurs via mutation followed by random drift, rather than by adaptive mutations being driven to fixation by **selection**. Adaptive mutations do occur, but they are rare. To be sure, more and more evidence of adaptive molecular evolution is being found; for example, a recent study suggested that as many as 45 percent of all amino acid substitutions in *Drosophila silivans* and *D. yakuba* have been fixed by natural **selection** (Smith and Eyre-Walker 2002). Still, the neutral theory is the starting point in any analysis of DNA sequence evolution. pag45

PURIFYING SELECTION (Chapter 12) occurs when new sequence variants are selected against, causing $f < 1$ and $k < v$. Under strong purifying **selection**, most nonsynonymous mutations are selected against, but synonymous mutations still accumulate, since changes at these sites do not challenge the protein's amino acid sequence. One index of purifying **selection** in a protein-coding gene, therefore, is a low ratio of nonsynonymous to synonymous substitutions. pag454

POSITIVE SELECTION-substitution of a mutation that increases fitness-accelerates the accumulation of nonsynonymous mutations over and above the mutation rate (the rate of fixation of neutral mutations). If the number of advantageous substitutions in a gene exceeds the number of neutral substitutions (i.e., if $\theta > 1$), positive Darwinian selection has acted on the gene. pag454

High values of d , indicate that there has been strong positive **selection** on lysin. Similarly, many of the proteins produced by the accessory glands of male *Drosophila*, which are transferred to females along with sperm during mating, undergo rapid sequence evolution. pag454

However, more than 10 percent of noncoding DNA is highly conserved between long-diverged species, such as humans and mice, suggesting a function maintained by purifying **selection** (Shabalina et al. 2001). Moreover, many noncoding regions, including introns, are transcribed into RNA sequences such as "lincRNAs" that are usually about 22 bp long. pag456

TEs tend to occur in regions between genes and in introns, probably because those that occur within coding regions often cause deleterious mutations and are eliminated by purifying **selection**. pag460

The paralogs are therefore no longer redundant, so both are preserved by natural **selection**, and may later undergo further functional specialization and evolutionary change. pag470

The great morphological complexity and diversity that we see in multicellular organisms is produced by developmental processes that have evolved in response to natural **selection**. pag473

These examples suggest several questions: What are the selective pressures that favor such a novel evolutionary trajectory? How could such a profound alteration of early development evolve so many times? And, perhaps most challenging, what genetic and developmental processes are involved in these evolutionary alterations? It is likely that **selection** for rapid development promotes the evolution of direct development. pag474

The field of evolutionary developmental biology, or EDB (often called "evo-devo"), seeks to understand the mechanisms by which development has evolved, both in terms of developmental processes (for example, what novel cell or tissue interactions are responsible for novel morphologies in certain taxa) and in terms of evolutionary processes (for example, what **selection** pressures promoted the evolution of these novel morphologies). pag474

Natural **selection** acts on phenotypes produced by development, but ultimately we want to understand how the modes by which development produces those phenotypes affect evolutionary potentials and trajectories. pag474

Traditional neo-Darwinian theory explains how natural **selection**, genetic drift, and gene flow, acting on the raw material of genetic variation, have produced the astonishing variety of organisms. pag490

Therefore, it appears that within each species, the entire enhancer has evolved in a concerted fashion to maintain its function. If the fixation (by **selection** or drift) of a nucleotide substitution in one position in the enhancer caused a minor alteration in stripe expression, that change might provide **selection** pressure for a compensatory substitution elsewhere in the enhancer in order to maintain the stripe expression. pag496

During these brief periods (of hundreds of thousands of years), the rate of change per generation is roughly the same as rates measured for characteristics that have been altered by novel **selection** pressures within the last few centuries (see Chapter 4) pag502

Selection, rather than genetic drift, may well be the cause of these rapid changes. pag502

Thus rates of evolution of quantitative traits, determined from the fossil record or from comparisons among living species, are consistent with evolution by natural selection and/or genetic drift, with information on mutation and genetic variation, and with observations on short-term rates of evolution that have been inferred from responses to laboratory selection (see Chapter 13), responses of natural populations to environmental change (see Chapter 13), and divergence among populations and among closely related species (see Chapter 15).pag502

Mayr's model of speciation requires that genetic drift (the founder effect) move a small population from the vicinity of one adaptive peak across an adaptive valley (Le. Oppos11, g the action of natural selection) to the slope of a different adaptive peak. As "ve sa"" ill Chapter '16, this is unlikely to occur unless selection is very weak or unless the population is so small that it is at risk of losing genetic variation altogether.pag503

Moreover, geographic variation within species, as well as the rapid adaptive evolution of populations exposed to new selection pressures; show that speciation is not required for adaptive phenotypic change (Levinton 2001).pag503

Stabilizing selection for a constant optimum phenotype. It may seem unlikely that natural selection could favor the same character state over millions of years, during which both physical and biotic environmental factors would almost inevitably change. pag504

Thus it is likely that the evolution of one mimetic pattern from another "vas initiated by a mutation of large enough effect to provide substantial resemblance to a different model species, followed by selection of alleles with smaller effects that "fine-tuned" the phenotype (Figure 21.6). Genetic analysis of the color patterns of *P. dardmllis* supports this hypothesis (Ford 197]).pag507

Ne may postulate that such conservatism has been caused by consistent stabilizing selection or by inadequate variation for selection to act on.pag508

By occupying one niche (e.g., host plant, climatic zone) rather than another, a species subjects itself to some selective pressures and screens off others; it may even be said to "construct" or determine its own niche, and therefore many aspects of its potential evolutionary future (Lewontin 2000; Odling-Smee et al. 2003). Niche conservatism implies consistent selection. pag508

Second, and more generally, if there is gene exchange among individuals that inhabit the ancestral niche (e.g., microhabitat) and those that inhabit a novel niche, and if there is a fitness trade-off between character states that improve fitness in the two environments, then selection will generally favor the ancestral character state (i.e., stabilizing selection will prevail) simply because most of the population occupies the ancestral environment (Holt 1996).Pag508-509

In organisms that lack habitat selection behavior, selection for ancestral character states reduces fitness in the novel environment, so that a population in that environment may be a "sink" population, incapable of persistence. Moreover, in animals that are capable of habitat selection, the differential in fitness between individuals that occupy ancestral versus novel environments favors choice of the ancesh" al environment. Both factors will result in the habitat tracking described above.pag509

is buffering, or CANALIZATION, in some cases can evolve by natural selection for a consistent phenotype, although such evolution may occur only under restricted conditions (Wagner et al. 1997).pag509

How do major changes in characters evolve, and how do new features originate? These questions have two distinct meanings. First, we can ask what the genetic and developmental bases of such changes are—the subject of Chapter 20. Second, we can ask what role natural selection plays in their evolution. For instance, we may well ask whether each step, from the slightest initial alteration of a feature to the full complexity of form displayed by later descendants, could have been guided by selection, page 510

The first person to recognize this potential problem was Darwin himself, in *The Origin of Species*: "That the eye, with all its inimitable contrivances for adjusting the focus to different distances, for admitting different amounts of light, and for the correction of spherical and chromatic aberration, could have been formed by natural selection seems, I freely confess, absurd in the highest possible degree." page 512

But he then proceeded to supply examples of animals' eyes as evidence that "if numerous gradations from a perfect and complex eye to one very imperfect and simple, each grade being useful to its possessor, can be shown to exist; if further, the eye does vary ever so slightly, and the variations be inherited, which is certainly the case; and if any variation or modification in the organ be ever useful to an animal under changing conditions of life, then the difficulty of believing that a perfect and complex eye could be formed by natural selection, though insuperable by our imagination, can hardly be considered real." page 512

This nonrandomness strongly suggests that the trend was caused by natural selection rather than genetic drift. page 515

These trends can be attributed to individual selection. A good example of a trend due to species selection is the increase in the ratio of nonplanktonic to planktonic species in several clades of Cenozoic gastropods (Figure 21.16). page 515

On the other hand, selection might favor PARCELLATION of a highly integrated network of characters into different modules, each of a few functionally related characters, and each able to evolve independently of other modules (Figure 21.18). Wagner and Altenberg (1996) suggest that metazoan animals have tended to evolve toward greater modularity hence greater evolvability—but this idea has not yet been tested. page 517

And even though natural selection within populations increases mean fitness (specifically, relative fitness), fitness values are always context-dependent. page 518

Likewise, although we might suppose that species longevity would be a measure of increased adaptedness, this need not be so. The consequence of natural selection is the adaptation of a population to the currently prevailing environment, not to future environments, so selection does not imbue a species with insurance against environmental change. page 518

The word progress usually implies movement toward a goal, as well as improvement or betterment. The processes of evolution, such as mutation and natural selection, cannot imbue evolution with a goal. page 519

The Pope's position was close to the argument generally known as theistic evolution, which holds that God established natural laws (such as natural selection) and then let the universe run on its own, without further supernatural intervention. page 524

Genesis was billions of years long.) Other creationists allow that mutation and natural selection can occur, and even that very similar species can arise from a common ancestor. page 525

Thus science, as a social process, is tentative; it questions belief and authority; it continuously tests its views against evidence. Scientific claims, in fact, are the outcome of a process of natural selection, for ideas (and scientists) compete with one another, so that the body of ideas in a scientific field grows in explanatory content and power (Hull 1998). pag526

But this history of evolutionary change is explained by evolutionary theory, the body of statements (about mutation, selection, genetic drift, developmental constraints, and so forth) that together account for the various changes that organisms have undergone, pag527

Of course, Darwin made this particular theological argument passe by providing a natural mechanism of design: natural selection. 'Moreover, Darwin and subsequent evolutionary biologists have described innumerable examples of biological phenomena that are hard to reconcile with beneficent intelligent design. pag530

Just as Voltaire showed (in Candide) that cruelties and disasters make a mockery of the idea that this is "the best of all possible worlds," biology has shown that organisms have imperfections and anomalies that can be explained only by the contingencies of history, and characteristics that make sense only if natural selection has produced them. pag530

Instead, adaptation is based on a combination of a random process (mutation) that cannot be trusted to produce the needed variation (and often does not) and a process that is the very epitome of waste and seeming cruelty (natural selection, which requires that great numbers of organisms fail to survive or reproduce). It would be hard to imagine a crueller instance of natural selection than sickle-cell anemia, "whereby part of the human population is protected against malaria at the expense of hundreds of thousands of other people, who are condemned to die because they are homozygous for a gene that happens to be worse for the malarial parasite than for heterozygous carriers (see Chapter 12). Indeed, Darwin's theory of the cause of evolution was, widely rejected just because people found it so distasteful, even horrifying, to contemplate . pag530

The life histories of parasites, whether parasitic wasp or human immunodeficiency virus, ill fit our concept of an intelligent, kindly designer, but are easily explained by natural selection (see Chapter 18). pag531

No one has yet demonstrated a characteristic of any species that serves only to benefit 21 different species, or only to enhance the so-called balance of nature-for, as Darwin saw, "such could not have been produced through natural selection." pag531

Are they predicted by intelligent design theory? Likewise, no theory of design can predict or explain features that we ascribe to sexual selection, such as males that remove the sperm of other males from the female's reproductive tract, or chemicals that enhance a male's reproductive success but shorten his mate's life span. Nor can we rationalize why a beneficent designer would shape the many other selfish behaviors that natural selection explains, such as cannibalism, siblicide, and infanticide. pag531

We know also that most natural populations carry a great deal of genetic variation that can yield rapid responses to artificial or natural selection (see Chapters 9,11, and 12). We have seen allele frequency differences among recently established populations that can be confidently attributed to genetic drift (see Chapter 10). Evolutionary biologists have documented literally hundreds of examples of natural selection acting on genetic and phenotypic variation (see Chapters 12 and 13). pag531

They have described hundreds of cases in which populations have responded to directional **selection** and have adapted to new environmental factors, ranging from the evolution of resistance to insecticides, herbicides, and antibiotics to the evolution of different diets (see Chapter 13). pag531-532

But no scientific observations have ever cast serious doubt on the reality of the basic mechanisms of evolution, such as natural **selection**, nor on the reality of the basic historical patterns, such as transformation of characters and the origin of all known forms of life from common ancestors. pag532

Order in nature, such as the structure of crystals, arises from natural causes and is not evidence of intelligent design. The order displayed by the correspondence between organisms' structures and their functions is the consequence of natural **selection** acting on genetic variation, as has been observed in many experimental and natural populations (see Chapters 13 and 14). Darwin's realization that the combination of a random process (the origin of genetic variation) and a nonrandom process (natural **selection**) can account for adaptations provided a natural explanation for the apparent design and purpose in the living world and made a supernatural account unnecessary and obsolete. pag533

Most mutations are indeed harmful and are purged from populations by natural **selection**. Some, however, are "beneficial" as shown in many experiments (see Chapters 8 and 13). Complex adaptations usually are based not on single mutations, but on combinations of mutations that jointly or successively increase in frequency due to natural **selection**. pag533

"New" characters, in most cases, are modifications of pre-existing characters, which are altered in size, shape, developmental timing, or organization (see Chapters 3, 4, and 21). This is true at the molecular level as well (see Chapter 19). Natural **selection** "creates" small modifications by increasing the frequencies of alleles at several or many loci so that combinations of alleles, initially improbable because of their rarity, become probable. Observations and experiments on both laboratory and natural populations have demonstrated the efficacy of natural **selection**. pag533

This is true, but natural **selection** is a deterministic, not a random, process. The random processes of evolution—mutation and genetic drift—do not result in the evolution of complexity, as far as we know. Indeed, when natural **selection** is relaxed, complex structures, such as the eyes of cave-dwelling animals, slowly degenerate, due in part to fixation of neutral mutations by genetic drift. pag534

Another example is the classic study of industrial melanism in the peppered moth by H. B. D. Kettlewell, who is accused of having obtained spurious evidence for natural **selection** by predatory birds by pinning moths to unnatural resting sites (tree trunks). pag535

Likewise, both natural **selection** and rapid evolutionary changes have been demonstrated in so many species that these principles would stand firmly even if the peppered moth story were completely false. (Kettlewell's evidence that birds differentially attack dark and light peppered moths was based on a variety of experiments, and other investigators have added to this evidence since then. pag535

Of course, the creationists who cite these examples of supposed flaws and frauds realize that the strength of evolutionary biology does not rest on these studies. After all, most creationists accept natural **selection** and "microevolution" such as changes in moth coloration. Rather, they attempt to persuade their readers to doubt the truthfulness of evolutionary scientists and to justify their disbelief in evolution. pag535

In fact, none of the evolutionary biologists who hold these positions deny the central proposition that adaptive characteristics evolve by the action of natural **selection** on random mutations. All these debates arise from differing opinions on the relative frequency and importance of factors known to influence evolution: large-effect versus small-effect mutations, genetic drift versus natural **selection**, individual **selection** versus species **selection**, adaptation versus constraint, and so forth (see Chapters 11, 20, and 21). These arguments about the relative importance of different processes do not at all undermine the strength of the evidence for the historical fact of evolution—i.e., descent with modification from common ancestors. On this point, there is no disagreement among evolutionary biologist. pag536

Furthermore, evolutionary biologists have developed methods for determining where natural **selection** has acted on a DNA sequences (see Chapters 12 and 19), a first step in understanding how the gene and its protein product malfunction. pag538

EVO-DEVO

The field of evolutionary developmental biology, or EDB (often called "**evo-devo**"), seeks to understand the mechanisms by which development has evolved, both in terms of developmental processes (for example, what novel cell or tissue interactions are responsible for novel morphologies in certain taxa) and in terms of evolutionary processes (for example, what selection pressures promoted the evolution of these novel morphologies). Pág 474

DESENVOLVIMENTO

These chapters provide the basis for understanding the evolution of life histories, genetic systems, ecological interactions, genes and genotypes, and **development**. I then return to macroevolution, approached as a synthesis of evolutionary process and pattern. Preface xii

The ever-quickenning pace of research and the variety of novel techniques, especially in molecular, genomic, and **developmental** evolutionary biology, make it increasingly difficult for anyone person to keep abreast of and be capable of evaluating research across the entire field of evolutionary studies, Preface xii

So I'm very grateful to Scott Edwards (Harvard University) and John True (State University of New York at Stony Brook) for joining me in this venue, and contributing chapters on evolution of genes and genomes (Chapter 19) and on evolutionary **developmental** biology (Chapter 20), respectively. They have brought to these subjects knowledge and critical understanding well beyond any effort I might have made.

Preface

xiii

The **development**, or ONTOGENY, of an individual organism is not considered evolution: individual organisms do not evolve. Groups of organisms, which we may call populations, undergo descent with modification. Populations may become subdivided, so that several populations are derived from a common ancestral population. If different changes transpire in the several populations, the populations diverge. The changes in populations that are considered evolutionary are those

Pág2

Molecular biology has provided tools for studying a vast number of evolutionary topics, such as mutation genetic variation, species differences, **development**, and the phylogenetic history of life. Pág 11

EVOLUTIONARY **DEVELOPMENTAL** BIOLOGY is an exciting field devoted to understanding how **developmental** processes both evolve and constrain evolution. It is closely tied to **developmental** biology, one of the most rapidly moving fields of biology today. EVOLUTIONARY GENOMICS, concerned with variation and evolution in multiple genes or even entire genomes, is being born. Pág 11

Embryological similarities of Homologous characters include some features that appear during **development**, but would be unnecessary if the **development** of an organism were not a modification of its ancestors' ontogeny. Pág 48

Homologous characters generally have similar genetic and **developmental** underpinnings; although these foundations sometimes have undergone substantial divergence among species (see Chapter 20). Pág 49

For example, the structural correspondence between the hind limbs of birds and crocodiles is more evident in the embryo than in the adult because many of the bird's bones become fused as **development** proceeds. Pág 51

The convergent evolution (convergence), superficially similar features are formed by different **developmental** pathways (Lauder 1981). The eyes of vertebrates and cephalopod mollusc (such as squids and octopuses) are an example of convergent evolution (Figure 3.5). Pág 51

Parallel evolution (parallelism), on the other hand, is thought to involve similar **developmental** modifications that evolved independently (often in closely related organisms, because they are likely to have similar **developmental** mechanisms to begin with). Pág 51

The genetic and **developmental** basis of this evolutionary transformation is the same in both groups and occurs in some other crustacean lineages as well. Pág 52

For example, one genus has direct **development** without a tadpole stage, and another gives birth to live young. Pág 54

One of Darwin's most enthusiastic supporters the German biologist Ernst Haeckel, reinterpreted such patterns to mean that "ontogeny recapitulates phylogeny"; that is, that the **development** of the individual organism repeats the evolutionary history of the adult forms of its ancestors. Pág 56

Until a few decades ago, classification and phylogenetic studies relied chiefly on analyses of morphological characters, including their change during embryonic **development**. In the course of their work, systematic and comparative morphologists documented many common patterns of evolution. Today, one of the most active research areas concerns the genetic and **developmental** basis of such evolutionary changes (see Chapter 20). Some of these patterns are individualization, heterochromy, allometry, heterotopy, and changes in complexity (Rensch 1959; Müller 1990; Raff 1996; Wagner 1996). Pág 56

The bodies of many organisms consist of MODULES distinct units that have distinct genetic specifications, **developmental** patterns, locations, and interactions 'with other modules (Raff 1996). Some modules (e.g., leaves of many plants, teeth of many fishes) lack distinct individual identities

and may be considered aspects of a single character. Pág 56

HETEROCHRONY. Heterochromy (Gould 1977; McKinney and McNamara 1991) is broadly defined as an evolutionary change in the timing or rate of **developmental** events. Many phenotypic changes appear to be based on such changes in timing, but several other **developmental** mechanisms can produce similar changes (Raff 1996). Pág 56

Relatively global heterochronic changes, affecting many characters simultaneously, are illustrated by cases in which the time of **development** of most somatic features (those other than the gonads and related reproductive structures) is altered relative to the time of maturation of the gonads (i.e., initiation of reproduction). Pág 57

In contrast, evolution of delayed maturity may result in reproduction at a larger size, associated with the extended **development** of "hyper-adult" features. Such an evolutionary change is called peramorphosis. The large size of the human brain, for example, has been ascribed to humans' extended period of growth (McNamara 1997). Pág 57

Both paedomorphosis and peramorphosis can result from evolutionary changes in either the rate of development or the duration of **development** due to a change in α or ω (Figure 3.16). Peramorphosis can result if the duration of **development** is extended (a change from ω to $\omega + \Delta\omega$; Figure 3.16B). Pág 58

For example, the gigantic antlers of the extinct Irish elk (*Megaceros giganteus*), which are larger in relation to body mass than those of any other deer, are a peramorphic feature associated with the animal's extended **development** to a larger body size (Figure 3.17). Pág 58

In most vertebrates, the notochord degenerates after its expression in early embryonic **development**, but it is retained in the embryo because it induces the **development** of the central nervous system. Rupert Riedl (1978) suggested that such a character carries a BUIWENj meaning a suite of other features that depend on it for their **development** or proper function. Pág 83

Multicellularity is a prerequisite for large size and for the **development** of elaborate organ systems. The evolution of tissues and organs required the evolution of gene regulatory mechanisms: ways of controlling the expression of different genes in different cells. Pág 96

Mutations in any of the many different genes that contribute to the normal **development** of some characteristics can also result in similar phenotypes Pág 169

Among the most fascinating mutations are those in the "master control genes" that regulate the expression of other genes in **developmental** pathways. Pág 175

These genes derive their name from homeotic mutations in *Drosophila*, which redirect the **development** of one body segment into that of another. Mutations in the Antennapedia gene complex, for example, cause legs to develop in place of antennae (Figure 8.14.). Another master control gene, Pax6, switches on about 2500 other genes required for eye **development** in mammals, insects, and many other animals (Celis and Ikeo 1999). Mutations in this gene cause malformation or loss of eyes. Pág 175

It cannot be stressed too strongly that even the most drastic mutations cause alterations of one or more pre-existing traits. Mutations with phenotypic effects alter **developmental** processes, but they cannot alter **developmental** foundations that do not exist. "We may conceive of winged horses and angels, but no mutant horses or humans, will ever sprout wings from their shoulders, for the

developmental foundations for such wings are lacking. Pág 178

Mutations occur at random. It is extremely important to understand what this statement does and does not mean. It does not mean that all conceivable mutations are equally likely to occur because, as we have noted, the **developmental** foundations for some imaginable transformations do not exist. Pág 178

Phenotype refers to a characteristic in an individual organism, or in a group of individuals that are alike in this respect. Phenotypic variation is largely the result of genetic differences among individuals, but can also be the result of the direct effects of environmental variation on **development**. Figure 9.1 shows instances of both types of phenotypic variation. Pág 190

Quantitative characters often vary both because of genes and because of nongenetic environmental factors, and by "**developmental** noise." The latter term refers to ineradicable variations in **developmental** processes that produce variation among individuals, as well as variation within individuals (e.g., asymmetry between the two sides of the same animal, which obviously has shared both the same genotype and the same environment). Pag 207

Often simplifying, we can imagine that each genotype in a population has an average phenotypic value (of, say, body length), but that individuals with that genotype vary in their phenotypes due to environmental effects or **developmental** noise. Pág 209

Thus the **developmental** process is adaptive: it reacts to the environment by producing different phenotypes, suitable for different conditions, at different stages. Pag 248

Modern biology views the **development**, physiology, and behavior of organisms as the results of purely mechanical processes, resulting from interactions between programmed instructions and environmental conditions or triggers. Pag 250-251

Five toes may probably not an option for birds because of genetic **developmental** constraint. Thus, if we ask why a species has one feature rather than another the answer may be adaptation or it may be phylogenetic history. Pág 261

A genotype is likely to have different phenotypic expressions as a result of environmental influences on **development**, so the fitness of a genotype is the mean of the fitness of its several phenotypes, weighted by their frequencies. Pág 271

The phenotypic variance (V_p) in a phenotypic trait is the sum of the variance due to differences among genotypes (the genetic variance, V_G) and the variance due to direct effects of the environment and **developmental** noise (the environmental variance, V_E). Pág 299

The number of loci that contribute to variation in a character may be less than the number that actually contribute to its **development**. However, only variable loci can be detected- and detecting those that have small phenotypic effects is not easy. Pág 301

Thus the lack of correspondence between genome size and phenotypic complexity in eukaryotes was dubbed the C-value paradox, as researchers discovered that not all the DNA in a genome carries information that is used during the **development** and functioning of an organism. Genomes contain a great deal of non informative, highly repetitive DNA that varies greatly in amount among species. pag 459

The great morphological complexity and diversity that we see in multicellular organisms is

produced by **developmental** processes that have evolved in response to natural selection. Pág 473

But how do these **developmental** processes evolve? Direct **development** in animals illustrates many of the issues involved in addressing this question. Pág 473

Direct **DEVELOPMENT** occurs when embryos develop directly into adultlike forms instead of progressing through a larval stage (**INDIRECT DEVELOPMENT**). This striking divergence in **developmental** mode has evolved independently in many animal lineages, including sea urchins, ascidians, frogs, and salamanders (Figure 20.1). Pág 473

The evolutionary forces and genetic mechanisms promoting such radical, and sometimes rapid, changes in **development** and life history have mystified biologists for over a century. Comparisons of embryogenesis and larval morphogenesis, especially among marine invertebrates, are central topics in both classical **developmental** biology and modern evolutionary **developmental** biology. Pág 473

These examples suggest several questions: What are the selective pressures that favor such a novel evolutionary trajectory? How could such a profound alteration of early **development** evolve so many times? And, perhaps most challenging, what genetic and **developmental** processes are involved in these evolutionary alterations? It is likely that selection for rapid **development** promotes the evolution of direct **development**. But even though some of the genes that underlie these alternative **developmental** trajectories are beginning to be uncovered, the **developmental** mechanisms involved—and more importantly, the reasons why these mechanisms are apparently more flexible in some groups of organisms than others—are still mysteries. Pág 474

The field of evolutionary **developmental** biology, or EDB (often called "evo-devo"), seeks to understand the mechanisms by which **development** has evolved, both in terms of **developmental** processes (for example, what novel cell or tissue interactions are responsible for novel morphologies in certain taxa) and in terms of evolutionary processes (for example, what selection pressures promoted the evolution of these novel morphologies). Pág 474

Two of the main questions or themes that concern evolutionary **developmental** biologists are, first, what role has developmental evolution played in the history of life on Earth? And second, do the **developmental** all trajectories that produce phenotypes bias the production of variation or constrain trajectories of evolutionary change? Natural selection acts on phenotypes produced by **development**, but ultimately we want to understand how the modes by which development produces those phenotypes affect evolutionary potentials and trajectories. Pág 474

Biologists dating back to Geoffroy Saint-Hilaire (1772-1844), Karl Ernst von Baer (1792-1876), and Darwin himself were fascinated by the patterns of similarity and divergence in **development** among species. However, until quite recently, the fields of evolutionary biology and **developmental** biology proceeded along mostly separate paths, with seemingly distinct research programs and methodologies (Gould 1977; Depew and Weber 1994; Wilkins 2002). Pág 474

A mutation in another Hox gene, Antp, causes the misexpression of Antp protein in the cells that normally give rise to the antennae, resulting in the replacement of antennae with legs (see Figure 8.14). Antp is normally expressed only in the second thoracic segment (T2), where it controls the **development** of T2-specific body structures, including legs. Pág 475

Perhaps the most important type of data sought in **developmental** genetics and evolutionary **developmental** biology are the expression patterns of specific genes, and the proteins they encode,

during **development**. These patterns are SPATIO-TEMPORAL with a spatial component (referring to specific cells, tissues, segments, or structures) and a temporal component (referring to specific **developmental** stages). Gene expression patterns can be visualized by three methods, each requiring different tools and hence currently usable for certain species, but not others. Pág 476

We can hardly overstate the importance of the Hox gene discoveries for our understanding of how animal diversity evolved. For the first time, a common **developmental** genetic framework unified the ontogeny of all metazoans; before then, few biologists imagined that vertebrates and invertebrates would share such fundamental developmental genetic underpinnings. Pág 478

Patterns of gene expression (see Box A) are now frequently used together with morphological comparative embryological and phylogenetic data to infer the **developmental** genetic origins and histories of morphological characters. Pág 478

However, **developmental** genetic data, such as phenotypic information from mutants or individuals that have been genetically manipulated to under- or over-express a gene or protein of interest, are required to definitively demonstrate that a particular gene is required for the **development** of a tissue or structure. Pág 478

We would therefore expect genetically and **developmentally** similar characters to be homologous and phylogenetically homologous structures to have similar genetic and **developmental** bases. Pág 479

the same **developmental** genetic machinery in the ontogeny, but they are clearly not historically homologous within a species. Pág 479

The second molar of the lynx is not phylogenetically homologous to the second molar of other carnivores; it is homoplasious. However, from a **developmental** genetic standpoint, it may represent the "same" tooth, because the mechanisms producing it may be very similar or identical to those producing the structure in other carnivores (Raff 1996). Pág 480

Another conflict between phylogenetic and biological homology is that phylogenetically homologous traits often have different **developmental** and genetic foundations. For example, digits differentiate sequentially from back (postaxial) to front (preaxial) in all tetrapods except salamanders, whose digits differentiate in the reverse order. Pág 480

Conversely, **developmentally** and functionally similar structures in different taxa may not be phylogenetically homologous. In perhaps the best example, animal eyes evolved independently in very diverse taxa, but in all of these taxa, a highly conserved transcription factor, Pax6, controls eye **development**. We will examine these examples in more detail later in this chapter. Pág 480

The concept of biological homology suggests that a feature may be homologous among species at one level of organization (e.g., phenotypic), but not at another level (e.g., genetic or **developmental**). Pág 480

The genes that regulate morphogenesis function in hierarchies or networks termed **developmental** pathways or **developmental** circuits (Box B). These genes encode signaling proteins that relay molecular signals between cells, transcription factors, which respond to signaling pathways by increasing (up-regulating) or decreasing (down-regulating) transcription at target genes, and structural genes, which encode the proteins that actually do the work of **development** and physiology (e.g., enzymes and cytoskeletal proteins). Pág 480

Hox genes are examples of homeotic selector genes, which control cascades of gene expression (i.e. transcription) during the patterning and **development** of particular tissues, organs, or regions of the body. pág 481

Most cell Signaling pathways are used multiple times during **development**, suggesting that morphogenetic novelty may often evolve by re-deploying these pathways in different tissues and at different **developmental** stages.

pág 481

Cell signaling pathways and transcription factors are linked into **developmental** pathways (also called **developmental** circuits). Such circuits are involved, for example, in patterning the Drosophila wing, which takes place in the wing imaginal disc (Figure 2). The end result of **developmental** circuit's fire patterns of gene expression that guides the **development** of an adult structure such as the Drosophila wing. pág 481-482

Normal wing **development** requires this pattern of expression of vestigial. Pág 482

Several **developmental** pathways that control the formation of major organs or appendages seem to be largely controlled by highly conserved transcription factors (reviewed in Carroll et al. 2001). The Distalless gene, for example, encodes a transcription factor that governs the **development** of body outgrowths that differentiate into very diverse structures in different phyla (Figure 20.8) (Panganiban et al. 1997). Pág 483

Mutations in the mouse homologue of eyeless, which is called Pax6, also cause reduction of the eyes. Ptx6^{eyeless} activates the transcription of a hierarchy of regulatory proteins that control the **development** and differentiation of the eye. Pág 483

These DNA sequences bind particular sets of transcription factors in specific cells or at specific **developmental** stages. For example, several genes expressed in the developing Drosophila wing are regulated by the transcription factors Scalloped and Vestigial, which activate genes required for wing **development** (Guss et al. 2001). The noncoding DNA (introns) of these genes contains one to several binding sites for Scalloped and Vestigial; each 8 to 9 nucleotides long (see Figure 3 in Box B). Pág 484

A particular gene often has a number of different enhancers. This regulatory modularity is thought to enable evolutionary changes in the **development** of specific tissues and body structures. Pág 484

The degree to which the **development** of different body structures is independent is referred to as MODULARITY, and the individual structures or units can be thought of as MODULES. How is modularity achieved by **developmental** pathways? Insights about gene regulation, of the kind described above, will be the key to answering this question.

Pág 486

Many genes and signaling pathways have multiple **developmental** roles. For example, the transcription factor Distalless is required to organize the **development** of legs, wings, and antennae of all insects, but in some butterflies, it is also expressed later in specific positions on the developing wing, where it is involved in setting up the color patterns known as "eyespot" (see Figure 20.16A) Pág 486

Developmental biologists have used the terms recruitment (Wilkins 2002) and co-option (reviewed by True and Carroll 2002) to refer to the evolution of novel functions for pre-existing genes and **developmental** pathways. Pág 486

Co-option of single genes for new functions may be common. The members of many gene families have diversified into different **developmental** and physiological roles (Chapter 19). Pá 486

Alternatively, a **developmental** pattern originally expressed in one region of the embryo may become expressed in a different region, leading to a duplication of that structure in the new region (Figure 20.15B). Pá 488

Much of morphological evolution has entailed HETEROCHRONY--evolutionary changes in the timing of **development** (see Chapter 3). The **developmental** genetic basis of heterochrony has been little studied in model organisms, but genetic approaches have been used to study neoteny in salamanders (Voss and Shaffer 2000; Voss et al. 2003). Pá 488

The threshold size for hom **development** has diverged from the ancestral condition in both introduced populations, even though variation of this magnitude was not evident in the founding populations (Figure 20.18). Pá 490

Thus genetic constraints, such as paucity of variation and genetic correlation, are closely related to **developmental** constraints. Pá 491

Developmental constraints. Maynard Smith et al. (1985) defined a **developmental** constraint as "a bias on the production of various phenotypes caused by the structure, character, composition, or dynamics of the **developmental** system." The two most common phenomena attributed to **developmental** constraint are absence or paucity of variation, including the absence of morphogenetic capacity (i.e., lack of cells, proteins, or genes required for the **development** of a structure), and strong correlations among characters, which may result from interaction between tissues during development or the involvement of the same genes or **developmental** pathways in multiple morphogenetic processes. Pá 491

Developmental constraints can be revealed by embryological and genetic manipulations in the laboratory. In a classic experiment, Pere Alberch and Emily Gale (1985) used the mitosis-inhibiting chemical colchicine to inhibit digit **development** in the limb buds of salamanders (*Ambystoma*) and frogs (*Xenopus*) (Figure 20.19). Pá 491

Although the digit number variation in this study was produced artificially, the results suggest that naturally occurring variation in **developmental** systems may be constrained by intrinsic, species-specific **developmental** programs. Although in practice it is very difficult to rule out selective constraints, **developmental** or genetic constraints might explain some evolutionary patterns. Pá 491-492

The **developmental** system may impose a bias such that certain kinds of variation are produced and not others, enabling particular evolutionary trajectories to be taken. Pá 492

One of several possible explanations for this pattern is canalization: the evolution of modifications of the **developmental** system such that the most highly advantageous phenotype is more reliably produced (Waddington 1942; see Chapter 13). Pá 493

Similarities in embryological stages among higher taxa. Such similarities might result from the need to conserve early **developmental** processes so as not to disturb the later events that depend on them (Riedl 1978). Pá 493

The few QTL studies that implicate specific genes suggest that **developmental** regulatory loci are commonly involved in morphological differences between species, and that these loci can include major **developmental** regulatory genes such as *Lbx*, as we saw above. Thus the many crucial **developmental** functions of these genes do not preclude their involvement in short-term evolutionary change. Pág 493

Developmental genetic data from *D. melanogaster* indicate that *nan*'s role is to produce sexual dimorphism in specific abdominal segments by integrating information about anterior-posterior position in the abdomen, which is conferred by expression of the Hox gene *Abdominal B* (*AbdB*), and about sexual identity, which is determined by expression of the transcription factor *doublesex* (*dsx*). Pág 493

As the field of evolutionary **developmental** biology unfolds, one of its most important and fascinating endeavors will be to elucidate the **developmental** genetic and evolutionary mechanisms involved in the appearance of traits unique to humans, such as our large brain size, craniofacial morphology, vertebral, limb, and digit innovations, reduced hair cover, and, of course, our complex behavioral and cultural traits (reviewed by Carroll) Pág 496

Comparative genomic data indicate that many or most of the DNA-level changes responsible for altered gene expression in the regulation of **developmental** and *Sh1.1ct1.lraJ* proteins that we share with our primate and mammalian relatives. Pág 497

Many of the initial clues to the genetic bases of human traits come from studying human variation, including genetic disorders, and **development** in mammalian model species, such as the mouse. Pág 497

Contemporary macroevolutionary studies draw on the fossil record, on phylogenetic patterns of evolutionary change, on evolutionary **developmental** biology, and on our understanding of genetic and ecological processes. Pág 512

Internal genetic or **developmental** constraints. Eldredge and Gould (1972) proposed that stasis is caused by internal genetic or **developmental** constraints, which would be manifested by lack of genetic variation or by genetic correlations too strong to permit characters to evolve independently to new optima. Pág 504

Thus mutations that reduce the function of this master gene interfere with a complex **developmental** pathway, and **development** is routed into a "default" pathway that produces the features of the second thoracic segment (including wings). The whole system can be shut down in a single step by turning a master switch, but that does not mean that the system came into existence by a single step. Pág 507

Development appears ordinarily to be "buffered" against phenotypic expression of this genetic variation. This buffering, or canalization, in some cases can evolve by natural selection for a consistent phenotype, although such evolution may occur only under restricted conditions (Wagner et al. 1997). Pág 509

Whatever the cause maybe, it is clear that some **developmental** pathways produce highly buffered, almost invariant characteristics. Pág 509

Development can therefore impose constraints on the rate or direction of evolution of a character. The consequences of such constraints are made clear when an adaptive function is performed not by the structure we might expect, but by another structure that has been modified instead. The giant

panda, for example, has six apparent fingers, evidently useful for manipulating the bamboo on which it feeds. The outermost "finger" (or "thumb"), however, is not a true digit, but a sesamoid bone that develops from cartilage (Figure 21.8). Pág 509

How do major changes in characters evolve, and how do new features originate? These questions have two distinct meanings. First, we can ask what the genetic and developmental bases of such changes are—the subject of Chapter 20. Second, we can ask what role natural selection plays in their evolution. Pág 510

The boundaries that enforce passive trends may be due to either functional or developmental genetic constraints Pág 515

The thoracic segments of insects, for example, have acquired individual developmental identities and are unlikely to regain the homogeneous condition postulated for ancestral arthropods Pág 515

Another possible reason for the loss of evolve ability is that the genetic and developmental bases of different characters might become more integrated over time (the opposite of parcellation; see Figure 21.18), leading to greater genetic correlations or to longer or more intricate developmental pathways. Pág 517

It has been proposed that early steps in a developmental pathway may become more phylogenetically conservative over evolutionary time because they carry a heavy "burden": later steps depend on them and could easily go awry if the earlier steps were altered (Riedl 1978; Wimsatt 1986). Pág 51

It is not known if developmental integration increases and prevents large phenotypic changes from evolving later, or if increasing numbers of species occupy major resources, so that there is less room for ecological and morphological divergence of newly arisen species (Foote 1997). Pág 518

Some of them even seem to accept certain aspects of evolution, such as development of different species from common ancestors. However, they argue that many biological phenomena are too complicated to have arisen by natural processes and can only be explained by intelligent design (ID). Pág 525

But this history of evolutionary change is explained by evolutionary theory, the body of statements (about mutation, selection, genetic drift, developmental constraints, and so forth) that together account for the various changes that organisms have undergone, Pág 525

Homology of structures is often more evident in early developmental stages than in adult organisms, and contemporary developmental biology demonstrates that Hox genes and other developmental mechanisms are shared among animal phyla that diverged from common ancestors a billion or more years ago (see Chapter 20). Pág 529

Order and complexity can increase in local, open systems due to an influx of energy. This is evident in the development of individual organisms, in which biochemical reactions are powered by energy derived ultimately from the Sun. Pág 533

"New" characters, in most cases, are modifications of pre-existing characters, which are altered in size, shape, developmental timing, or organization (see Chapters 3, 4, and 21). Pág 533

But the various vertebrate embryos really do share profoundly important similarities (such as the notochord and pharyngeal pouches, often misnamed "gill slits") and really are more similar, overall, than the animals are later in **development**. Pág 535

GENE HOX

Michael Averoff and Nipam Patel (1997) studied differences in the expression of two "master" regulatory genes (**Hox genes**, which will be discussed in great detail in Chapter 21). Pág 51

Regulatory genes that govern the differentiation of body parts (such as the **Hox genes**; see Chapter 20) may have undergone major evolutionary changes at this time. Pág 98

The **Hox genes** are the best-known class of homeotic selector genes, which control the patterning of specific body structures, as we saw in Chapter 8. **Hox genes** control the identity of segments along the anterior-posterior body axis of all metazoans Pág 475

Mutations in the **Hox genes** often cause transformations of one type of segment into another. In *Drosophila*, for example, a mutation of the Ultrabithorax (Ubx) gene transforms the third thoracic segment (T3), which normally bears the tiny halteres (the *Drosophila* homologue of the hindwing of four-winged insects), into a second thoracic segment (T2), which bears wings (Figure 20.2). A mutation in another **Hox gene**, Antennapedia (Antp), causes the misexpression of Antp protein in the cells that normally give rise to the antennae, resulting in the replacement of antennae with legs (see Figure 8.14). Antp is normally expressed only in the second thoracic segment (T2), where it controls the development of T2-specific body structures, including legs. Pág 475

Termed the Antennapedia complex and the bithorax complex. The pioneering genetic work on the bithorax complex was done between the 1940s and the 1970s by E. B. Lewis and that on the Antennapedia complex in the 1970s and 1980s by Thomas Kaufman and his colleagues. Pág 475

They also discovered that the eight *Drosophila* **Hox genes** are members of a single gene family, and that the proteins they encode share a particular amino acid sequence that binds DNA, subsequently named the homeobox (in the gene) or the homeodomain (in the protein). Pág 475

This finding supported Lewis's idea, proposed in the 1960s, that the **Hox genes** regulate the transcription of other genes. Other researchers were stunned to discover that all other animal phyla also possess a set of **Hox genes**. These genes have homeodomain sequences similar to those of their homologues in *Drosophila* and have the same gene order and orientation as in *Drosophila* (except that they form a single gene complex in most animals). Mammals have four **Hox gene** complexes (denoted Hoxa, Hoxb, Hoxc, and Hoxd) in different parts of the genome, and a total of 13 different **Hox genes** (as opposed to only 8 in *Drosophila*), although not all of the complexes have all 13 members (see Figure 20.5). Pág 475

Staining for **Hox** proteins or mRNA (see Box A) showed that the anterior-posterior expression of the **Hox genes** corresponds to their mutant phenotypes. Pág 475

Mapping the presence and absence of **Hox genes** on the metazoan phylogenetic tree shows their evolutionary history (Figure 20.5). Two **Hox genes** have been found in radially symmetrical Cnidaria (jellyfishes, corals), which are the sister group of the Bilateria. Several novel **Hox genes** arose in the lineage leading to all Bilateria, representing new Hox classes (as evidenced by their

homeodomain sequences) that presumably can define increasing degrees of anterior-posterior axis identity. Pág 477

We can hardly overstate the importance of the **Hox gene** discoveries for our understanding of how animal diversity evolved. For the first time, a common developmental genetic framework unified the ontogeny of all metazoans; before then, few biologists imagined that vertebrates and invertebrates would share such fundamental developmental genetic underpinnings. Pág 478

ESPECIAÇÃO

Speciation is the origin of two or more species from a single common ancestor. **Speciation** usually occurs by the genetic differentiation of geographically segregated populations. Because of the geographic segregation, interbreeding does not prevent incipient genetic differences from developing. Pág 11

The hypothesis that Eldredge and Gould introduced is that characters evolve primarily in concert with true **speciation**-that is, the branching of an ancestral species into two species (Figure 4.18C). They based their hypothesis on a model, known as "founder-effect **speciation**" or "peripatric **speciation**," proposed by Ernst Mayr in 1954, which we will consider in Chapter 16. Pág 86

This proposition is contradicted by considerable evidence from populations of living species (see Chapters 9 and 13), and Eldredge and Gould's hypothesis that evolutionary change requires **speciation** is not widely accepted. Furthermore Pág 86

Except for two species that colonized Maui from Hawaii, colonization has proceeded from older to younger islands and each island has been colonized only once. Within each island, the rate of **speciation** has been quite high. Pág 125

Within the last 50 years, global warming-almost certainly caused by humans burning fossil fuels-has noticeably altered the geographic distributions of many species (Parmesan et al. 1999; Root et al. 2003). On a scale of millions of years, extinction, adaptation, **speciation**, climate change, and geological change create the potential for entirely different assemblages of species. Pág 139-140

Thus the extent to which the equilibrium species number falls short of the maximal number of species that could coexist depends on how high the extinction rate is, relative to the **speciation** rate. Pág 142

In both plants and animals, taxa with high rates of origination (**speciation**) also have high rates of extinction (Nee et al. 1983; Stanley 1990). That is, they have high rates of turnover. Pág 144

Population dynamics. Species with low or fluctuating population sizes are especially susceptible to extinction. Some authors believe that **speciation** is also enhanced by small or fluctuating population sizes, although this hypothesis is controversial. Pág 145

Geographic range. Species with broad geographic ranges tend to have a lower risk of extinction because they are not extinguished by local environmental changes. They also have lower rates of **speciation** (Jablonski and Roy 2003), probably because they have a high capacity for dispersal. Pág 145

Distinguish between the rate of **speciation** in a higher taxon and its rate of diversification. What are the possible relationships between the present number of species in a taxon, its rate of **speciation**, and its rate of diversification? Pág 160

Then the rate of **speciation** would be greater in orchids than in irises, and the number of species of orchids would grow more rapidly. (The Orchidaceae, with about 19,500 species, is in fact the largest family of plants; the Iridaceae has a mere] 750 species.)
Pág 259

The average state of species overall "ould change because of this difference iJl the "birth rate" of n€\v species with one or another feature (**speciation** rate), analogously to a change in the proportions of different phenotypes within a population that differ in reproductive rate (Figure 11.16). Pág 259

In the orchid/ires example, there is species selection/or specialized pollination (i.e., specialized pollination causes a higher **speciation** rate). Because of the correlation between petiole structure and mode of pollination, there has also been selection 0/ (but not selection for) h-visted petioles. Pág 260

The increasing incidence of twisted petioles among these plant species is an effect of a fortuitous association with **speciation** rate. Pág 260

In fact, the polymorphism may have been maintained by selection for so long that **speciation** has occurred in the interim. In that case, both lineages of genes may have been inherited by two (or more) species, and some gene copies in each species may be genealogically more closely related to genes in the other species than to other genes in the same species. Pág 290

Thus rUlla\·vay sexual selection can £0110\." Different paths in different populations, so that poplllotiollS Illoy diverge in/lote choice oldd becollle reprodllctively isolated. Sexual selection is therefore a powerful potential cause of **speciation** (see Chapter 16).
Pág 335

In speciation lie the origin of diversity, and the study of **speciation** bridges microevolution and macroevolution. Pag .353

The most important consequence of **speciation** is that different species undergo independent divergence, maintaining separate identities, evolutionary tendencies, and fates (Wiley 1978). Some authors have also suggested that **speciation** may facilitate the evolution of ne\v morphological and other phenotypic characters-that is, that a characteristic that would not evolve in a single, unbranched lineage may be able to do so if the lineage branches. (This view, however, is not widely accepted.) Pág 354

Some steps toward **speciation** may occur fast enough for us to study directly, but the full history of the process is usually too prolonged for one generation, or even a few generations, of scientists to observe. Pág 354

Conversely, **speciation** is often too fast to be hilly documented LI1 the fossil record, and even an ideal fossil record could not document some of the genetic processes in **speciation** that are still inadequately wlderstood. Thus the study of **speciation** is based largely on inferences from living species. Pag 354

Probably no definition of "species" suffices for all the contexts in which a species-like concept is used. Jerry Coyne and Allen Orr (2004), the authors of a recent comprehensive book on **speciation**, note that species can be defined in a way that

Pág 354

This definition would presumably apply to both sexual and asexual organisms. According to this definition, **speciation** would occur whenever a population undergoes fixation of a genetic difference--even a single DNA base pair--that distinguishes it from related populations. The study of **speciation**, then, would be simply the study of divergence between populations. Pág 355

This generalization is called Haldane's rule, and it appears to be one of the most consistent generalizations that can be made about **speciation** (Coyne and Orr 1989b).

Pág 362-363

Any such character difference may have evolved partly in geographically segregated populations before they became different species, partly during the process of **speciation**, and partly after the reproductive barriers evolved. Pág 364

The strength of both prezygotic and postzygotic isolation increases gradually with the time since the separation of the populations (Figure 15.11). That is, **speciation** is a gradual process. Pág 365

In the early stages of **speciation**, hybrid sterility or inviability is almost always seen in males only; female sterility or inviability appears only when taxa are older. Thus postzygotic isolation evolves more rapidly in males than in females. Pág 466

The analyzing barriers to gene exchange, we wish to know whether the genetic differences required for **speciation** consist of few or many genes and how those genes act. Because some genetic differences accrue after **speciation** has occurred, we must compare populations that have speciated very recently, or are still in the process of doing so, in order to answer these questions. Pág 466

The role of structural alterations in postzygotic isolation and **speciation** is controversial (King 1993; Rieseberg 2001; Coyne and Orr 2004). An important question is whether heterozygosity for chromosome rearrangements causes reduced fertility (postzygotic isolation) in hybrids due to segregation of aneuploid gametes in meiosis. Pág 369

A possible cause or contributor to **speciation** in insects is cytoplasmic incompatibility, caused by endosymbiotic bacteria in the genus *Wolbachia* that are inherited in egg cytoplasm, but are not transmitted by sperm (Werren 1998). Pág 370

There are other reproductive barriers between these species, including sexual isolation, so it is unclear if cytoplasmic incompatibility may not have been the cause of **speciation** in this case. Pág 371

Hybridization in nature interests evolutionary biologists because the hybridizing population's sometimes represent intermediate stages in the process of **speciation**. In some cases, hybridization may be the source of new adaptations or even of new species (Arnold 1997). Pág 373

These possibilities will be discussed in the following chapter as we examine the processes of **speciation**. Pág 376

A recent book by J. A. Coyne and H. A. Orr, *Speciation* (Sinauer Associates, Sunderland, MA, 2004) is the most comprehensive book on **speciation** in more than 40 years. The authors analyze

hypotheses and data about **speciation** carefully and summarize a great amount of relevant literature. They provide an extensive discussion of species concepts and a justification of the biological species concept in particular.

Pág 377

But if the permanence of these distinctions depends on reproductive isolation, and if we consider reproductive isolation a defining feature of species, then the central question about **speciation** must be how genetically based barriers to gene exchange arise. Pág 379

The problem of **speciation**, then, is how **new** different populations can be formed without intermediates. This problem holds, whatever the character that confers prezygotic or postzygotic isolation may be. Pág 380

The many conceivable solutions to this problem are the **MODES OF SPECIATION**. The modes of **speciation** that have been hypothesized can be classified by several criteria (Table 16.1), including the geographic origin of the barriers to gene exchange, the genetic bases of the barriers, and the courses of evolution of the barriers. Pág 380

Speciation may occur in three kinds of geographic settings that blend one into another (Figure 16.1). Allopatric **speciation** is the evolution of reproductive barriers in populations that are prevented by a geographic barrier from exchanging genes at more than a negligible rate. A distinction is often made between allopatric **speciation** by vicariance (divergence of two large populations; Figure 16.1A) and peripatric **speciation** (divergence of a small population from a widely distributed ancestral form; Figure 16.1B) Pág 380

In parapatric **speciation**, neighboring populations, between which there is modest gene flow, diverge and become reproductively isolated (Figure 16.1C). Sympatric **speciation** is the evolution of reproductive barriers within a single, initially randomly mating population (Figure 16.1D). Allopatric, parapatric, and sympatric **speciation** form a continuum, differing only in the degree to which the initial reduction of gene exchange is accomplished by a physical barrier extrinsic to the organisms (as in allopatric **speciation**) or by evolutionary change in the biological characteristics of the organisms themselves (as in sympatric **speciation**). Pág 380

Allopatric **speciation** is widely acknowledged to be a common mode of **speciation**; the incidence of parapatric and sympatric **speciation** is debated. Pág 380-381

From a genetic point of view the reproductive barriers that arise may be based on genetic divergence (allele differences at, usually, several or many loci), cytoplasmic incompatibility, or cytological divergence (polyploidy or structural rearrangement of chromosomes). We will devote most of this chapter to **speciation** by genetic divergence. Pág 381

The causes of evolution of reproductive barriers, as of any characters, are genetic drift and natural selection of genetic alterations that have arisen by mutation. Peripatric **speciation**, a hypothetical form of **speciation** that is also referred to as **TRAI'SILENCE** or **SPECIATION BY PEAK SHIFT**, requires both genetic drift and natural selection. Both sexual selection and ecological causes of natural selection may result in **speciation** pag 381

All evolutionary biologists agree that allopatric **speciation** occurs, and many hold that it is the prevalent mode of **speciation**, at least in animals (Mayr 1963; Coyne and Orr 2004).

Pág 381

Speciation can often be related to the geological history of barriers. For example, the emergence of the Isthmus of Panama in the Pliocene divided many marine organisms into Pacific and Caribbean populations, some of which have diverged into distinct species. Pag 381-382

Allopatric **speciation** is also supported by negative evidence. No pairs of sister species of birds occur together on any isolated island, implying that **speciation** does not occur on land masses that are too small to provide geographic isolation between populations (Coyne and Price 2000).Pag 382

Tim Barraclough and Alfried Vogler (2000) reasoned that over time, the amount of overlap between the geographic ranges of species that have formed by allopatric **speciation** can only increase from zero, whereas overlap between species that originated by sympatric **speciation** should stay the same or decrease.Pag 383

Several groups showed increasing overlap with time, as expected from allopatric **speciation** (Figure 16.5A,B), whereas two groups of insects displayed a pattern consistent with the possibility of sympatric **speciation** (Figure 16.5CD). Pag 383

Models of vicariant allopatric **speciation** have been proposed based on genetic drift, natural selection, and a combination of these two factors. The combination of genetic drift and selection is discussed later, in relation to peripatric **speciation**.Pag 383

The allele substitutions could be caused by either genetic drift or natural selection. For the moment, we will leave open the possibility of **speciation** by random fixation of alleles, and consider the ways in which natural selection may contribute to the origin of species. Pag 384

The most widely held view of vicariant allopatric **speciation** is that it is caused by vicariant selection, which causes the evolution of genetic differences that create prezygotic and/or postzygotic incompatibility. Some—perhaps most—of the reproductive isolation evolves while the populations are allopatric, so that a substantial or complete barrier to gene exchange exists when the populations meet again if their ranges expand (Mayr 1963). Thus **speciation** is usually an effect—a by-product—of the divergent selection that occurred during allopatry. The divergent selection may be ecological selection or sexual selection. Pag 384

In many of these studies, partial sexual isolation or postzygotic isolation developed, demonstrating that substantial progress toward **speciation** can be observed in the laboratory, and that it can arise as a correlated response to divergent selection.Pag 385

A good example is the case of the two monkey flowers (*Mimulus*) described in Chapter 15, which have become adapted to different pollinators (see Figure 15.7). Three-spined sticklebacks (*Gasterosteus*) have undergone PARALLEL **SPECIATION** in several Canadian lakes, where a limnetic (open-water) "ecotype" coexists with a benthic (bottom-feeding) "ecomorph" that is smaller and differs in shape.

Pag.385

These ecomorphs are sexually isolated and have evolved independently in each lake; that is, **speciation** has occurred in parallel (Figure 16.8A)Pag 385

Molecular data also are beginning to provide evidence of a role for natural selection in **speciation**. The few genes that contribute to reproductive isolation and that have been sequenced, such as *Ucp66* in *Drosophila* (see Figure 15.15), show the high rate of amino acid replacing substitutions that indicates directional selection Pag 386

Models of sexual selection of male traits by female choice show that divergent traits and preferences can evolve in different populations of an ancestral species, resulting in **speciation** (Lande 1981; Pomiankowski and [wasa 1998; Turelli et al. 2001). The expected result would be the diversity of different male traits that distinguish species of hummingbirds (see Figure 15.6) and many other groups of animals. Pág 386

It is very likely that sexual selection has been an important cause of **speciation**, especially in highly diverse groups, such as African lake cichlids, Hawaiian *Drosophila*, pheasants, and birds of paradise, in which males are commonly highly (and diversely) colored or ornamented (Panhuis et al. 2001) Pág 386

Because sister clades, by definition, are equal in age, the difference in diversity implies a higher rate of **speciation** (or possibly a lower extinction rate) in clades that experience strong sexual selection. Diversity of species and subspecies has like wise been correlated, with the evolution of sexually selected feather ornaments, such as crests and elongated tail feathers (Iv0Uer and Cuervo 1998). Pág 386

Sexual selection in these cichlids has probably contributed to their extraordinarily high rate of **speciation** Pág 387

It is now generally agreed that natural selection can enhance prezygotic reproductive isolation between hybridizing populations, but how often this process plays a role in **speciation** is not known (Howard 1993; Noor 1999; Turelli et al. 2001). Pág 387

Thus recombination between loci that reduce the fitness of hybrids and loci that govern assortative mating is a powerful factor working against the reinforcement of prezygotic isolation. (It also reduces the likelihood of sympatric evolution of assortative mating, as you will see in the section below on sympatric **speciation**.) Pág 388

One of Ernst Mayr's most influential and controversial hypotheses was founder effect **speciation** (1954), which he later termed peripatric speciation (1982b). He based this hypothesis on the observation, in many birds and other animals, that isolated populations with restricted distributions, in locations peripheral to the distribution of a probable "parent" species, often are highly divergent, to the point of being classified as different species or even genera. Pág 389

Speciation by peak shift is considered unlikely by many theoretical population geneticists (Charlesworth and Rouhani 1988; Turelli et al. 2001). In their view, reproductive isolation is caused by the low fitness of heterozygous hybrids; that is, by a deep adaptive valley Pág 390

In summary, divergence of localized populations from more widespread, slowly evolving parent populations may, well prove to be a common pattern of **speciation**. So far, there is little evidence that this divergence is frequently due to peak shifts initiated by genetic drift and completed by selection, rather than natural selection alone. Pág 392

Allopatric, parapatric, and sympatric **speciation** form a continuum, from little to more to much gene exchange between the diverging groups that eventually evolve biological barriers to gene exchange. Pág 392

Even in allopatric **speciation**, there may be some gene flow between populations, but it is very low compared with the divergent action of natural selection and/or genetic drift. Parapatric **speciation** is

the same process, but since the rate of gene flow is higher, the force of selection must be correspondingly stronger to engender genetic differences that create reproductive isolation. Págs 392

As we have seen, a parapatric or sympatric distribution of sister species does not necessarily provide evidence that they arose by parapatric or sympatric **speciation**, because species' distributions change over time. Because sympatric species may have originated by allopatric **speciation**, distributional evidence must be cautiously interpreted (Cline and Lovejoy 1998). Págs 392

Parapatric **speciation** can theoretically occur if gene flow between populations that occupy adjacent regions with different selective pressures is much weaker than divergent selection for different gene combinations (Endler 1977). Págs 392-393

Parapatric **speciation** undoubtedly occurs and may even be common, but it is very difficult to demonstrate that it provides a better explanation than allopatric **speciation** for real cases (Coyne and Orr 2004). Possibly the best-documented example of the parapatric origin of reproductive isolation is attributable not to these theories, but to selection for isolation—i.e., reinforcement. Págs 393

Sympatric **speciation** is a highly controversial subject. **Speciation** would be sympatric if a biological barrier to gene exchange arose within an initially randomly mating population without any spatial segregation of the incipient species—that is, if **speciation** occurred despite high initial gene flow. The difficulty any model of sympatric **speciation** must overcome is how to reduce the frequency of the intermediate genotypes that would act as a conduit of gene exchange between the incipient species. Ernst Mayr (1952, 1963) was the most vigorous and influential critic of the sympatric **speciation** hypothesis, demonstrating that many supposed cases are unconvincing and that the hypothesis must overcome severe theoretical difficulties. Under certain special circumstances, however, these difficulties are not all that severe (Diehl and Bush 1989; Dieckmann and Doebeli 1999; see Twelli et al. 2001). Págs 393

Sympatric **speciation** is somewhat more probable in several variant models. For example, suppose that insect genotypes A₁A₁ and A₂A₂ are best adapted to different host plants, and that locus B affects the insect's choice of host plant. Assume that the insects mate on the host plant chosen. Many herbivorous insects do exactly that; in fact, Guy Bush (1969) proposed this model based on his study of true fruit flies (Tephritidae). In such insects, a genetic difference in host preference (or, more generally, habitat preference), if it affects both sexes, automatically causes assortative mating. **Speciation** then occurs by sympatric evolution of ecological isolation (see Table 15.2) rather than by sexual isolation as such. Págs 394

However, if host preference is a continuous, polygenic trait, reproductive isolation will not evolve unless selection is strong (Figure 16.16B). Somewhat similar models describe sympatric **speciation** by adaptation to a continuously distributed resource, such as prey size (Dieckmann and Doebeli 1999; Kondrashov and Kondrashov 1999). Some authors have questioned how realistic these models are (Gavrilets 2004; Coyne and Orr 2004). Págs 394

EVIDENCE ON SYMPATRIC SPECIATION. Because the conditions required for sympatric **speciation** to occur are theoretically more limited than those for allopatric **speciation**, and because there is so much evidence for allopatric **speciation**, sympatric **speciation** must be demonstrated rather than assumed for most groups of organisms. Such demonstration may be quite difficult. Nevertheless, many possible examples, supported by varying degrees of evidence, have been proposed. Págs 394

"Host races" of specialized herbivorous insects—partially reproductively isolated subpopulations that feed on different host plants—have often been proposed to represent sympatric **speciation** in progress. Pag 394-395

It has often been suggested that the enormous diversity of cichlid fishes in the African Great Lakes (see Figure 3.24) arose by sympatric **speciation**. However, there are plentiful opportunities for allopatric **speciation** within each lake, because most of these species are sedentary and are restricted to one or another of several distinct habitats (rocky shore, soft bottom, etc.) that are discontinuously distributed along the lake periphery. Indeed, separated conspecific populations of these cichlids differ genetically, even over short distances (Rico et al. 2003). The likelihood of such "microallopatric" **speciation** seems remote, though, in two groups of cichlid species that are confined to two small crater lakes (Schliewen et al. 1994). Pág 396

Mitochondrial DNA sequence data indicate that the cichlids in each lake are monophyletic, suggesting that **speciation** has occurred within the crater lakes. The lakes lie in simple coralline basins that lack habitat heterogeneity and opportunity for spatial isolation. This example, and a pair of apparent species of Arctic charr (*Salvelinus pinus*, a relative of brook trout) in a glacial lake in Iceland (Gislason et al. 1999), may provide the most convincing examples of completed **speciation** without spatial separation. Pág 396

A tetraploid, for example, has four chromosome complements in its somatic cells. Polyploid populations are reproductively isolated by postzygotic barriers from their diploid (or other) progenitors and are therefore distinct biological species. **Speciation** by polyploidy is the only known mode of allopatric **speciation** by a single genetic event. Pág 396

A milestone in the study of **speciation** was the experimental production of a natural polyploid species by Arne Miintzing in 1930. Miintzing suspected that the mint *Gnaphalium tetrahil*, with $2n = 32$ chromosomes, might be an allotetraploid derived from the diploid ($2n = 16$) ancestors *C. pubescens* and *C. speciosa*. Pag 397

Decades later, Pamela and Douglas Soltis (1991) found that the tetraploid species have exactly the combinations of DNA markers from the diploid species that are predicted by Ownbey's hypothesis. DNA studies also show that each of the allopolyploid species has arisen independently several times by hybridization between its diploid parents (Figure 16.19B). Thus allopolyploids exemplify "parallel **speciation**" Pág 397

This process has been called recombinational **speciation** or HYBRID **SPECIATION** (Grant 1981). Pag 398

Recombinational **speciation** seems to be rare in animals, but may be more common in plants (Rieseberg and Wendel 1993; Rieseberg 1997). Diploid species of hybrid origin have been identified by morphological, chromosomal, and molecular characters. Pág 398

Because recombination breaks down the initial associations among genetic markers derived from the two parent species, the sizes of chromosomal blocks derived from each parent can be used to estimate how long it took for **speciation** to occur. On this basis, one of the hybrid species, *H. mitchellii*, is estimated to have arisen within about 60 generations (Ungerer et al. 1998). Pág 398

The phrase "rate of **speciation**" has several meanings (Coyne and Orr 2004). One is the **TRAIT SUBSTITUTION TIME** or **TIME FOR SPECIATION** (TFS), the time required for (nearly) complete reproductive isolation to evolve, once the process has started (Figure 16.21A). Another is the **BIOLOGICAL SPECIATION INTERVAL** (BSI), the average time between the origin of a new

species and when that species branches (speciates) again. The BSI includes not only the TFS, but also the "waiting time" before the process of **speciation** begins again. Pág 399

The diversification rate, R , or increase in species number per unit time, equals the difference between the rates of **speciation** (S) and extinction (E). R can be estimated for a monophyletic group if the age of the group (I) can be estimated and if we assume that the number of species (N) has increased exponentially according to the equation

Pág 400

(33 my) appear to speciate especially slowly. Whatever approach is taken, **speciation** rates clearly vary greatly—as we would expect from theories of **speciation**. We expect the process of **speciation** (TFS) to be excruciatingly slow if it proceeds by mutation and drift of neutral alleles; we expect it to be faster if it is driven by ecological or sexual selection, and to be accelerated if reinforcement plays a role. Pág 401

Some possible modes of **speciation**, such as polyploidy, recombinational **speciation**, sympatric **speciation**, and **speciation** by peak shifts, should be very rapid when they occur—although they may occur rarely, resulting in long intervals (B51) between **speciation** events. As we have already seen, substantial reproductive isolation apparently evolved within about a century in the apple maggot fly *Rhagoletis pomonella* and the hybrid sunflower species *Helianthus annuus*; on the other hand, some sister taxa of snapping shrimps (*Alpheidae*) on opposite sides of the Isthmus of Panama have not achieved full reproductive incompatibility in the 3.5 My since the isthmus arose (Knowlton et al. 1993). Pág 401

What characteristics favor high rates of **speciation**? The best way to determine whether a characteristic affects the rate of diversification is to compare the species diversity of replicated sister groups that differ in the characteristic of interest (a replicated sister group comparison; see Figures 7.18 and 16.9). [Many features are correlated with diversification rate in various groups of organisms, but it is often hard to tell whether they enhance the **speciation** rate or diminish the extinction rate Pág 401

Among characteristics studied so far, those that seem most likely to have increased **speciation** rate as such seem to be animal (rather than wind) pollination in plants and features that indicate intense sexual selection in animals (Coyne and Orr 2004). Pág 401

The most important consequence of **speciation** is that it is the sine qua non of diversity. For sexually reproducing organisms, every branch in the great phylogenetic tree of life represents a **speciation** event, in which populations became reproductively isolated and therefore capable of independent, divergent evolution, including, eventually, the acquisition of those differences that mark genera, families, and still higher taxa. **Speciation**, then, stands at the border between microevolution—the genetic changes within and among populations—and macroevolution—the evolution of the higher taxa in all their glorious diversity. Pág 401

In their hypothesis of punctuated equilibrium, Eldredge and Gould (1972) (see also Stanley 1979; Gould and Eldredge 1993) proposed that **speciation** may be required for morphological evolution to occur at all. From the observation that many fossil lineages change little over the course of millions of years (see Chapter 7), they proposed that in broadly distributed species, internal constraints may prevent adaptive evolution. They suggested, based on Mayr's (1954) proposal that founder events trigger rapid evolution from one genetic equilibrium to another, that most evolutionary changes in morphology are triggered by and associated with peripatric **speciation**. Pág 401

Population geneticists generally reject this hypothesis; after all, morphological characters vary among populations of a species, just as they do among reproductively isolated species (Charlesworth et al. 1982). Thus, as Gould (2002) himself concluded, there is no reason to think that **speciation** (acquisition of reproductive isolation) triggers morphological evolution. Nevertheless, morphological change might be associated with **speciation** in the fossil record because reproductive isolation enables morphological differences between populations to persist in the long term (Futuyma 1987). Pág 401

Much of the divergence that has occurred will then be lost by interbreeding. If reproductive isolation has evolved (Figure 16.24). A succession of **speciation** events, each "capturing" further change in a character, may result in a long-term trend. Pág 402

Likewise, gradual morphological evolution in trilobites was more pronounced in stable than in unstable environments (Sheldon 1990). Perhaps, then, as Ernst Mayr (1963, p. 621) said, "**Speciation** ... is the method by which evolution advances. Without **speciation**, there would be no diversification of the organic world, no adaptive radiation, and very little evolutionary progress. The species, then, is the keystone of evolution." Pág 402

The simplest interpretation of this pattern is that the association between *B. lcl/llem* and aphids dates from the origin of this insect family, that there has been little if any cross infection between aphid lineages, and that the bacteria have diverged in concert with **speciation** of their hosts. Pág 431

When gene duplication precedes **speciation** and the duplicates diverge in sequence both within and between species, the major clusters in the resulting phylogenetic tree will correspond to the different paralogs. Within each paralog, the phylogenetic relationships of the species sampled will be reflected (Figure 19.21A). Pág 469

This interval is roughly the same as, or even greater than, the time required for **speciation** that has been estimated from genetic differences between sister species of living organisms (see Chapter 16). Thus duration of 1 or 2 million years per **speciation** event is more than enough to account for the evolution of great diversity, even in the most rapidly proliferating groups. Pág 502

The fossil record would provide some support for Eldredge and Gould's theoretical model if morphological change were ordinarily accompanied by bifurcation of a lineage, i.e., true **speciation**. It can be difficult to distinguish change with bifurcation from "punctuated gradualism" (see Chapter 4), but there are some convincing examples of both gradual change without **speciation** (e.g., the rodent example in Figure 4.19) and morphological change associated with true **speciation** (e.g., the bryozoan genus *Metrarjwbdotos*, in Figure 4.20). Obviously, we would expect to find some instances of coupled **speciation** and morphological divergence in the fossil record, since fossils of different species could be distinguished except by phenotype. But the punctuated equilibrium hypothesis requires that morphological evolution be almost inevitably accompanied by **speciation**, and it is not clear that the evidence supports this expectation. Pág 503

Mayr's model of **speciation** requires that genetic drift (the founder effect) move a small population from the vicinity of one adaptive peak across an adaptive valley (i.e., opposing the action of natural selection) to the slope of a different adaptive peak. As we saw in Chapter 16, this is unlikely to occur unless selection is very weak or unless the population is so small that it is at risk of losing genetic variation altogether. Consequently, many population geneticists are skeptical that peripatric **speciation** is at all common, and so far there is little evidence that species are formed in this way.

Pág 503

Moreover, geographic variation within species, as well as the rapid adaptive evolution of populations exposed to new selection pressures; show that **speciation** is not required for adaptive phenotypic change (Levinton 2001). Therefore, few evolutionary biologists espouse the theoretical model of Eldredge and Gould (1972), and even its authors have agreed that **speciation** is not a necessary trigger of adaptive, directional morphological evolution (Eldredge 1989; Gould 2002, p. 796). (Nonetheless, **speciation** may contribute to an a genetic evolution, as we will see in the following section.)Pág 503

111US, although **speciation** may not cause anagenetic adaptive change, it may confer long life sllch changes, leading to a possible association between **speciation** and morphological evolution (i.e., the pattern of punctuated equilibrium).Pág 505

Evidence of sllstained evolution in stable environments has led some paleontologists to the same conclusion (Sheldon 1987; see Figure 4.3), and there is considerable evidence that the drastic climatic fluctuations in the Pleistocene inhibited both **speciation** and persistent adaptive phenotypiC change (Jansson and Dynesius 2002 Pág 505

The mean character state among species in a clade can also change due to a correlation with **speciation** or extinction rates (see Figure 11.16). Pág 514

However, they more than compensate by their higher rate of **speciation**, probably because their lower rate of dispersal reduces the rate of gene flow among populations (Hansen 1980; jebloński and Lutz 1983).Pág 515

Trends due to lineage sorting by species hitchhiking are probably very common because if anyone character causes one clade to become richer in species t.han other clades due to its effect on th rate of **speciation** or extinction, then all the other features of that clade will also tend toward greater frequencies Pág 515

Speciation generally takes a very long time, but some processes of **speciation** can also be observed. Substantial reproductive isolation has evolved in laboratory populations, and species of plants that apparently originated by polyploidy and by hybridization have been "re-created" de novo by crossing their suspected parent forms and selecting for the species' diagnostic characters (see Chapter 16). Pág 532

DERIVA

Evolutionary biology is a unified whole: just as carbohydrate metabolism and amino acid synthesis cannot be divorced in biochemistry, so it is for topics as seemingly different as the phylogeny of species and the theory of genetic **drift**. Preface xv

The rate of mutation is too low for mutation by itself to shift a population from one genotype to another. Instead, the change in genotype proportions within a population can occur by either of two principal processes: random fluctuations in proportions (genetic **drift**), or nonrandom changes due to the superior survival and/or reproduction of SOIU€ genotypes compared with others (Le., natural selection). Natural selection and random genetic **drift** can operate simultaneously. Pág 10

This hypothesis, developed especially by Motoo Kimura (1924--1994), holds that most of the evolution of DNA sequences occurs by genetic **drift** rather than by nah.ual selection. EVOLUTIONARY DEVELOPMENTAL BIOLOGY is an exciting Held devoted to understanding hm.v developmental processes both envolve and constrain evolution.Pág 11

A body of ideas about the causes of evolution, including mutation, recombination, gene flow, isolation, random genetic drift, the many forces of natural selection, and other factors, constitute our current theory of evolution, or "evolutionary theory." Pág 14

Similarly, among a finite number of offspring, both the genotype frequencies and the allele frequencies may differ from those in the previous generation, purely by chance. Such random changes are called random genetic drift. Pág 196

The central question was, "Do forces of natural selection maintain this variation, or is it neutral, subject only to the operation of random genetic drift?" Pág 204

Gene flow, if unopposed by other factors, homogenizes the populations of a species—that is, it brings them all to the same allele frequencies unless it is sufficiently counterbalanced by the divergent forces of genetic drift or natural selection (see Chapters 10 and 12). Pág 216

But at the same time, there are important random processes in evolution, including mutation (as discussed in Chapter 8) and random fluctuations in the frequencies of alleles or haplotypes: the process of random genetic drift. Pág 226

Genetic drift and natural selection are the two most important causes of allele substitution—that is, of evolutionary change—in populations. Genetic drift occurs in all natural populations because, unlike ideal populations at Hardy-Weinberg equilibrium, natural populations are finite in size. Random fluctuations in allele frequencies can result in the replacement of old alleles by new ones, resulting in non-adaptive evolution. That is, while natural selection results in adaptation, genetic drift does not—so this process is not responsible for those anatomical, physiological, and behavioral features of organisms that equip them for reproduction and survival. Genetic drift nevertheless has many important consequences, especially at the molecular genetic level: it appears to account for much of the difference in DNA sequences among species. Pág 226

Because all populations are finite, alleles at all loci are potentially subject to random genetic drift—but all are not necessarily subject to natural selection. For this reason, and because the expected effects of genetic drift can be mathematically described with some precision, some evolutionary geneticists hold the opinion that genetic drift should be the "null hypothesis" used to explain an evolutionary observation unless there is positive evidence of natural selection or some other factor. This perspective is analogous to the "null hypothesis" in statistics: the hypothesis that the data do not depart from those expected on the basis of chance alone." According to this view, we should not assume that a characteristic, or a difference between populations or species, is adaptive or has evolved by natural selection unless there is evidence for this conclusion. Pág 226

The theory of genetic drift, much of which was developed by the American geneticist Sewall Wright starting in the 1930s, and by the Japanese geneticist Motoo Kimura starting in the 1950s, includes some of the most highly refined mathematical models in biology. (But fear not! We shall skirt around almost all the math.) We will first explore the theory and then see how it explains data from real organisms. In our discussion of the theory of genetic drift, we will describe random fluctuations in the frequencies (proportions) of two or more kinds of self-reproducing entities that do not differ all average (or differ very little) in reproductive success (fitness). Pág 226

The concept of random genetic drift is so important that we will take steps in developing the idea. Pág 227

As allele frequencies in a population change by genetic **drift**, so do the genotype frequencies, which conform to Hardy-Weinberg equilibrium among the new zygotes in each generation. Pág 228

Bear in mind that this model, as developed so far, includes only the effects of random genetic **drift**. It assumes that other evolutionary processes—namely, mutation, gene flow, and natural selection—do not operate. Pág 228

Let us take another, more traditional, approach to the concept of random genetic **drift**. As Slime that the frequencies of alleles A1 and A2 are p and q in each of many independent populations, each with N breeding individuals (representing 2N gene copies in a diploid species). Pág 229

Since no stabilizing force returns the allele frequency toward 0.5, p will eventually wander (**drift**) either to approach 0: the allele is either lost or fixed. (Once the frequency of an allele has reached either 0 or 1, it cannot change unless another allele is introduced into the population, either by mutation or by gene flow from another population.) Pág 229

Therefore, the genetic variation at a locus declines and is eventually lost. As the frequency of one of the alleles approaches 1.0, the frequency of heterozygotes, $H \sim 2p(1 - p)$, declines. The rate of decline in heterozygosity is often used as a measure of the rate of genetic **drift** within a population. Pág 231

Evolution by genetic **drift** proceeds faster in small than in large populations. In a diploid population, the average time to fixation of a newly arisen neutral allele that does become fixed is $4N$ generations, on average. That is a long time if the population size (N) is large. Pág 231

Thus the rate of genetic **drift** of allele frequencies, and of loss of heterozygosity, will be greater than expected from the population's census size, corresponding to what we expect of a smaller population. In other words, the population is effectively smaller than it seems. Pág 231

The effective size (denoted N_e) of an actual population is the number of individuals in an ideal population (in which every adult reproduces) in which the rate of genetic **drift** (measured by the rate of decline in heterozygosity) would be the same as it is in the actual population. Pág 231

For instance, if we count 10,000 adults in a population, but only 1000 of them successfully breed, genetic **drift** proceeds at the same rate as if the population size were 1000, and that is the effective size, N_e . Pág 231

The random genetic **drift** that ensues is often called a founder effect. If the new population rapidly grows to a large size, allele frequencies (and therefore heterozygosity) will probably not be greatly altered from those in the source population, although some rare alleles will not have been carried by the founders. Pág 232

If the colony remains small, however, genetic **drift** will alter allele frequencies and erode genetic variation. If the colony persists and grows; new mutations eventually restore heterozygosity to higher levels (Figure 10.6). Pág 232

Peter Buri (1956) described genetic **drift** in an experiment with *Drosophila melanogaster*. He initiated 107 experimental populations of flies, each with 8 males and 8 females, all heterozygous for two alleles (bw and b⁷⁵) that affect eye color (by which all three genotypes are recognizable). Pág 232

By generation 19,30 populations had lost the bw7S allele, and 28 had become fixed for it; among the unfixed populations, intermediate allele frequencies were quite evenly distributed. The results nicely matched those expected from genetic drift theory (see Figure 10.4). Pá 233

They found that average heterozygosity (R) declined steadily after each bottleneck episode, and that the smaller the bottlenecks were, the more rapidly it declined. On the whole, R closely matched the values predicted by the mathematical theory of genetic drift. Pá 234

We therefore attempt to infer causes of evolution (such as genetic drift or natural selection) by interpreting patterns. Such inferences are possible only on the basis of theories that tell us what pattern to expect if one or another cause has been most important. Pá 234

Patterns of molecular genetic variation in natural populations often correspond to what we would expect if the loci were affected by genetic drift. For example, Robert Selander (1970) studied allozyme variation at two loci in house mice (*Mus musculus*) from widely scattered barns in central Texas. Pá 234

Having estimated the population size in each barn, Selander found that although small and large populations had much the same mean allele frequencies, the variation (variance) in allele frequency was much greater among the small populations, as we would expect from random genetic drift (Table 10.1). Pá 234

Moreover; the effective size was probably even lower, because less than 20 percent of males typically succeed in mating. The hypothesis that genetic drift was responsible for the monomorphism a likely hypothesis according to the model we have just described—is supported by the historical data. Pá 234

Whether or not random genetic drift has played an important role in the evolution of many of the morphological and other phenotypic features of organisms is a subject of considerable debate. There is no question, however, that at the levels of DNA and protein sequences, genetic drift is a major factor in evolution. Pá 235

This belief was based on numerous studies of genes with morphological or physiological effects. But in the 1960s, the theory of evolution by random genetic drift of selectively neutral alleles became important as of two kinds of molecular data became available. In 1966, Lewontin and Hubby showed that a high proportion of enzyme loci are polymorphic. Pá 235

He argued that such constancy would not be expected to result from natural selection, but would be expected if most evolutionary changes at the molecular level are caused by mutation and genetic drift. These authors and others (King and Jukes 1969) initiated a controversy about molecular polymorphism and evolution, known as the "neutralist-selectionist debate," that is still not entirely resolved. Although everyone now agrees that some molecular variation and evolution is neutral (i.e., a result of genetic drift), "selectionists" think a larger fraction of molecular evolutionary changes are due to natural selection than "neutralists" do. Pá 236

The neutral theory of molecular evolution holds that although a small minority of mutations if DNA or protein sequences are advantageous and are fixed by natural selection, and although many mutations are disadvantageous and are eliminated by natural selection, the great majority of those mutations that are fixed are effectively neutral with respect to fitness and are fixed by genetic drift. Pá 236

It is important to recognize that the neutral theory does not hold that the morphological, physiological, and behavioral features of organisms evolve by random genetic drift. Pág 236

By effectively neutral, we mean that the mutant allele is so similar to other alleles in its effect on survival and reproduction (i.e., fitness) that changes in its frequency are governed by genetic drift alone, not by natural selection. Pág 236

Then natural selection and genetic drift operate simultaneously, but because genetic drift is stronger in small than in large populations, the changes in the mutant allele's frequency will be governed almost entirely by genetic drift if the population is small enough. Therefore a particular allele may be effectively neutral, relative to another allele, when the population is small, but not when the population is large.) Pág 236

The number of new mutations is, on average, $U \times 2N_e$ since there are $2N_e$ gene copies that could mutate. From genetic drift theory, we have learned that the probability that a mutation will be fixed by genetic drift is its frequency, p , which equals $1/(2N_e)$ for a newly arisen mutation. Pág 237

From genetic drift theory, we have learned that the probability that a mutation will be fixed by genetic drift is its frequency, p , which equals $1/(2N_e)$ for a newly arisen mutation. Pág 237

Notice that, surprisingly, the rate of substitution does not depend on the population size: each mutation drifts toward fixation more slowly if the population is large, but this is compensated for by the greater number of mutations that arise. Pág 237

But new neutral alleles arise continually by mutation, and although many are immediately lost by genetic drift, others drift to higher frequency and persist for some time in a polymorphic state before they are lost or fixed Pág 238

Although the identity of the several or many alleles present in the population changes over time, the level of variation reaches an equilibrium when the rate at which alleles arise by mutation is balanced by the rate at which they are lost by genetic drift. Pág 238

If the neutral mutation rate is U for replacement changes and U_s for synonymous changes, then, according to the neutral theory, the ratio of replacement to synonymous differences should be the same as U/U_s for both polymorphisms and substitutions, if indeed the replacement changes are subject only to genetic drift. Pág 238

If most replacement substitutions are advantageous rather than neutral, they will increase in frequency and be fixed more rapidly than by genetic drift alone. Pág 238-239

A measure of the variation in allele frequency among populations is F_{ST} (see Chapter 9). The rate at which populations drift toward fixation of one allele or another is inversely proportional to the effective population size, N_e (or N , for simplicity). However, the drift toward fixation is counteracted by gene flow from other populations, at rate m . These factors strike a balance, or equilibrium, at which the fixation index. Pág 241

This assumption can be evaluated by the degree of consistency among different loci for which F_{ST} is estimated. Genetic drift and gene flow affect all loci the same way, whereas natural selection affects different loci more or less independently. Pág 241

This might not be the case if, for example, the sampled sites have only recently been colonized and the populations have not yet had time to differentiate by genetic drift. Their genetic similarity would then lead us to overestimate the rate of gene flow. Pág 241

Earlier in this chapter, we introduced the principle of genetic drift by showing that because gene lineages within a population become extinct by chance over the course of time, all gene copies in a population today are descended from one gene copy that existed at some time in the past. Pág 241

Because the smaller the effective size (N_e) of a population, the more rapidly genetic drift transpires, the existing gene copies in a small population must stem from a more recent common ancestor than the gene copies in a large population (compare parts A and B in Figure 10.15). Pág 242

If one neutral allele replaces another in a population by random genetic drift (see Chapter 10), then the bearers of that allele in that population have had a greater rate of increase than the bearers of the other.

Pág 251

We can ascribe genetic changes to natural selection rather than random genetic drift only if we observe consistent, nonrandom changes in replicate populations, or measure numerous individuals of each phenotype and find an average difference in reproductive success. Pág 252

Second, Ule hait may have evolved by random genetic drift rather than by natural selection. Pág 261

Natural selection is not the same as evolution. Evolution is a multi-step process: the origin of genetic variation by mutation or recombination, followed by changes in the frequencies of alleles and genotypes, caused chiefly by genetic drift or natural selection. Neither natural selection nor genetic drift occurs it's for the origin of variation, Pág 270

Unlike genetic drift, will breeding, and gene flow, which act at the same rate on all loci in a genome, the allele frequency changes caused by natural selection in a sexually reproducing species proceed largely independently at different loci. Pág 270

In the following discussion, we make the simplifying assumptions that the population is very large, so genetic drift may be ignored; that mating occurs at random; that mutation and gene flow do not occur; and that selection at other loci does not affect the locus we are considering Pág 273

As we saw in Chapter 9, studies of natural populations revealed instead a wealth of variation. The factors that might be responsible for this variation are: (1) recurrent mutation producing deleterious alleles, subject to only weak selection; (2) gene flow of locally deleterious alleles from other populations in which they are favored by selection; (3) selective neutrality (i.e., genetic drift); and (4) maintenance of polymorphism by natural selection. The last of these hypotheses has championed by British ecological geneticists led by E. B. Pág 280

The effect of random genetic drift is negligible if selection on a locus is strong relative to the population size—that is, if s is much greater than $1/(4N_e)$. Conversely, if s is much less than $1/(4N_e)$, selection is so weak that the allele frequencies change mostly by genetic drift: the alleles are nearly neutral. Pág 287

The effect of population size on the efficacy of selection has several important consequences. First, a population may not attain exactly the equilibrium allele frequency predicted from its genotypes' fitness; instead, it is likely to wander by genetic drift in the vicinity of the equilibrium frequency.

Second, a slightly advantageous mutation is less likely to be fixed by selection if the population is small than if it is large, because it is more likely to be lost simply by chance. Conversely, deleterious mutations can become fixed by genetic drift, especially if selection is weak and the population is small. Population bottlenecks provide temporary conditions under which genetic drift may counteract selection so that a deleterious allele may increase in frequency. For example, slightly deleterious mutations might be fixed, contributing to divergence among populations at the molecular level. [pág 287](#)

The principle that genetic drift could prevail over selection might be especially important if heterozygotes are inferior in fitness, so that the adaptive landscape has two peaks (see Figure 12.70). Selection cannot move a population down the slope of one peak and across a valley to the slope of another peak, even if the second peak is higher: a population does not first become poorly adapted so that it can then become better adapted (Figure 12.20A). [pág 288](#)

But during episodes of very low population size, allele frequencies may fluctuate so far by genetic drift that they cross the adaptive valley—after which selection can move the population "uphill" to the other peak (Figure 12.20B). The probability that such a peak shift will occur (Barton and Charlesworth 1984) depends on the population size and on the difference in height (mean fitness) between the valley and the initially occupied peak. [Pág 288](#)

Thus, when there are multiple stable equilibria, genetic drift and selection may cooperate to accomplish what selection alone cannot, moving a population from one adaptive peak to another. [Pág 288](#)

Because these grasshoppers are flightless and quite sedentary, local populations are small, providing the opportunity for genetic drift to occasionally initiate a peak shift whereby a new chromosome arrangement is fixed. [Pág 288](#)

As we saw in Chapter 10, for example, that at equilibrium between mutation and genetic drift, the expected amount of sequence variation in a diploid population, as expressed by the frequency of heterozygotes per nucleotide site, [Pág 288-289](#)

Consider two unlinked loci, one that has been evolving solely by genetic drift (Figure 12.21A) and one that has experienced a selective sweep (Figure 12.21B). [Pág 289-290](#)

In a genealogy of sequences sampled from a population, the common ancestor of all the sequences may be older than if they had been evolving solely by genetic drift because selection has maintained two gene lineages longer. [Pág 290](#)

When Tishkoff and collaborators performed computer simulations of various possible histories of change, they found that in simulations involving genetic drift, but not selection, levels of microsatellite variation were much higher than those observed, and levels of linkage disequilibrium were lower. [Pág 293](#)

Linkage disequilibrium may be caused by genetic drift. If the recombination rate is very low, the four gamete types in the example above may be thought of as if they were four alleles at one locus. One of these "alleles" may drift to high frequency by chance, creating an excess of that combination relative to others. [pág 304](#)

This is because more genetic variation is introduced by mutation in large than in small populations, large populations lose variation by genetic drift more slowly, and selection is more efficient in large populations. (Recall from Chapter 12 that whether allele frequency changes are affected more by

selection or by genetic drift depends on the relationship between the coefficient of selection and the population size.) Pág 308

Neo-Darwinian theory offers two possible explanations: either mutations that cause degeneration of an unused character become fixed by genetic drift because variation in the character are selectively neutral, or there is selection against an unused organ, perhaps because it interferes with some important function or requires energy and materials that could better be used for other purposes Pág 310

If alleles that contribute to variation in a polygenic trait are selectively neutral, variation and evolution of the trait are affected only by mutation (which increases variation) and genetic drift (which erodes it). The variance that arises per generation by mutation, V_m , is proportional to the number of mutating loci, the mutation rate per loci, and the average phenotypic effect of a mutation Pág 311

At equilibrium, when mutation is balanced by genetic drift, the genetic variance and heritability should, theoretically, reach a stable value, which should be quite high if the effective population size is large. Pág 311

As mutations that affect the character arise and are fixed by genetic drift, the mean will fluctuate at random. If a number of isolated populations are derived from an initially uniform ancestral population, mutation and genetic drift can cause genetic divergence among them in a polygenic character, just as they do at a single locus (see Chapter 10). Pág 311

He found that almost all the features had evolved at much lower rates than expected under mutation and genetic drift. Only the cranial capacity of Homo Sapiens has evolved at rates that may be higher than expected from the neutral model. Pág 311

Moreover populations in which stabilizing selection favors the same phenotype can diverge in genetic composition as mutation and genetic drift create turnover in alleles at the contributing loci. Pág 312

Others are adaptive differences related to ecological factors, such as temperature tolerance and habitat use; still others are presumably neutral differences that have arisen by mutation and genetic drift Pág 365

Prescribes found that in both species lineages, amino acid-replacing nucleotide substitutions have occurred in the N1p96 gene at a high rate relative to synonymous substitutions, a clear indication that natural selection, rather than genetic drift, has driven divergence (Figure 15.15). Why selection favored changes in this protein is not yet known. Pág 368-369

According to the COALESCENT THEORY described in Chapter 10, genetic drift in each species eventually results in the loss of all the ancestral lineages of DNA sequence variants except one; that is, coalescence to a common ancestral gene copy occurs in each species. (This process can also be caused by directional selection for a favorable mutation.) Gene lineages are lost by genetic drift at a rate inversely proportional to the effective population size. Pág 372

If we considered species to be merely populations with distinguishing characteristics, the question of how they originate would be easily answered: natural selection or genetic drift can fix novel alleles or characteristics (see Chapters 10-13). Pág 379

The causes of evolution of reproductive barriers, as of any characters, are genetic **drift** and natural selection of genetic alterations that have arisen by mutation. Peripatric speciation, a hypothetical form of speciation that is also referred to as TRAI'SILENCE or SPECIATION BY PEAK SHIFT, requires both genetic **drift** and natural selection. Pág 381

Because both natural selection and genetic **drift** cause populations to diverge in genetic composition, it is probably inevitable that if separated long enough, geographically separated populations will become different species. Pág 381

Models of vicariant allopatric speciation have been proposed based on genetic **drift**, natural selection, and a combination of these two factors. The combination of genetic **drift** and selection is discussed later, in relation to peripatric speciation. Pág 383

Therefore these allele substitutions can occur by natural selection (if the fitnesses differ) or by genetic **drift** (if they do not). Pág 384

This model is supported by genetic data showing that reproductive isolation is based on epistatic interactions (called Dobzhansky-Muller incompatibilities) among several or many loci (see Chapter 15). The allele substitutions could be caused by either genetic **drift** or natural selection. Pág 384

He reasoned that allele frequencies at some loci would differ from those in the parent population because of accidents of sampling in the, genetic **drift**-simply because a small number of colonists would carry only some of the alleles from the source population, and at altered frequencies. Pág 389

The process begins when genetic **drift** in the small, newly founded population shifts allele frequencies from the vicinity of one adaptive peak to the slope of the other. Pág 390

If the adaptive valley is very deep (i.e., if there is strong selection against heterozygotes), genetic **drift** is unlikely to move allele frequencies across the valley from one peak to another, unless the founder population is very small. Pág 390

Other models, however, show that peak shifts may be more likely if different assumptions are made (Price et al. 1993; Wagner et al. 1994; Gavrilets 2004). For example, a small population may move by genetic **drift** along an "adaptive ridge" to the other side of an adaptive valley from the parent population (Figure 16.12B). Pág 390

Thus genetic **drift** seems to have affected the pattern of courtship behavior, which might lead to sexual isolation Pág 392

In summary, divergence of localized populations from more widespread, slowly evolving parent populations may well prove to be a common pattern of speciation. So far, there is little evidence that this divergence is frequently due to peak shifts initiated by genetic **drift** and completed by selection, rather than natural selection alone. Pág 392

Even in allopatric speciation, there may be some gene flow between populations, but it is very low compared with the divergent action of natural selection and/or genetic **drift**. Pág 392

Whatever approach is taken, speciation rates clearly vary greatly-as we would expect from theories of speciation. We expect the process of speciation (TFS) to be excruciatingly slow if it proceeds by mutation and **drift** of neutral alleles; we expect it to be faster if it is driven by ecological or sexual selection, and to be accelerated if reinforcement plays a role. Pág 401

Thus the zero-mutation class declines over time because its members experience new deleterious mutations. Moreover, due to genetic **drift** in a finite population, the zero class may be lost by chance, despite its superior fitness. (The smaller the population, the more likely this is to happen.) Thus all remaining genotypes have at least one deleterious mutation. Sooner or later, by the same process of **drift**, the one-mutation class is lost, and all remaining individuals carry at least how mutations. The accidental loss of superior genotypes continues, and is an irreversible process—a ratchet. This reduction of fitness is likely to lower population size, and this, in turn, increases the rate at which the least mutation-laden genotypes are lost by genetic **drift**. Thus there may be an accelerated decline of fitness—a "mutational meltdown"—leading to extinction (Lynch et al. 1993). Pág 420

Only in the second half of the twentieth century did it become possible to compare the genes and molecules more clearly both the evolutionary relationships among species and population processes such as gene flow and genetic **drift**. Pág 449

These discoveries do not alter the fact that the genome as a whole is subject to the same principles of mutation, **drift** and adaptive evolution that have been studied for decades—although we can add a wealth of recent insights into chromosome evolution and genome structure to the evolutionary principles covered earlier in this book. Pág 451

The neutral theory states that the vast majority of evolutionary change in genes and chromosomes occurs via mutation followed by random **drift**, rather than by adaptive mutations being driven to fixation by selection. Pág 452

The neutral theory considers polymorphisms within species to be a transient state, one in which a new allele that has arisen by mutation is on its way to either fixation or loss by **drift**. Pág 453

Traditional neo-Darwinian theory explains how natural selection, genetic **drift**, and gene flow, acting on the raw material of genetic variation, have produced the astonishing variety of organisms. Pág 490

Therefore, it appears that within each species, the entire enhancer has evolved in a concerted fashion to maintain its function. If the fixation (by selection or **drift**) of a nucleotide substitution in one position in the enhancer caused a minor alteration in stripe expression, that change might provide selection pressure for a compensatory substitution elsewhere in the enhancer in order to maintain the stripe expression. Pág 498

At these low rates, even genetic **drift**, to say nothing of natural selection, could explain the net change in the feature, if the rate of evolution were constant (see Chapter 13). Pág 502

Selection, rather than genetic **drift**, may well be the cause of these rapid changes. Thus rates of evolution of quantitative traits, determined from the fossil record or from comparisons among living species, are consistent with evolution by natural selection and/or genetic **drift**, with information on mutation and genetic variation, and with observations on short-term rates of evolution that have been inferred from responses to laboratory selection (see Chapter 13), responses of natural populations to environmental change (see Chapter 13), and divergence among populations and among closely related species (see Chapter 15). Pág 502

Mayr's model of speciation requires that genetic **drift** (the founder effect) move a small population from the vicinity of one adaptive peak across an adaptive valley (i.e., despite the action of natural selection) to the slope of a different adaptive peak. Pág 503

Either driven or passive trends could have any of several causes. Neutral evolution by mutation and genetic drift results in increasing variance among lineages (see Chapter 12) and could produce a passive trend if variation were bounded as in Figure 21.13A.

Pág 514

So is evolution a fact or a theory? The light of these definitions, evolution is a scientific fact. That is, the descent of all species, with modification, from common ancestors is a hypothesis that in the last 150 years or so has been supported by so much evidence, it has so successfully resisted all challenges, that it has become a fact. But this history of evolutionary change is explained by evolutionary theory, the body of statements (about mutation, Selection, genetic drift, developmental constraints, and so forth) that together account for the various changes that organisms have undergone, pág 527

This is true, but natural selection is a deterministic, not a random, process. The random processes of evolution-mutation and genetic drift-do not result in the evolution of complexity, as far as we know. Indeed, when natural selection is relaxed, complex structures, such as the eyes of cave-dwelling animals, slowly degenerate, due in part to fixation of neutral mutations by genetic drift.

Pág 534

All these debates arise from differing opinions on the relative frequency and importance of factors known to influence evolution: large-effect versus small-effect mutations, genetic drift versus natural selection, individual selection versus species selection, adaptation versus constraint, and so forth (see Chapters 11, 20, and 21). Pág 536

MACROEVOLUÇÃO

These authors argued persuasively that mutation, recombination, natural selection, and other processes operating within species (which Dobzhansky termed microevolution) account for the origin of new species and for the major, long-term features of evolution (termed macroevolution).

Pág 9

The study of macroevolution has been renewed by provocative interpretations of the fossil record and by new methods for studying phylogenetic relationships. As molecular methods have become more sophisticated and available, virtually new fields of evolutionary study have developed

Pág 11

On this occasion, we present several examples of macroevolutionary change-the origin of higher taxa over long periods of geological time.

Pág 71

Moreover they give the lie to claims by antievolutionists that the fossil record fails to document macroevolution. Anyone educated in biology should be able to counter such charges with examples such as these. Pág 71-72

In speciation lie the origin of diversity, and the study of speciation bridges microevolution and macroevolution Pág 353

The phenomena of evolution are often divided into microevolution (meaning, mostly, processes that occur within species) and macroevolution, which is often defined as "evolution above the species level." "Macroevolution" has slightly different meanings to different authors. Pág 501

"**Macroevolution**" has slightly different meanings to different authors. To Stephen Jay Gould (2002, p. 38), it meant "evolutionary phenomenology from the origin of species on up." These phenomena include patterns of origination, extinction, and diversification of higher taxa, the subject of Chapter 7. Pág 501

To other authors, **macroevolution** is restricted to the evolution of great phenotypic changes, or the origin of characteristics that diagnose higher taxa (e.g., Levinton 2001). The subject matter of **macroevolutionary** studies, however defined, includes patterns that have developed over great periods of evolutionary time—patterns that are usually revealed by paleontological or comparative phylogenetic studies, even if their explanation lies in genetic and ecological processes that can be studied in living organisms. Pág 501

Much of the modern study of **macroevolution** stems from themes and principles developed by the paleontologist George Gaylord Simpson (1947, 1953), who focused on rates and directions of evolution perceived in the fossil record, and Bernhard Rensch (1959), a zoologist who inferred patterns of evolution from comparative morphology. Pág 502

Contemporary **macroevolutionary** studies draw on the fossil record, on phylogenetic patterns of evolutionary change, on evolutionary developmental biology, and on our understanding of genetic and ecological processes. Pág 502

That is, Eldredge and Gould applied Mayr's model of founder effect speciation (*peripatric speciation*) to **macroevolutionary** change, proposing that most morphological characters cannot evolve (because of internal genetic constraints) except when genetic drift initiates a shift to a new adaptive equilibrium (see Chapter 16). Pág 502-503

Although the theoretical model of punctuated equilibrium described above is almost certainly wrong, the controversy over the model had the healthy effect of drawing attention to many interesting questions about **macroevolution**. Pág 504

A common theme in the evolution of a feature alters the selective regime, leading to its modification. This principle, already recognized by Darwin, is one of the most important in **macroevolution** (Mayr 1960), and every group of organisms presents numerous examples. Pág 512

RESTIÇÃO

Eldredge and Gould had not further proposed that, except in populations that are undergoing speciation, morphological characters generally cannot evolve, due to internal genetic "**constraints**." Pág.86

Such a locus is said to have many functional **constraints**. On the other hand, if the protein can function well despite any of many amino acid changes (i.e., it is less constrained), $d_{N/S}$ will be higher. Pág 236

According to the neutral theory, the rate of allele substitution over time and the equilibrium level of heterozygosity are both proportional to the neutral mutation rate, μ . If, because of differences in **constraint** or other factors, various kinds of DNA sequences or base pair sites differ in their rate of neutral mutation, those sequences or sites that differ more between related species should also display greater levels of variation within species. Pág 238

That suggests that monogamy evolved only once, and has been retained by all callitruicids for unknown reasons: perhaps monogamy is advantageous for all the species, or perhaps an internal **constraint** of some kind prevents the evolution of polygamy even if it would be adaptive pág 264

It cannot fix the best of all conceivable variants if they do not arise, or have not yet arisen, and the best possible variants often fall short of perfection because of various kinds of **constraints**. For example, with a fixed amount of available energy or nutrients, a plant might evolve higher seed numbers, but only by reducing the size of its seeds or some other part of its structure (see Chapter 17). Pá g 264

Thus genetic correlations, owing in some cases to trade-offs of this kind, can sometimes act as genetic constraints on evolution. Whether or not a genetic correlation acts as a long term **constraint** depends on several factors, such as how readily the genetic correlation changes. Pá g 316

From the observation that many fossil lineages change little over the course of millions of years (see Chapter 7), they proposed that in broadly distributed species, internal **constraints** may prevent adaptive evolution. They suggested, based on Mayr's (1954) proposal that founder events trigger rapid evolution from one genetic equilibrium to another, that most evolutionary changes in morphology are triggered by and associated with peripatric speciation. Pá g 401

Because traits evolve so as to maximize fitness, we might naively expect organisms to evolve ever greater fecundity, ever longer life, and ever earlier maturation. That all organisms are nevertheless limited in these respects may be attributed to various **constraints**. Pá g 408

Other **constraints**, termed PHYSIOLOGICAL or GENETIC **CONSTRAINTS**, are less well understood, but may be detected by comparisons among different genotypes or phenotypes. Some such **constraints** constitute trade offs, whereby the advantage of a change in a character is correlated with a disadvantage in other respects. Pá g 409

In this example, λ increased from less than 1 to approximately 1, as expected if **constraints** were relaxed following loss of function. Pá g 454

Traditional neo-Darwinian theory explains how natural selection, genetic drift, and gene flow, acting on the raw material of genetic variation, have produced the astonishing variety of organisms. But does it explain why organisms have not evolved certain features, or in certain directions? Does it explain why there are no live-bearing turtles, for instance, or why frogs have no more than four digits on their forelimbs? Such questions have led evolutionary biologists to ask what the **constraints** on evolution might be. Pá g 490

Physical constraints. Some structures do not evolve because the properties of biological materials (e.g., bones, epidermis, DNA, RNA, etc.) do not permit them. Physical **constraints** can be phylogenetically local. Insects, for example, conduct oxygen and carbon dioxide by means of diffusion in narrow tubes, or tracheae, which branch through hollow the body. Limits on diffusion rates are thought to set an upper limit on insect body size. Pá g 491

Genetic **constraints**. Genetic variation in a particular phenotype may not be present, as discussed in Chapter 13. Developmental pathways are expected to have varying degrees of tolerance for variation in their components, and their limits of tolerance may limit variation in the resulting traits. Moreover, if two traits share a common pathway of morphogenesis, the genes underlying that pathway will have strong pleiotropic effects, resulting in genetic correlations that limit the freedom with which those traits can vary relative to each other (see Chapter 13). Thus genetic **constraints**,

such as paucity of variation and genetic correlation, are closely related to developmental **constraints**. 4. Developmental **constraints**. Maynard Smith et al. (1985) defined a **constraint** as "a bias on the production of various phenotypes caused by the structure, character, composition, or dynamics of the developmental system." The two most common phenomena attributed to developmental **constraints** are absence or paucity of variation, including the absence of morphogenetic capacity (i.e., lack of cells, proteins, or genes required for the development of a structure), and strong correlations among characters, which may result from interaction between tissues during development or the involvement of the same genes or developmental pathways in multiple morphogenetic processes. Pág 491

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Although in practice it is very difficult to rule out selective **constraints**, developmental or genetic **constraints** might explain some evolutionary patterns: Pág 492

Morphological stasis over long periods of evolutionary time. The absence of evolutionary change has many possible explanations, of which developmental **constraint** is one (see Chapter 21). Pág 493

Similarities in embryological stages among higher taxa. Such similarities might result from the need to conserve early developmental processes so as not to disturb the later events that depend on them (Riedl 1978). von Baer's law (see Figure 3.12) may be a consequence of developmental **constraints**. For example, the notochord, which persists throughout life in the most "primitive" vertebrates, is almost completely lost in the postembryonic forms of "advanced" vertebrates, but is needed in the embryo in order to induce the differentiation of central nervous system tissues. Pág 493

Several kinds of **constraints** on evolution may determine that certain evolutionary trajectories are followed and not others. Developmental systems are thought to impose some **constraints** on morphological evolution. Some **constraints** may be restricted to certain clades (i.e., may be phylogenetically "local"). Pág 498

Internal genetic or developmental **constraints**. Eldredge and Gould (1972) proposed that stasis is caused by internal genetic or developmental **constraints**, which would be manifested by lack of genetic variation or by genetic correlations too strong to permit characters to evolve independently to new optima. But although such **constraints** may indeed play a role in evolution, as we will see below, they cannot explain the constancy of size and shape of many quantitative characters, which are almost always genetically variable and only imperfectly correlated with one another (see Chapter 13) Pág 504

Development can therefore impose **constraints** on the rate or direction of evolution of a character. The consequences of such **constraints** are made clear when an adaptive function is performed not by the structure we might expect, but by another structure that has been modified instead. The giant panda, for example, has six apparent fingers, evidently useful for manipulating the bamboo on which it feeds. The outermost "finger" (or "thumb"), however, is not a true digit, but a sesamoid bone that develops from cartilage (Figure 21.8) Pág 509

Decoupling the multiple functions of an ancestral feature frees it from functional **constraints** and may lead to its elaboration. For example, the locomotory muscles of many "reptiles" insert on the ribs, so that these animals cannot breathe effectively while running. Pág 511

David Wake ("1982) has proposed that the loss of lungs in the largest family of salamanders (Plethodontidae) has relieved a functional **constraint** on the evolution of the tongue. In other salamanders, the bones that support the tongue are also used for moving air in and out of the lungs. Pág 511

The boundaries that enforce passive trends may be due to either functional or developmental genetic **constraints**. Pág 515

But this history of evolutionary change is explained by evolutionary theory, the body of statements (about mutation, selection, genetic drift, developmental **constraints**, and so forth) that together account for the various changes that organisms have undergone, Pág 527

EFEITO FUNDADOR

Restrictions in size through which populations may pass are called bottlenecks. A particularly interesting bottleneck occurs when a new population is established by a small number of colonists, or founders---sometimes as few as a single mating pair (or a single unispermated female, as in insects in which females store sperm). The random genetic drift that ensues is often called a **founder effect**. If the new population rapidly grows to a large size, allele frequencies (and therefore heterozygosity) will probably not be greatly altered from those in the source population, although some rare alleles will not have been carried by the founders. If the colony remains small, however, genetic drift will alter allele frequencies and erode genetic variation. If the colony persists and grows; new mutations eventually restore heterozygosity to higher levels (Figure 10.6). Pág 232

THE HYPOTHESIS. One of Ernst Mayr's most influential and controversial hypotheses was **founder effect** speciation (1954), which he later termed *peripatric speciation* (1982b). He based this hypothesis on the observation, in many birds and other animals, that isolated populations with restricted distributions, in locations peripheral to the distribution of a probable "parent" species, often are highly divergent, to the point of being classified as different species or even genera. For example, the small lizard *Uta stansburiana* exhibits only subtle geographic variation throughout western North America, but populations on different islands in the Gulf of California vary so greatly in body size, scalation, coloration, and ecological habits that some have been named separate species (Soule 1966). Pág 389

Mayr proposed that genetic change could be very rapid in localized populations founded by a few individuals and cut off from gene exchange with the main body of the species. He reasoned that allele frequencies at some loci would differ from those in the parent population because of accidents of sampling in the genetic drift---simply because a small number of colonists would carry only some of the alleles from the source population, and at altered frequencies. (He termed this initial alteration of allele frequencies the **FOUNDER EFFECT**; see Chapter 10.) Because epistatic interactions among genes affect fitness, this initial change in allele frequencies at some loci would alter the selective value of genotypes at other interacting loci. Pág 389

The environment of peripheral populations often differs substantially from that occupied by more central populations, both in abiotic factors such as climate and in the species composition of the community. Thus peripheral populations often diverge simply because of natural selection, not because of **founder effects**. Pág 391

Peripatric speciation, or **founder effect** speciation, is a hypothetical form of allopatric speciation in which genetic drift in a small peripheral population initiates rapid evolution, and reproductive isolation is a by-product. The likelihood of this form of speciation differs greatly depending on the mathematical model used. Although the geographic pattern of speciation predicted by this hypothesis may be common, there is little evidence for the process of drift-induced speciation. Pág 403

That is, Eldredge and Gould applied Mayr's model of **founder effect** speciation (peri patri speciation) to macroevolutionary change, proposing that most morphological characters cannot evolve (because of internal genetic constraints) except when genetic drift initiates a shift to a new adaptive equilibrium (see Chapter 16). Pág 502

Founder effect The principle that the founders of a new population carry only a fraction of the total genetic variation in the source population. Pág 548

RIDLEY

SELECÃO

When Darwin put forward his theory of evolution by natural **selection**, he lacked a satisfactory theory of inheritance, and the importance of natural **selection** was widely doubted until it was shown in the 1920s and 1930s how natural **selection** could operate with Mendelian inheritance. pag1

The two key events in the history of evolutionary thought are therefore Darwin's discovery of evolution by natural **selection** and the synthesis of Darwin's and Mendel's theories as a synthesis variously called the modern synthesis, the synthetic theory of evolution, and neo-Darwinism. pag1

It considers the conditions for natural **selection** to operate, and the main kinds of natural **selection**. One crucial condition is that the population should be variable, that is, individuals should differ from one another; the chapter shows that variation is common in nature. New variants originate in mutation. pag1

However, a beautifully simple and easily understood idea of evolution by natural **selection** can be scientifically tested in all these fields. pag4

In Darwin's theory as in modern evolutionary biology the problem is solved by natural **selection**. pag4

Natural **selection** means that some kinds of individual in a population tend to contribute more offspring to the next generation than do others. pag4

Wallace had independently arrived at a very similar idea to Darwin's natural **selection**. pag10

The reactions to Darwin's two connected theories of evolution and natural **selection** differed. pag10

While evolution of a sort was being accepted, natural **selection** was just as surely being rejected. People disliked the theory of natural **selection** for many reasons. This first chapter is not going to explain the arguments in any depth. pag12

One of the deepest hitting criticisms of the theory of natural **selection** pointed out that it could hardly operate at all if heredity blended (Section 2.9, p. 37). pag12

At a more popular level, many objections were raised against natural **selection**. One was that natural **selection** explains evolution by chance. This was (and still is) a misunderstanding of natural **selection**, which is a non-random process. Almost every chapter in this book after Chapter 4 illustrates how natural **selection** is non-random, but the topic is particularly discussed in Chapters 4 and 10. Chapters 6–7 discuss an evolutionary process called random drift. Random drift is random, but it is a completely different process from natural **selection**. pag12

A second objection was that gaps exist between forms in nature as gaps that could not be crossed if evolution was powered by natural **selection** alone. pag13

In Darwin's theory, organs evolve gradually, and each successive stage has to be advantageous in order that it can be favored by natural **selection**. pag 13

Biologists who accepted the criticism sought to get round the difficulty by imagining processes other than **selection** that could work in the early stages of a new organ's evolution pag13

In Darwin's time, the debate was about the relative importance of natural **selection** and the inheritance of acquired characteristics; but by the 1880s the debate moved into a new stage. pag13

Weismann initially suggested that practically all evolution was driven by natural **selection**, but he later retreated from this position. pag13

Around the turn of the century, Weismann was a highly influential figure, but few biologists shared his belief in natural **selection**. Some, such as the British entomologist Edward Bagnall Poulton, were studying natural **selection**. However, the majority view was that natural **selection** needed to be supplemented by other processes. An influential history of biology written by Erik Nordenskiöld in 1929 could even take it for granted that Darwin's theory was wrong. About natural **selection**, he concluded "that it does not operate in the form imagined by Darwin must certainly be taken as proved;" the only remaining question, for Nordenskiöld, was "does it exist at all?" pag13

The early Mendelians, such as Hugo de Vries and William Bateson, all opposed Darwin's theory of natural **selection**. pag13

Darwin's theory than were the Mendelians. W.F. Weldon, for instance, was a biometrician, and he attempted to measure the amount of **selection** in crab populations on the seashore. pag14

The next step was to show that natural **selection** could operate with Mendelian genetics. pag15

Their synthesis of Darwin's theory of natural **selection** with the Mendelian theory of heredity established what is known as neo- Darwinism, or the synthetic theory of evolution, or the modern synthesis, after the title of a book by Julian Huxley, *Evolution: the Modern Synthesis* (1942). pag15

The ideas of Fisher, Haldane, and Wright are known mainly from their great summary works all written around 1930. Fisher published his book *The Genetical Theory of Natural Selection* in 1930. pag15

Haldane published a more popular book, *The Causes of Evolution*, in 1932; it contained a long appendix under the title "A mathematical theory of artificial and natural **selection**," summarizing a series of papers published from 1918 onwards. pag15

These classic works of theoretical population genetics demonstrated that natural **selection** could work with the kinds of variation observable in natural populations and the laws of Mendelian inheritance. pag15

E.B. Ford (1901–88) began in the 1920s a comparable program of research in the UK. He studied **selection** in natural populations, mainly of moths, and called his subject "ecological genetics." pag16

Robson and Richards suggested that the differences between species are non-adaptive and have nothing to do with natural **selection**. Richard Goldschmidt (1878–1958), most famously in his book

on *The Material Basis of Evolution* (1940), argued that speciation was produced by macromutations, not the **selection** of small variants. pag17

It then considers how Darwin's theory almost required heredity to be Mendelian, because natural **selection** can hardly operate at all with a blending mechanism of inheritance. pag21

The measuring conditions must be such as to minimize, and ideally to eliminate, the action of natural **selection** pag31

Natural **selection** usually cannot be completely neutralized, however, and the estimates that we have for mutation rates are only approximate. pag31

The problem was Darwin's lack of a sound theory of heredity, and indeed it had even been shown in Darwin's time that natural **selection** would not work if heredity was controlled in the way that, before Mendel, most biologists thought it was. pag38

Why does this preservation of genes matter for Darwinism? Our full discussion of natural **selection** comes in later chapters, and some readers may prefer to return to this point after they have read about natural **selection** in more detail; but even with only the elementary account of natural **selection** in Chapter 1, it is possible to understand why Darwin, so to speak, needed Mendel. Figure 2.11 illustrates the argument. pag39

This objection to the theory of natural **selection** was known to Darwin. Darwin was very worried by it and never did find a wholly satisfactory way round it. pag41

There is ample time for natural **selection** to increase the proportion of light green individuals, and eventually there would be enough of them for there to be a chance that two will mate together and produce some AA homozygotes among their offspring. pag41

Thus natural **selection** is a powerful process with Mendelian heredity, because Mendelian genes are preserved over time; whereas it is at best a weak process with blending inheritance, because potentially favorable genes are diluted before they can be established. pag41

The change, from a viral population that was susceptible to 3TC to a viral population that was resistant to 3TC, is an example of evolution by natural **selection**. pag45

In a typical artificial **selection** experiment, a new generation is formed by allowing only a selected minority of the current generation to breed (Figure 3.3)pag47

The procedure is routinely used in agriculture an artificial **selection** has, for example, been used to alter the numbers of eggs laid by hens, the meat properties of bullocks, and the milk yield of cows. pag47

Artificial **selection** can produce dramatic change, if continued for long enough. A kind of artificial **selection**, for example, has generated almost all our agricultural crops and domestic pets. No doubt the artificial **selection** in these cases abegun thousands of years ago in some cases an employed less formal techniques than would a modern breeder. pag48

What degree of difference, in these taxonomic terms, has been produced by artificial **selection** in domestic animals? All domestic pigeons can interbreed, and are members of the same species in a reproductive sense. pag50

The evidence from domestic animals suggests that artificial **selection** can produce extensive change in phenotypic appearance a enough to produce new species and even new genera a but has not produced much evidence for new reproductive species. pag50

No one will have any difficulty in seeing how the examples of evolution in action, from moths and artificial **selection**, suggest that species are not fixed in form. pag59

The theory of evolution has a mechanical, scientific theory for adaptation: natural **selection**.3. pag67

This chapter first establishes the conditions for natural **selection** to operate, and distinguishes directional, stabilizing, and disruptive forms of **selection**. pag71

The excess fecundity, and consequent competition to survive in every species, provide the preconditions for the process Darwin called natural **selection**. Natural **selection** is easiest to understand, in the abstract, as a logical argument, leading from premises to conclusion. pag74

Variation in individual characters among the members of the population. If we are studying natural **selection** on body size, then different individuals in the population must have different body sizes. (See Section 1.3.1, p. 7, on the way biologists use the word “character.”). pag74

If these conditions are met for any property of a species, natural **selection** automatically results. And if any are not, it does not. Thus entities, like planets, that do not reproduce, cannot evolve by natural **selection**. Entities that reproduce but in which parental characters are not inherited by their offspring also cannot evolve by natural **selection**.
pag74

The increase in the frequency of drug-resistant HIV is almost certainly driven by natural **selection**. The virus satisfies all four conditions for natural **selection** to operate. pag75

The virus reproduces; the ability to resist drugs is inherited (because the ability is due to a genetic change in the virus); the viral population within one human body shows genetic variation in drug-resistance ability; and the different forms of HIV have different fitnesses. In a human AIDS patient who is being treated with a drug such as 3TC, the HIV with the right change of amino acid in their reverse transcriptase will reproduce better, produce more offspring virus like themselves, and increase in frequency. Natural **selection** favors them. pag75

Natural **selection** produces evolution when the environment changes; it will also produce evolutionary change in a constant environment if a new form arises that survives better than the current form of the species. pag75

Natural **selection** can not only produce evolutionary change, it can also cause a population to stay constant. If the environment is constant and no superior form arises in the population, natural **selection** will keep the population the way it is. Natural **selection** can explain both evolutionary change and the absence of change. pag75

Natural **selection** also explains adaptation. The drug resistance of HIV is an example of an adaptation (Section 1.2, p. 6). The discriminatory reverse transcriptase enzyme enables HIV to reproduce in an environment containing nucleoside inhibitors. The new adaptation was needed because of the change in the environment. pag75

The action of natural **selection** to increase the frequency of the gene coding for a discriminating reverse transcriptase resulted in the HIV becoming adapted to its environment. Over time, natural **selection** generates adaptation. Pag75-76

Over time, natural **selection** generates adaptation. The theory of natural **selection** therefore passes the key test set by Darwin (Section 1.3.2, p. 8) for a satisfactory theory of evolution. pag76

In HIV, natural **selection** adjusted the frequencies of two distinct types (drug susceptible and drug resistant). However, many characters in many species do not come in distinct types. pag76

Natural **selection** is then directional: it favors smaller individuals and will, if the character is inherited, produce a decrease in average body size (Figure 4.2a). Directional **selection** could, of course, also produce an evolutionary increase in body size if larger individuals had higher fitness. pag76

The **selection** favoring small size in the salmon population was intense, because fishing effort is highly efficient and about 75–80% of the adult salmon swimming up the rivers under investigation were caught in these years. The average weight of salmon duly decreased, by about one-third, in the next 25 years. pag76

A second (and in nature, more common) possibility is for natural **selection** to be stabilizing (Figure 4.2b). The average members of the population, with intermediate body sizes, have higher fitness than the extremes. Natural **selection** now acts against changes in body size, and keeps the population constant through time. pag76

Studies of birth weight in humans have provided good examples of stabilizing **selection**. pag76

Stabilizing **selection** has probably operated on birth weight in human populations from the time of the evolutionary expansion of our brains about 1–2 million years ago until the twentieth century. pag77

However, in the 50 years since Karn and Penrose's (1951) study, the force of stabilizing **selection** on birth weight has relaxed in wealthy countries (Figure 4.4b), and by the late 1980s it had almost disappeared. pag77

Selection has relaxed because of improved care for premature deliveries (the main cause of lighter babies) and increased frequencies of Caesarian deliveries for babies that are large relative to the mother (the lower survival of heavier babies was mainly due to injury to the baby or the mother during birth). By the 1990s in wealthy countries, the stabilizing **selection** that had been operating on human birth weight for over a million years had all but disappeared. pag80

The third type of natural **selection** occurs when both extremes are favored relative to the intermediate types. This is called disruptive **selection** (Figure 4.2c). T.B. Smith has described an example in the African finch *Pyrenestes ostrinus*, informally called the black-bellied seedcracker (Smith & Girman 2000) (see Plate 2, between pp. 68 and 69). pag80

In an environment with a bimodal resource distribution, natural **selection** drives the finch population to have a bimodal distribution of beak sizes. Natural **selection** is then disruptive. pag80

Disruptive **selection** is of particular theoretical interest, both because it can increase the genetic diversity of a population (by frequency-dependent **selection** a Section 5.13, p. 127) and because it can promote speciation (Chapter 14). Pag80-81

A final theoretical possibility is for there to be no relation between fitness and the character in question: then there is no natural **selection** (Figure 4.2d; Figure 4.4b provides an example or a near example). pag81

Natural **selection** will operate whenever the four conditions in Section 4.2 are satisfied
pag81

Not all the characters of organisms are inherited; and natural **selection** will not adjust the frequencies of non-inherited characters. But many are inherited, and natural **selection** can potentially work on them. The third and fourth conditions do need further comment. pag81

When we move on to look at natural **selection** in more detail, we can assume that in natural populations the requirement of variation, as well as of reproduction and heredity, is met. pag84

If natural **selection** is to operate, it is not enough that characters vary. The different forms of the character must also be associated with reproductive success (or fitness) a in the degree to which individuals contribute offspring to the next generation.
pag85

Examples such as HIV, or the pink salmon, show that natural **selection** can operate; but that leaves open the question of how often natural **selection** operates in natural populations, and in what proportion of species. pag86

We could theoretically find out how widespread natural **selection** is by counting how frequently all four conditions apply in nature. That, however, would at the least be hard work. The evidence of variation in phenotypic characters and of ecological competition suggests that the preconditions required for natural **selection** to operate are widespread, indeed probably universal. pag86

It is logically possible that individual reproductive success varies in all populations in the manner of Figure 4.8, but that natural **selection** does not operate in any of them, because the variation in reproductive success is not associated with any inherited characters. Pag 86

The argument is one of plausibility, rather than certainty: it is not logically inevitable that in a population showing (inherited) variation in a phenotypic character there will also be an association between the varying character and fitness. But if there is, natural **selection** will operate. Pag 86-87

The variation that exists in a population is the resource on which natural **selection** works. Imagine a population evolving increased body size. To begin with there is variation and average size can increase. Pag 87

The evolution of humans more than 8 feet high would be impossible if natural **selection** only had the currently existing variation to work on.pag87

Given that resistance to 3TC requires a change in only one amino acid, we can see that natural **selection** is an overwhelmingly powerful counterforce against human medicine operating with single-drug treatments.Pag 88

Natural **selection** imposes direction on evolution, using undirected variation. In this section, we define the alternative viewpoint (the theory of directed variation) and consider why it is not accepted. pag88

The simplest case is when the population is large, large enough that we can ignore random effects; models of this kind are called deterministic. In Chapter 5, we look at a simple deterministic model of natural **selection**. pag93

We also look at how natural **selection** can maintain variation at a single locus, in three circumstances, and look at examples of each. pag93

Chapter 7 looks at the relative contributions of random drift and natural **selection** to molecular evolution. The question of their relative contributions has stimulated one of the richest research programs in evolutionary biology. We shall concentrate on modern research, but look at its conceptual roots too. pag93

In Chapter 8, we move on to consider natural **selection** working simultaneously on more than one locus. Linkage between loci complicates the one-locus model. With more than one locus, the genes at different loci may interact and influence each other's fitness. pag93

We then move on to models of natural **selection**, concentrating on the specific case of **selection** against a recessive homozygote. Pag 96

The second half of the chapter is mainly about how natural **selection** can maintain genetic polymorphism. We look at **selection**–mutation balance, heterozygous advantage, and frequency-dependent **selection**; and we finish by looking at models that include migration in a geographically subdivided population. The theory in this chapter all assumes that the population size is large enough for random effects to be ignored. Chapters 6 and 7 consider how random effects can interact with **selection** in small populations. Pag 96

Natural **selection** can operate in two ways: by differences in survival among genotypes or by differences in fertility. There are two theoretical extremes. At one, the surviving individuals of all genotypes produce the same number of offspring, and **selection** operates only on survival; at the other, individuals of all genotypes have the same survival, but differ in the number of offspring they produce (that is, their fertility). Both kinds of **selection** probably operate in many real cases, but the models we shall consider in this chapter all express **selection** in terms of differences in chance of survival. This is not to suggest that **selection** always operates only on survival; it is to keep the models simple and consistent. Pag 98

The model, in the general form of Figure 5.1, may look rather complicated. However, we can cut it down to size by making some simplifying assumptions. The first two simplifying assumptions to consider are random mating and no **selection** (no differences in survival between genotypes from stages 4 to 5). Pag 98

After reaching those frequencies immediately, in one generation, the population stays at the Hardy Weinberg equilibrium for as long as the population size is large, there is no **selection**, and mating is random. Pag 100

We can now see that it is possible to calculate, from gene frequencies alone, what the genotype frequencies will be in the next generation, provided that mating is random, there is no **selection**, and the population is large. Pag 100

The Hardy–Weinberg theorem depends on three main assumptions: no **selection**, random mating, and large population size. In a natural population, any of these could be false; we cannot assume that natural populations will be at the Hardy–Weinberg equilibrium. Pag 102

In fact all three populations are at Hardy–Weinberg equilibrium. We shall see in Section 5.6 that the same calculations do not correctly predict the genotype frequencies after **selection** has operated. Pag 103

We have no good reason to think that genotypes in natural populations will generally have Hardy–Weinberg frequencies, because it would require both no **selection** and random mating, which are rarely found. The interest of the theorem lies elsewhere, in three other areas. Pag 103

If we compare genotype frequencies in a real population with Hardy–Weinberg ratios, then if they deviate it suggests something interesting (such as **selection** or non-random mating) may be going on, which would merit further research. Pag 103

A simple model of **selection** can concentrate on how the genotype frequencies are modified between birth and the adult reproductive stage (from stage 2 to stage 3 of Figure 5.3). Pag 104

We shall start with the simplest case. It is the case of natural **selection** operating on only one genetic locus, at which there are two alleles, one dominant to the other. Pág 104

Haldane (1924) first produced this particular model of **selection**. One important feature of the model is that it shows how rapidly, in evolutionary time, natural **selection** can produce change. Pag 107

A quantitative model such as Haldane's was needed to answer the quantitative question of how rapidly **selection** can drive evolution. Pag 108

All we need to know for these estimates is that natural **selection** is acting a just how it is acting, whether by bird predators or other factors, is another question. Pag 108

It may be that **selection** initially favored a melanic allele with no or weak dominance, and subsequently some other melanic alleles with stronger dominance. Pag 108

The melanic form was first seen in 1848; but it was probably not a new mutation then. It probably existed at a low frequency in the population, in what is called “mutation–**selection** balance.” Mutation–**selection** balance means that the gene is disadvantageous, and exists at a low frequency determined by a balance between being formed by mutation and being lost by **selection** (Section 5.11). pag110

The gene frequency changes have undoubtedly occurred, and provide an excellent example of evolution by natural **selection**. Now we can move on to ask what the agent, or agents, of natural **selection** were in this example. Pag 112

In conclusion, the industrial melanism of the peppered moth is a classic example of natural **selection**. It can be used to illustrate the one-locus, two-allele model of **selection**. The model can be used to make a rough estimate of the difference in fitness between the two forms of moth using their frequencies at different times; the fitnesses can also be estimated from mark–recapture experiments. Good evidence exists that bird predation is at least partly the agent of **selection**, but some biologists suggest other factors are at work too. Pag 104

DDT becomes ineffective so quickly now because DDT-resistant mosquitoes exist at a low frequency in the global mosquito population and, when a local population is sprayed, a strong force of **selection** in favor of the resistant mosquitoes is immediately created. Pag 115

It is only a matter of time before the resistant mosquitoes take over. A graph such as Figure 5.7 allows a rough estimate of the strength of **selection**. Pag 115

If we define p as the frequency of R and q as the frequency of r , equation 5.5 again gives the change in gene frequency: **selection** is working against a recessive gene. Pag 116

It appears that in Figure 5.7 the resistant mosquitoes had about twice the fitness of the susceptible ones which is very strong **selection**. Pag 117

In the absence of DDT, the resistance disappeared, which suggests that the amplified genotype has to be maintained by **selection**. Pag 117

But however that may be, pesticides did not exist during the hundreds of millions of years that insects lived for before they were introduced in the 1940s, and the rapid evolution since then of resistance to pesticides provides a marvellously clear example of evolution by natural **selection** (Section 10.7.3, p. 276, extends the story, and Box 8.1, p. 213, looks at drug resistance in the malaria organism itself). Pag 119

The time it takes for resistance to evolve will be influenced by several factors. Two such factors can be seen in the simple models of **selection** we have been considering. Pag 119

The frequency of an advantageous dominant gene increases much more rapidly by natural **selection** than does the frequency of an advantageous recessive gene. Pag 119

Natural **selection** cannot “see” the gene until it is found in a homozygote. If the gene is dominant, it is immediately expressed and natural **selection** immediately favors it. Pag 119

A review of research on natural **selection** in the wild by Endler in 1986 contains a table (24 pages long) listing all the work he had located. Pag 120

Fitnesses have only been measured in a minority and an unknown minority of those 24 pages’ worth of studies of natural **selection**, but the number could still be non-trivial.) pag 120

Evolutionary change in which natural **selection** favors a rare mutation at a single locus, and carries it up to fixation, is one of the simplest forms of evolution. pag 120

But things can be more complicated in nature. We have considered **selection** in terms of different chances of survival from birth to adulthood; but **selection** can also take place by differences in fertility, if individuals of different genotypes after they have survived to adulthood produce different numbers of offspring. pag 121

The model of **selection** at one locus revealed how a favorable mutation will spread through a population. But what about unfavorable mutations? Natural **selection** will act to eliminate any allele that decreases the fitness of its bearers, and the allele’s frequency will decrease at a rate specified by the equations of Section 5.6; but what about a recurrent disadvantageous mutation that keeps arising at a certain rate? **Selection** can never finally eliminate the gene, because it will keep on reappearing by mutation. pag 121

In this case, we can work out the equilibrium frequency of the mutation: the equilibrium is between the mutant gene's creation, by recurrent mutation, and its elimination by natural **selection**. pag121

However, the general idea of this section is that a balance between **selection** and mutation can exist and explain genetic variation will be used in later chapters. pag123

Genes and genes are both removed by **selection**. The A genes are removed because they appear in the inferior AA homozygotes and the a genes because they appear in aa homozygotes. At the equilibrium, both genes must have the same chance of being removed by **selection**. pag124

When heterozygotes are fitter than the homozygotes, therefore, natural **selection** will maintain a polymorphism. The result was first proved by Fisher in 1922 and independently by Haldane. pag124

Allison (1954) showed that, although SS is almost lethal, the heterozygote AS is more resistant to malaria than the homozygote AA. (Allison's was the first demonstration of natural **selection** at work in a human population.). pag126

Selection causes deviations from the Hardy–Weinberg frequencies. Take the genotype AA as an example. pag126

The next interesting complication is to consider **selection** when the fitness of a genotype depends on its frequency. pag127

Frequency-dependent **selection** means that natural **selection** is acting and the fitnesses of the genotypes vary with the frequency of the genotypes. pag127

Then, if one of the host genotypes is in high frequency, natural **selection** will favor the parasite genotype that can penetrate that common kind of host. The result is that a high frequency automatically brings a disadvantage to a host genotype, because it creates an advantage for the kind of parasite that can exploit it. pag127

Natural **selection** favors a gene when it is rare, but works against it when it is common. The result is that genotypes equilibrate at some intermediate frequency. pag128

The purpose of Sections 5.11–5.13 has been to illustrate the different mechanisms by which natural **selection** can maintain polymorphism. In Chapter 6 we look at another mechanism that can maintain polymorphism a genetic drift. pag129

We might suspect that **selection**, or some other factor, was favoring homozygotes. In fact both subpopulations are in perfectly good Hardy–Weinberg equilibrium and the deviation is due to the unwitting pooling of the separate populations. pag130

The transfer of genes is called gene flow. If the two populations originally had different gene frequencies and if **selection** is not operating, migration (or, to be exact, gene flow) alone will rapidly cause the gene frequencies of the different populations to converge. We can see how rapidly in a simple model. pag131

Migration will generally unify gene frequencies among populations rapidly in evolutionary time. In the absence of **selection**, migration is a strong force for equalizing the gene frequencies of populations within a species. pag132

Individuals of mixed parentage are usually categorized as African American and, if we ignore the possibility of **selection** favoring the M allele in the USA, we can treat the change in gene frequency in the African American population as due to “migration” of genes from the European American population. pag132

If **selection** is working against an allele within one subpopulation, but the allele is continually being introduced by migration from other populations, it can be maintained by a balance of the two processes. pag133

We can analyze the balance between the two processes by much the same arguments as we used above for **selection** mutation balance and heterozygous advantage. The simplest case is again for one locus with two alleles. Imagine **selection** in one subpopulation is working against a dominant allele. The fitnesses of the genotypes are: pag132

The allele has frequency p in the local population. Suppose that in other subpopulations, natural **selection** is more favorable to the gene A, and it has a higher frequency in them, p_m on average. p_m will then be the frequency of A among immigrants to our local population. In the local population, genes are lost at a rate ps per generation. pag133

The third possibility is an exact balance between migration and **selection**. There will be equilibrium (with local frequency of A = p^*) if: pag133

In the first case, migration unifies the gene frequencies in both populations, much in the same manner as Section 5.14.2: migration is so strong relative to **selection** that it is as if **selection** were not operating. pag133

This theory is also relevant in the question of the relative importance of gene flow and **selection** in maintaining biological species (Section 13.7.2, p. 369). pag133

We see how drift is more powerful in small than large populations, and how in small populations it can counteract the effects of natural **selection**. pag137

We also imagine that natural **selection** is not operating: all genotypes have the same fitness. What will the gene frequencies be in the next generation? The most likely answer is 0.5 A and 0.5 a. pag138

The easiest case in which to see the effect of random sampling is when natural **selection** is not acting. When the genotypes at a locus all produce the same number of offspring (they have identical fitness), the condition is called selective neutrality. pag138

Natural **selection** is not acting, and we might expect the gene frequencies to stay constant over time. Indeed, according to the Hardy–Weinberg theorem, the genotype frequencies should be constant at p^2 , $2pq$, and q^2 (where p is the frequency of the gene A and q is the frequency of the gene a). pag138

Genetic drift is not confined to the case of selective neutrality. When **selection** is acting at a locus, random sampling also influences the change in gene frequencies between generations. The interaction between selection and drift is an important topic in evolutionary biology, as we shall see in Chapter 7. However, the theory of drift is easiest to understand when **selection** is not complicating the process and in this chapter we shall mainly look at the effect of drift by itself. pag138

Natural **selection** would be determining which horses survived and which died. If we looked at the genotypic frequencies among the smashed horses at the bottom of the ravine they would differ from those among the survivors. pag139

Population geneticists study how far back the coalescent exists for a gene, depending on population size, demography, and **selection**. pag144

This chapter discusses the relative importance of two processes in driving molecular evolution: random drift and natural **selection**. pag155

The relative contributions of **selection** and drift to non-synonymous (Amino acid altering) changes are less clear. Natural **selection** can leave its signature in the statistical properties of DNA sequences, and the modern genomic era of biology has made it possible to study **selection** and drift in new ways. The chapter finishes by looking at four of these. pag155

Polymorphism within a species, and evolutionary change between species, can be explained by two processes: natural **selection** and drift. This chapter will be looking at the contributions of drift and **selection** in molecular evolution. The subject hardly existed before the 1960s. pag156

The neutral theory does not suggest that random drift explains all evolutionary change. Natural **selection** is still needed to explain adaptation. It is, however, possible that the adaptations we observe in organisms required only a small proportion of all the evolutionary changes that have actually taken place in the DNA. pag156

“Genetic variant” could be substituted for “mutation” throughout this paragraph.) Given a mutation of a certain **selection** coefficient, the theory of random drift or **selection** (as described in Chapters 5 and 6) applies in a mathematically automatic way. pag156

If natural **selection** has produced most evolutionary change at the molecular level, many advantageous mutations must have occurred, but few neutral mutations. pag157

The neutral theory therefore does not rule out natural **selection**. It simply has a different use for it than has the **selectionist** theory of molecular evolution. pag158

The **selectionist** theory uses natural **selection** to explain both why mutations are lost (when they are disadvantageous) and are fixed (when they are advantageous). The neutral theory uses **selection** only to explain why disadvantageous mutation are lost; it uses drift to explain how new mutations are fixed. pag158

Selectionist and neutral theories of molecular evolution agree that **selection** drives adaptive evolution. The disagreement is over what fraction of molecular evolution is adaptive. pag158

The **selectionist** alternative is that the few hundred variants are not equivalent, but that one works better in one environment, another in another environment, and so on. Evolution then consists of the substitution of one variant for another when the environment changes. pag158

The direct way to test between them should simply be to measure the fitnesses of many genetic variants at a locus, and count the numbers with negative, neutral, or positive **selection** coefficients under certain environmental conditions pag159

The absolute rate of molecular evolution and degree of polymorphism, both of which have been argued to be too high to be explained by natural **selection**. pag159

The constancy of molecular evolution, which has been argued to be inconsistent with natural **selection**. pag159

The observation that functionally less constrained parts of molecules evolve at a higher rate, which has been argued to be the opposite of what the theory of natural **selection** would predict. pag159

In the second half of the chapter we shall look at some additional ways of testing between drift and **selection** that have become possible in the genomic era. pag159

Kimura (1968, 1983) thought that the rate of molecular evolution, and the amount of molecular variation, was too high for a process driven by natural **selection**. His arguments are now mainly of historic importance and are outlined in Box 7.1. pag161

Everyone would be dead. More realistic evolution will proceed at a lower rate, because the population must continue to exist in reasonable numbers while natural **selection** substitutes superior alleles. pag162

The rate of molecular evolution is clearly far higher than Haldane's estimated upper limit. Kimura concluded that most molecular evolution could not be driven by natural **selection**. pag162

Substitutional load arises when natural **selection** is substituting one (superior) allele for another (inferior) allele. While the inferior allele exists in the population, mean fitness is lower than if all individuals had the superior allele. The substitutional load is mathematically equivalent to another concept, defined by Haldane (1957), and called the "cost of natural **selection**." pag162

Until the disease-resistant genotype is being substituted by natural **selection**, the reproductive output of the birds will decrease. pag163

Substitutional load ultimately limits the rate of evolution whether **selection** is hard or soft, but the limit is much lower with hard **selection**. Much **selection** in fact is probably soft, and does not reduce the reproductive output of a population. pag163

The second counterargument is that natural **selection** can act jointly on many loci. In the argument above about heterozygous advantage, we assumed that each homozygous locus in an individual reduces fitness by a few percent. pag163

Natural **selection** may not work like that. An individual may be able to survive equally well with one, two, three, or 100 homozygous loci, and only after the number of homozygous loci goes over some threshold, such as 500, will that individual's fitness seriously decrease. pag163

A third counterargument is that genetic variation can be maintained by frequency-dependent **selection** without creating a genetic load. (The sex ratio, which maintains the X and Y chromosomes, is an example: see Section 12.5, p. 337.) Thus, even if Kimura's argument rules out heterozygous advantage as the explanation of much genetic variation, it does not rule out all forms of natural **selection**. pag163

Kimura concluded that it was impossible for natural **selection** to maintain all the

genetic variation observed at the molecular level. The genetic variation must be maintained by random drift, which explains polymorphism by a balance of drift and mutation (Section 6.6, p. 150). pag163

One is that the upper limits on the rate of evolution, and on the tolerable level of genetic variation, can be raised if we allow for soft **selection**. Haldane and Kimura's calculation assumed hard **selection**. pag163

Hard **selection** means that natural **selection** adds to the amount of mortality, decreasing the population size. We can distinguish between "background" mortality, due to normal ecological processes (Section 4.1, p. 72), and "selective" mortality, due to the action of natural **selection**. pag163

Natural **selection** is hard if it reduces the number of survivors below two. Natural **selection** is soft if converts some of the background ecological mortality into selective mortality. Population size is not reduced if **selection** is soft. pag163

Half the eggs die before growing up into adults, such that 500 adults compete for the 100 territories each generation (400 will fail a though the numbers might need adjusting if gender introduces complexities). Consider first extreme soft **selection**. pag163

Compare that with hard **selection**. A new disease arises that is only caught by territory holders. pag163

What does a constant rate imply about whether molecular evolution is mainly driven by natural **selection** or neutral drift? Kimura reasoned that constant rates are more easily explained by neutral drift than **selection**. pag165

Natural **selection**, Kimura argued, does not produce such constant change. Under **selection**, the rate of evolution is influenced by environmental change as well as the mutation rate; and it would require a surprisingly steady rate of environmental change, over hundreds of millions of years, in organisms as different as snails and mice and sharks and trees to produce the constant rate of change seen in Figure7.3. pag165

Moreover, if we look at characters, such as any adaptive morphological characters that have undoubtedly evolved by natural selection they do not seem to evolve at constant rates. Kimura (1983) discussed the evolution of the bird wing as an example. pag165

The wings of birds undoubtedly evolved by natural **selection**. The rate of change during wing evolution fluctuated between fast and slow. The rate of molecular evolution appears to be relatively constant, compared with morphological evolution. pag165

Morphological evolution has a different pattern, and is probably driven by the non-random process of **selection**. pag165

Population size only cancels out for purely neutral mutations. For a nearly neutral mutation, the relative power of drift and **selection** depends on population size. Nearly neutral mutations behave as neutral mutations in small populations, and their fate is determined by random drift. They behave as non-neutral mutations in large populations, and their fate is determined by **selection**. pag171

The chance that a slightly advantageous mutation is fixed by **selection** can be calculated and it is roughly $2s$. The mutation has a $1 - 2s$ chance of being lost by random factors.

pag172

Any one copy of the mutation may be lost by chance, but there are so many copies that one of them is likely to survive and be fixed by **selection**. pag172

Evolution, therefore, is arguably dominated by drift in small populations and by **selection** in large populations. pag172

A mutation that satisfies the inequality $4Ns < 1$ (or $Ns < 1$) is a nearly neutral mutation. The class of nearly neutral mutations includes purely neutral mutations ($s = 0$), together with mutations that have small non-zero **selection** coefficients. The conceptual interest of nearly neutral mutations is that they evolve by random drift rather than natural **selection**. pag172

In a species with large populations, natural **selection** is more powerful than drift. The slightly disadvantageous mutations will be eliminated and not contribute to the observed genetic variation in that species. In species with small populations, natural **selection** is weak relative to random drift. pag173

When population size increases, the slightly disadvantageous mutations will be eliminated by **selection** and the rate of evolution will slow down. pag173

In a species with a long generation length, such as a whale, we now have two factors to consider: (i) DNA is copied slowly per year, which reduces the mutation rate per year; and (ii) population sizes are small, which makes drift more powerful than **selection**. Slightly disadvantageous mutations are less likely to be eliminated by **selection**, and are more likely to be fixed by drift. Factor (i) slows the rate of evolution; factor (ii) speeds it up. pag174

The relative power of **selection** and drift on these mutations depends on population sizes. The nearly neutral theory, by plausible arguments about population size, can account for several observations that present problems for Kimura's purely neutral theory. pag174

The nearly neutral theory makes use of natural **selection**. In some circumstances (large population size), the theory draws on natural **selection**; in other circumstances (small population sizes), it does not. Nearly neutral theory might be thought to blur the distinction between "selectionist" and "neutralist" explanations of molecular evolution. pag174

However, a fundamental distinction remains. For any evolutionary change, in which one version of a gene is substituted for another, we can ask whether the force driving that change was natural **selection** or random drift. pag175

Natural **selection** against disadvantageous mutations has a subtler, more flexible form in the nearly neutral theory than in the purely neutral theory. Drift and **selection** combine in different ways in the two theories to explain the observed facts of molecular evolution. But a crucial similarity remains: both theories explain evolution by drift. Natural **selection** has only a negative role, acting against disadvantageous mutations. This contrasts with all "selectionist" theories of molecular evolution, in which molecular evolutionary change occurs because natural **selection** favors advantageous mutations. pag175

Alternatively, the gene copies that make up an allelic class may all have the same sequence because that sequence is maintained by natural **selection**; when a mutation arises, **selection** removes it. pag180

Mutations in non-synonymous sites have presumably not been retained because natural **selection** eliminated them. pag180

If it had turned out that the Adh-f allele was fixed for one DNA sequence at all sites, synonymous and non-synonymous, we should not know whether the uniformity was due to **selection** or identity by descent. We should be in the same position as we were in before Kreitman's DNA-level study. pag180

That polymorphism is known to be maintained by natural **selection**. Therefore, none of the amino acids in the 255 amino acid alcohol dehydrogenase enzyme of the fruitfly can be changed neutrally. pag180

Natural **selection** is powerfully maintaining the amino acid sequence, while synonymous changes evolve by drift. pag181

One is positive **selection** in favor of a change in gene function. The other is relaxed **selection**. pag181

However, natural **selection** could favor a change in the protein. Then the rate of non-synonymous evolution will increase, while the rate of synonymous change will continue as normal, by random drift. Thus an elevated dN/dS ratio can result when natural **selection** has favored a change in the protein coded by a gene. pag181

Alternatively, the dN/dS ratio can go up when natural **selection** is relaxed. Natural **selection** normally prevents amino acid changes. If natural **selection** is stopped from acting, the rate of amino acid evolution will increase. Changes that were disadvantageous become neutral in the absence of **selection**. Natural **selection** may be relaxed in humans, by medical care and other cultural practices that act against natural **selection**. More generally, a rapid increase in population size is a sign that **selection** has been relaxed. When a population colonizes some unexploited territory with abundant resources, there may be a phase of rapid population growth. Natural **selection** will probably be relaxed during this phase. pag181

The two explanations for elevated dN/dS ratios are frustrating because they are conceptually almost opposite. The same data may mean either that positive **selection**, in favor of change, has been acting, or that negative **selection**, against change, has been relaxed. The rate of non-synonymous evolution could go up either way. pag181

Wyckoff et al. thought of several ways round this dilemma. For instance, they looked for dN/dS ratios of more than one. Relaxed **selection** alone cannot take the ratio above one. When **selection** ceases to act on a DNA sequence, both non-synonymous and synonymous changes will be equally neutral and occur at the same rate. The dN/dS ratio will equal one. By contrast, positive **selection** in favor of change can take the dN/dS ratio much higher. If dN/dS > 1, it is a strong sign that natural **selection** has been driving change. pag182

Low, perhaps 0.1–0.2 (though the actual value can vary down the DNA). Interpretation: synonymous change is neutral; there is no evidence that **selection** is driving the change in amino acids. pag182

Between 0.2 and 1. Interpretation: either **selection** has been acting to change the amino acid sequence or **selection** has been relaxed; we do not know which. 3. dN/dS higher than 1. Interpretation: natural **selection** has been acting to change the amino acid sequence. pag182

Biologists have mainly been interested in using dN/dS ratios as evidence for positive **selection**. For them, relaxed **selection** is something to be ruled out. In the protamine gene, $dN/dS > 1$ and we have evidence of adaptive evolutionary change rather than relaxed **selection**. (Wyckoff et al. also presented other evidence for positive **selection** in protamine evolution, including evidence from the McDonald–Kreitman test that we discuss in the next section.). pag182

The relation between the two arguments in this section, and in the previous section, may be worth clarifying. It might seem that low dN/dS ratios were used as evidence of **selection** in the previous section and now high dN/dS ratios are being used as evidence of **selection** here. The answer is that the two sections are concerned with testing for different kinds of **selection**. Kreitman (1983) found synonymous, but no non-synonymous, variation between copies of one alcohol dehydrogenase allele in fruitflies. This shows that natural **selection** has been acting to prevent change. Wyckoff et al. (2000) found more non-synonymous than synonymous evolution in the protamine genes of apes. This shows, or at least suggests, that natural **selection** has driven adaptive evolutionary change. pag182

The elevated ratio is evidence of positive natural **selection**. In expensive and vital biomedical technologies, clues are valuable even when they are not decisive. pag183

A further test between drift and **selection** can be devised using the ratio of nonsynonymous to synonymous evolution. pag184

If **selection** is at work, the dN/dS ratio is not expected to be the same within and between species. pag184

If **selection** is at work, the dN/dS ratio is not expected to be the same within and between species. For instance, if natural **selection** favors a change in an amino acid in one species but not the other, the dN/dS ratio will be higher between than within a species. If natural **selection** favors a polymorphism, because of frequency-dependent **selection** or heterozygous advantage (Sections 5.12–5.13, pp. 123–8), the dN/dS ratio will be higher within a species than between. In summary, if the dN/dS ratio is similar for polymorphisms within a species and evolutionary change between species, that suggests random drift. If the ratio differs within and between species, that suggests natural **selection**. pag184

The dN/dS ratio is found to be larger between species rather than within. If that were true equally for all sites in the genome, the result could be explained either by positive **selection** for change or by the nearly neutral theory (with a population bottleneck during speciation). pag185

These sites have probably evolved by random drift. But at other sites, the amino acid has changed between related fruitfly species. It looks like **selection** has acted at those sites. pag185

More interestingly, the fraction of sites at which the dN/dS ratio is elevated between species can be used to estimate the fraction of evolutionary substitutions that have been driven by **selection**, as opposed to drift. In this way, Smith & Eyre-Walker (2002) estimated that 45% of non-synonymous substitutions between one pair of fruitfly species (*Drosophila simulans* and *D. yakuba*) were fixed by positive **selection**. pag185

The results so far are preliminary. They are based on a limited genomic sample from one small group of species. However, the results have great interest. They suggest that natural **selection** may be a major force, at least for substitutions that change amino acids. They also show how genomic data may be used to estimate the relative importance of **selection** and drift in molecular evolution. In the future, the sequences of chimp and human genomes will become available. Evolutionary

biologists can then scan down the sequences, to find sites where the dN/dS ratio is relatively high for comparisons between the species. Those sites may be the ones where **selection** has favored changes that have made us human.

Natural **selection** might work against GC to AT changes in regions of the DNA that need to be stably bonded. Secondly, different transfer RNAs are used by the different synonymous codons. (There are fewer kinds of tRNA than codons because of the phenomenon of “wobble. pag187

Thus, in high use genes natural **selection** works against codon changes. The cell benefits from having more of the codons corresponding to abundant tRNAs. In low use genes, changes are disadvantageous and the codon frequencies evolve by drift to be more equal. pag188

We have looked at five examples of the ways in which genomic sequences can be used to study natural **selection**. pag189

We have looked at five examples of the ways in which genomic sequences can be used to study natural **selection**. In the cases of the alcohol dehydrogenase gene and of codon bias, the effect of **selection** was negative: **selection** acted against disadvantageous mutations, preventing evolutionary change. Such evolutionary changes as do take place among synonymous codons are probably mainly driven by drift, but **selection** is acting to prevent some changes. The other three examples (elevated dN/dS ratios, different dN/dS ratios within and between species, and convergent evolution in lysozymes) illustrate positive **selection**: natural selecting actively favoring certain changes. The amino acid changes in the protamine and lysozyme genes have probably been driven by **selection** rather than drift. pag189

The examples illustrate two points. One is that the genomic era has opened up new ways to study **selection**. We saw earlier how natural **selection** can be studied ecologically, such as in the peppered moth or in insecticide resistance (Sections 5.7– 5.8, pp. 108–18). pag189

This kind of ecological research is not the only way that **selection** has been studied, but it contrasts with research in the genomic era. When we look at dN/dS ratios, for instance, we are not looking at organismic character states, nor measuring fitnesses. We are counting large numbers of evolutionary changes, statistically, in a mass of sequence data. In Section 8.10 (p. 210) we shall see another statistical method for detecting **selection** in sequence data, in the phenomenon of selective sweeps. pag189

Whole-genome analyses are being used to estimate the exact relative importance of **selection** and drift in amino acid substitutions. The lysozyme example shows how we can study the way selection works in an identified gene. It makes sense that **selection** as well as drift should matter in molecular evolution. The molecules in living bodies are well adapted, and natural **selection** must work at least occasionally to keep those adaptations up to date. pag189

Molecular evolution is now entering the genomics era. Genomic data hold out the promise both of revealing the localities within the DNA where natural **selection** acts, and also of estimating the fractions of evolutionary substitutions that have been driven by natural **selection** and by random drift. pag190

Genomic data can be used to study natural **selection**. 13 A high rate of non-synonymous evolution relative to synonymous evolution suggests that natural **selection** has been operating. pag191

How will natural **selection** act on a rare recombinant morph of *Papilio memnon*, such as *anura* in Java? Successful mimicry requires as complete a resemblance as possible Between a mimic and its model. pag197

In general, natural **selection** will act against any recombinants between the mimetic five-locus genotypes. A five-locus genotype that mimics one model species in all five respects will be favored. pag197

Selection has not been empirically confirmed to work against the recombinant forms of *P. memnon*, but the argument is quite convincing. pag197

In the absence of **selection**, the frequencies of each gene will be constant, but the frequencies of the haplotypes can be altered by recombination. pag200

In the absence of **selection**, the action of recombination will drive the haplotypes to these frequencies and then keep them there. pag202

Linkage equilibrium is, in a way, the analogy for a two-locus system of the Hardy–Weinberg equilibrium for the one-locus system. It describes the equilibrium that is reached in the absence of **selection**, and in an infinite, randomly mating population.

Pag 202

Deviations from Hardy–Weinberg proportions in a natural population suggest that **selection**, or non-random mating, or sampling effects may be operating. pag202

But **selection** is not the only possible reason for linkage disequilibrium, as the next section will reveal. pag204

In *Papilio* and in at least some of the HLA associations, it is probably due to **selection**. If **selection** favors individuals with particular combinations of alleles, then it produces linkage disequilibrium. But **selection** is not the only possible cause for linkage disequilibrium, and a full study of a real case must examine three other factors. Pag 205

The three processes other than **selection** probably account for some cases of linkage disequilibrium in nature. The process that has most interested evolutionary biologists, however, is natural **selection**. Let us now consider how we can model the effect of **selection** on haplotype frequencies. pag206

The effect of natural **selection** on haplotype frequencies in two-locus models, like its effect on gene frequencies in single-locus models, depends on the fitnesses of the genotypes. pag206

In general, **selection** can only produce linkage disequilibrium at equilibrium when the fitnesses of the genotypes at different loci interact epistatically. Not all epistatic fitness interactions generate doubly polymorphic equilibria with linkage disequilibrium. But all (or nearly all) such equilibria do have epistatic fitnesses. pag208

If it is high, then epistatic **selection** may be common. The argument works in one direction but not the other: because there are several possible causes of linkage disequilibrium (Section 8.7), its existence does not demonstrate epistatic **selection**. However, if linkage disequilibrium is absent or low, we can infer that epistatic **selection** is unimportant in nature. pag209

Suppose, for instance, that directional **selection** is substituting one allele A' for another (A) at one locus, and there is a neutral polymorphism (B, B') at a linked locus. Then whichever of B and B' happened to be linked with A' when it arose as a mutant will have its frequency increased. pag210

One consequence of hitch-hiking is that when natural **selection** fixes a new, favorable gene, the amount of genetic variation is reduced in the neighboring regions of the DNA.
pag210

Other nucleotide variants at neighboring sites in the DNA are eliminated, along with the inferior alleles at the locus where **selection** is acting. The result is reduced genetic diversity. (Genetic diversity can be measured by sequencing the DNA of many chromosomes from many fruitfly individuals, and counting the fraction of nucleotide sites that differ between two randomly picked chromosomes.). pag 210

The sweep reduces genetic diversity most at the locus where **selection** is acting. pag210

The homogenization (that is, reduction in diversity) of neighboring DNA when natural **selection** fixes a favorable new gene is called a selective sweep. As a mutation increases in frequency, it sweeps diversity out of the surrounding DNA. Pag 211

Local reductions in genetic diversity can be used as a “signature” of natural **selection** in DNA sequences. We can look down the DNA, and if we find a region of locally reduced diversity, one explanation is that natural **selection** has recently fixed a new gene somewhere in the region. Nurminsky et al.’s (2001) research on the gene called Sdic in *Drosophila melanogaster* is an example (Figure 8.6). The gene Sdic codes for a structure in the sperm. Figure 8.6b shows a trough in genetic diversity near Sdic, and this trough is part of Nurminsky et al.’s case that the version of Sdic in *D. melanogaster* has recently been fixed by natural **selection**. Pag211

A second alternative is background **selection**. Deleterious mutations occur in the DNA (Section 12.2.2, p. 321, looks at the deleterious mutation rate). Natural **selection** acts against deleterious mutations, removing them from the population. As **selection** clears out deleterious mutations, it also reduces the local genetic diversity because any variants linked to a deleterious mutation will be removed along with it. Pag212

This reduction could be either because of selective sweeps or background **selection**. Both processes reduce genetic diversity, and both operate more powerfully where the recombination rate is low.
pag212

Selective sweeps, in which the local genetic diversity is reduced, can be added to the other signatures of **selection** that we looked at in Section 7.8 (p. 179 a signatures such as the relative rates of non-synonymous and synonymous evolution). pag212

The test is most powerful if alternatives can be ruled out, and provides a further example of how DNA sequence data are allowing some novel tests of natural **selection**.
pag212

Natural **selection** favors individuals with genic associations like T–W2F2E2B2, whereas it works against recombinants like T+W2F2E2B2. An individual benefits from having the haplotypes that are in excess frequency in the population. pag213

The genetic basis of drug resistance would classically have been identified by crosses; but now we can use genomic data and statistical tests for signs of **selection**.
pag213

Selection could have acted recently on other genes, but a sign of **selection** is at least a clue that could lead to the detection of a drug-resistance gene. pag213

That locus shows a strong sign of recent **selection**. The genomic evidence alone would make us suspect that *pfcr* influences drug resistance. pag213

They can be used to find gene loci where **selection** has acted recently. pag213

Natural **selection** will favor recombinant individuals that do not have the A'B haplotype. pag214

In these two cases, natural **selection** carries the population to the gene frequency where mean fitness is at a maximum. With one favorable allele, the maximum mean fitness is where the allele is fixed and natural **selection** will act to fix the allele. With heterozygous advantage, the maximum mean fitness is where the smallest number of homozygotes are dying each generation and natural **selection** drives the population to an equilibrium where the amount of homozygote death is minimized. pag215

A question of interest in theoretical population genetics is whether natural **selection** always drives the population to the state at which the mean fitness is the maximum possible. Frequency-dependent **selection** (Section 5.13, p. 127) is a case in which natural **selection** may not act to maximize mean fitness. When a polymorphism is maintained by frequency-dependent **selection**, the fitness of each genotype is highest when it is rare. But when a genotype is rare, natural **selection** acts to increase its frequency, making it less rare. The effect of **selection** can then be to reduce mean fitness. pag215

If natural **selection** does not always maximize mean fitness, that opens up a further and still unanswered theoretical question of whether natural **selection** does act to maximize some other function, but we shall not pursue that question here. Whatever the answer to it, natural **selection** does still maximize simple mean fitness in many cases. For many purposes, we can safely think of natural **selection** as a hill-climbing process, by analogy with the hills in the adaptive topography (Figure 8.7). pag215

All the time, natural **selection** will be a hill-climbing process, directing the population up toward the currently nearest peak. When the surface changes, the direction to the nearest peak may change, and **selection** will then send the population off in the new upward direction. pag216

Natural **selection**, even in so far as it is a hill-climbing (i.e., mean fitness maximizing) process, is only a local hill-climbing process. In theory, the local fitness peak could be in the opposite direction from a higher, or global, peak (Figure 8.9). pag216

Natural **selection**, however, will direct the population to the local peak. Now suppose that the mean fitness of a population is a measure of the quality of its adaptations, such that a population with a higher mean fitness has better adaptations than a population with a lower mean fitness. pag216

Because natural **selection** seeks out only local peaks, natural **selection** may not always allow a population to evolve the best possible adaptations. A population could be stuck on a merely locally adaptive peak. Natural **selection** works against "valley crossing," where fitness is lower. (Mean fitness cannot always be equated with quality of adaptation. pag216

Wright was interested in how evolution could overcome the tendency of natural **selection** to become stuck at local fitness peaks. pag217

Surface. Once it had explored to the foot of another hill, natural **selection** could start it climbing uphill on the other side. If this process of drift and **selection** were repeated over and over again with

different valleys and hills on the adaptive topography, a population would be more likely to reach the global peak than if it was under the exclusive control of the locally maximizing process of natural **selection**. pag218

Wright's full shifting balance theory includes more than just **selection** and drift within a local population. He also suggested that populations would be subdivided into many small local populations, and drift and **selection** would go on in each. The large number of subpopulations would multiply the chance that one of them would find the global peak. pag217

Everything is included: multiple loci, fitness interactions, **selection** within and between populations, drift, and migration. (The theory of adaptive peaks is also relevant to speciation: Section 14.4.4, p. 394.). pag217

What facts are better explained by the shifting balance process than by simple natural **selection** within one population? For instance, the passion flower butterflies (*Heliconius*, Section 8.2 above) have many morphs, each mimicking a different model. Each morph probably occupies an adaptive peak. pag218

Can genetic drift drive populations across real adaptive valleys? Genetic drift is powerful when it is not opposed by **selection**: that is, when drift is between different neutral forms. However, in Wright's theory, drift has to work in opposition to **selection**. pag218

It can be fixed by normal natural **selection** within the population. The shifting balance process only helps if populations are so small that the best genotype happens never to have arisen in many local subpopulations. Supporters suggest that real populations are often as Wright suggested; critics doubt it. pag218

Do real fitness surfaces have multiple peaks? Fisher, for instance, doubted whether natural **selection** would actually confine populations to local peaks. pag218

In the extreme case, when there is infinity of dimensions, it is certain that natural **selection** will be able to hill climb all the way to the global peak without any need for drift. pag218

This is a highly interesting argument, though it is, of course, purely theoretical. It refutes Wright's theoretical claim that natural **selection** will get stuck at local peaks, but leaves open the empirical question of how important **selection** and drift have been in exploring the fitness surfaces of nature. pag218

With the theoretical apparatus in place, we can then apply it to a number of evolutionary questions: directional **selection**, in both artificial and natural examples, and stabilizing **selection** Pag 222

We look at the effect of **selection** on heritability, and at mutation–**selection** balance Pag 222

From the evidence we have met so far, we can predict that natural **selection** would favor larger finches when large fruits and seeds are abundant. pag223

The fluctuations in the direction of **selection** on beak shape with beaks evolving up in some years, down in other years, and staying constant in yet other years probably results in a kind of “stabilizing” **selection** over a long period of time such that the average size of beak in the population is the size favored by long-term average weather. (Later in the chapter, we shall see how

the degree of **selection** can be expressed more exactly; Figure 9.9 will show the results for 1976–77 and 1984–85.). pag225

However, even if different finches vary in their beak size for genetic reasons, that does not necessarily mean it can evolve by natural **selection**. As we shall see, we have to divide genetic influence into components that allow evolutionary change and those that do not. pag228

In the case of **selection**, the gene frequency in the next generation is easy to predict if we know **selection** allows only AA individuals to breed. In two-locus genetics, the procedure is the same. pag230

The proportion of variation due to the different effects matters when we wish to understand how a population will respond to **selection**. Pag 232

The proportion of the variation that is due to different values of A in different individuals tells us whether the population can respond to **selection**. pag232

The two other main methods are to measure the correlation between relatives and the response to artificial **selection**. pag236

How can quantitative genetics be applied to understand evolution? There are many ways, and we shall consider two of them here: directional **selection** and stabilizing **selection**. pag236

This section will be concerned with directional **selection**, which has particularly been studied through artificial **selection** experiments. Artificial **selection** is important in applied genetics, as it provides the means of improving agricultural stock and crops. pag237

If we wish to increase the value of a character by artificial **selection**, we can use any of a variety of **selection** regimes. One simple form is truncation **selection**: the selector picks out all individuals whose value of the character under **selection** is greater than a threshold value, and uses them to breed the next generation (Figure 9.6). pag237

(The response to **selection** or the parent–offspring regression can be used to estimate the heritability of a character; for a selected population, they are two ways of looking at the same set of measurements.) pag238

A real example of directional **selection** may not have the form of truncation **selection**. In truncation **selection**, all individuals above a certain value for the character breed and all individuals below do not breed. pag238

However, the same formula for evolutionary response works for all forms of directional **selection**. The difference between the mean character value in the whole population and in those individuals that actually contribute to the next generation (if necessary, weighted by the number of offspring they contribute) is the “**selection differential**” and can be plugged into the formula to find the expected value of the character in the next generation. pag238

A population can only respond to artificial **selection** for as long as the genetic variation lasts. Consider, for example, the longest running controlled artificial **selection** experiment. Since 1896, corn has been selected, at the State Agricultural Laboratory in Illinois, for (among other things) either high or low oil content. As Figure 9.7 shows, even after 90 generations the response to **selection** for high oil content has not been exhausted. pag238

At the loci controlling oil content, no additive genetic variance will then be left; heritability will have been reduced to zero and the response to artificial **selection** will come to a stop. Pag238-239

The population continues to respond to **selection** because heritability continues to be above zero. pag239

In other artificial **selection** experiments, the full process has been recorded. Figure 9.8 shows the response of a population of fruitflies to consistent directional **selection** for increased numbers of scutellar chaetae (i.e., bristles on a dorsal region of the thorax). pag239

A character such as beak size may be experiencing directional **selection** in a bird population. We can estimate the response to **selection** (R) by measuring the average size over a number of years. pag240

We can then use the two numbers to estimate the **selection** differential. The **selection** differential expresses how strongly **selection** is acting (in the case of directional **selection**, but not stabilizing **selection**). If the successful individuals are very different from the average individuals in the population, **selection** is strong, and the **selection** differential (S) will be large. If **selection** is weak, the successful individuals will be more like a random sample from the population as a whole and S will be small. pag241

If **selection** is weak, the successful individuals will be more like a random sample from the population as a whole and S will be small. pag240

In Darwin's finches, Gibbs & Grant (1987) measured the response to **selection** (R), and heritability, for several characters related to body size, and used these to estimate **selection** differentials. pag240

In Darwin's finches the measured relations between the **selection** differential, heritability, and response to **selection** all fit with the predictions of quantitative genetic theory. Any two of the three can be measured, and the third accurately predicted (Grant & Grant 1995). However, Section 9.12 below will look at some more puzzling cases in which a character is subject to directional **selection** (the value of S is nonzero), and has been shown to be genetically heritable, but shows no evolutionary response. pag240

Kingsolver et al. (2001) compiled the results of 63 studies of directional **selection**, on 62 species, performed by many different biologists and published between 1984 and 1997. Figure 9.10 shows the distribution of **selection** differentials found in the studies. For a survey of many characters, the **selection** differentials need to be "standardized." pag241

Artificial **selection** produces flies with a higher concentration of the vein-inducing substance and with correspondingly longer wing veins. pag245

Hence the observed response to **selection**. The relation of genotype and phenotype for vein length in Figure 9.13 is a hypothesis only; but it does show how in theory a bimodal response to **selection** could arise. Pag 245

The main points are that when the genotype–phenotype relation has the linear form of Figure 9.12a, there is a simple response to artificial **selection**. The population changes until the genetic variation is used up. However, we have no reason to think that this is the typical genotype–phenotype

relation. When the relation is more complex, the response to artificial **selection** can be interestingly different, as the bimodal response to **selection** on wing vein length in fruitflies illustrates. pag245

We saw earlier that directional **selection** reduces the amount of genetic variation for a character, and this can be measured as a decrease in heritability (see Table 9.2). But what about stabilizing **selection**? In nature, many (perhaps most) characters are subject to stabilizing **selection**, in which the extremes on either side of some optimum are selected against. (See Section 4.4, p. 78, where Figure 4.4 illustrates how birth weight in humans is an example of stabilizing **selection**.) pag245

Stabilizing **selection** will also tend to reduce heritable variation. Consider a character that is influenced by a large number of genes. Some of the genes increase the value of the character and some of them decrease it. pag245

Natural **selection** favors individuals with an intermediate phenotype, produced by any genotype made up of half + genes and half – genes. Here are three examples: pag245

All the offspring of genotype (3) have the optimal phenotype, whereas some of the offspring of genotypes (1) and (2) do not. In a population made up of these three genotypes, **selection** slightly favors genotype (3). If the environment were constant for a long time, always favoring the same phenotype, **selection** should eventually produce a uniform population with a genotype like (3). Pag 245-246

In conclusion, whether a character is subject to directional or stabilizing **selection**, the effect of **selection** is to reduce the amount of genetic variation, and the heritability. If **selection** were the only factor at work, and it worked steadily for a period of time, heritability would be reduced to zero pag247

If **selection**, whether directional or stabilizing, eliminates genetic variation, why does all this genetic variation exist? pag246

For characters subject to stabilizing **selection**, two processes can explain the existence of heritable genetic variation. One is mutation–**selection** balance. The character may have some optimum value, and natural **selection** eliminates genes that cause deviations from that optimum. But mutations will continually arise, causing no deviations from the optimum. The result is equilibrium, at which some genetic variation exists because **selection** cannot clear out mutations instantly with 100% efficiency. pag247

One, revived and developed by Lande (1976), considers stabilizing **selection** on a continuous character (such as body size) controlled by many loci. pag247

The other, revived and developed by Kondrashov & Turelli (1992), does not consider stabilizing **selection** on a phenotypic character, but supposes mutations are occurring at many loci and the great majority (many more than 50%) is deleterious. The result is a balance between **selection** and deleterious mutation at many loci. pag247

Natural **selection** can favor the maintenance of genetic variation. We look at the evidence in more detail in a later chapter about biological species (Sections 13.6–13.7, pp. 366–73). A simple version of the argument is as follows. Suppose, for example, that the members of a finch population have a range of beak sizes. pag248

If the seeds in the local environment are all the same size, then natural **selection** will produce a bird population with beaks of one size. If the seeds are a range of sizes, natural **selection** will favor a

range of beak sizes in the birds. The actual seed size distribution available to the bird population will depend on whether any competitors are present, as well as what seeds are produced by the local plants. However, although this “ecological” kind of **selection** can theoretically maintain genetic variation, we do not know whether it is in fact causing the genetic variation observed in the heritability measurements of Figure 9.14. pag248

A number of species have been the subjects of long-term studies in nature. Each generation, the action of natural **selection** is measured, as a **selection** differential. For example, in European collared flycatchers, the tarsus lengths of reproductively successful birds and of average birds have been measured from 1980 to 2000 (Figure 9.15a). (The tarsus is part of the bird’s leg.) pag248

In most years the **selection** differential is positive: the average number is about 0.2. (This is a “standardized **selection** differential,” and means that the successful birds have tarsus lengths 0.2 of a standard deviation longer than average birds.) The character is also heritable, with a heritability of about 0.35. Natural **selection** favors longer tarsuses in collared flycatchers, and collared flycatchers have genetic variation for tarsal size. pag248

The collared flycatcher is not the only species in which a character is apparently subject to directional **selection**, and apparently shows heritability, but is not showing an evolutionary response. pag249

A biologically more interesting possibility is that the effect of **selection**, to increase (for example) the tarsus length each generation, is balanced by some other force that decreases tarsus length by approximately the same amount pag249

If a large tarsus is advantageous, the effect of disadvantageous mutations each generation will be to reduce average tarsus length. Then, at equilibrium, the increase in tarsus length each generation by directional **selection** could be balanced by a decrease due to mutation. pag249

The lack of evolutionary response in heritable characters apparently subject to directional **selection** is not understood. Quantitative genetics is one of the oldest topics in evolutionary biology, and contains many solid findings. pag249

Effects. However, even with simple directional **selection**, the exact response depends on the underlying genetic control. For example, the possible threshold relation between the genotype and phenotype for the wing veins of the fruitfly generates an interesting bimodal response to **selection**. pag250

However, even here it can be argued that all but one of the genotypes should eventually be eliminated by **selection**. The argument appears to be contradicted by the facts, and biologists do not yet fully understand the observed values of heritabilities in natural populations. pag250

Chapter 10, however, argues that only natural **selection** can explain adaptation. Some characters, particularly molecular characters, have evolved by processes other than natural **selection**, but they are not adaptations pag253

Not all evolution proceeds by natural **selection**, but all adaptive evolution does. The chapter also looks at “gradualism” in Darwin’s theory and looks at the way new adaptations evolve by modifications of previously existing parts, and at the size of the genetic changes that occur during adaptive evolution pag253

In Chapter 11, we move on to ask what the entity is that adaptations evolve for the benefit of. Evolution by natural **selection** happens because adaptations benefit something, but what is it exactly a genes, whole genomes, individual organisms, groups of organisms, species, or what? This is the question of “What is the unit of **selection**?”

pag253

Only genes last long enough for natural **selection** to be able to adjust their frequencies over evolutionary time. Organismal adaptations usually result because gene reproduction is more closely tied to the reproduction of organisms than any other entity, and gene reproduction is maximized if adaptations are at the organismal level. pag253

We look first at the argument to show that natural **selection** is the only known explanation of adaptation; and second at whether natural **selection** can explain all adaptations, including such complex organs as the eye. pag255

The key difference between natural theology and Darwinism is that the former explains adaptation by supernatural action, and the latter by natural **selection**. pag256

Natural theology and natural **selection** are not the only explanations that have been put forward for adaptation. The inheritance of acquired characters (“Lamarckism”) suggests that the hereditary process produces adaptations automatically pag256

These theories differ from Darwinism. In Darwinism, variation is not directed toward improved adaptation. Instead, mutation is undirected and **selection** provides the adaptive direction in evolution (Section 4.8, p 88). pag256

It is one of the most fundamental claims in the Darwinian theory of evolution that natural **selection** is the only explanation for adaptation. The Darwinian, therefore, has to show that the alternatives to natural **selection** either do not work or are scientifically unacceptable. pag256

To provide a complete explanation for adaptation, it would have to fall back on another theory, such as God or natural **selection**. In the former case it would run into the difficulties we discussed above. In the latter case it is natural **selection**, not Lamarckism, that is providing the fundamental explanation of adaptation. Lamarckism could work only as a subsidiary mechanism; it could only bring adaptations into existence in so far as natural **selection** had already programmed the organism with a set of adaptive responses. Pure Lamarckism does not by itself explain adaptation. pag257

All theories of directed or designed mutation have the same problem. A theory of directed mutation, if it is to be a true alternative to natural **selection**, must offer a mechanism for adaptive change that does not **selection** do not explain adaptation at all.

pag257

Osborn, and others, believed that the trend was orthogenetic: that it arose not because of natural **selection** among random mutations but because titanotheres were mutating in the direction of the trend. pag258

In conclusion a strong argument can be made that natural **selection** is the only currently available theory of adaptation. The alternatives variously rely on chance, on unscientific causes, on processes that do not operate in fact, or are non-explanatory. pag259

So natural **selection** is our only explanation for adaptation. This statement, however, applies only to adaptation and not to evolution as a whole. Biologists, such as Gould & Lewontin (1979), have

pointed out that Darwin did not himself rely exclusively on natural **selection**, but admitted other processes too; and they urge that we should accept a “pluralism” of evolutionary processes, rather than relying exclusively on natural **selection**. pag259

They are different variants of one adaptation, and natural **selection** does not explain why one organism has one sequence variant, and another organism has another. We need drift as well as **selection** in a full theory of evolution. pag259

The fact that processes beside natural **selection** can cause evolutionary change does not alter the argument of Section 10.1. It just goes to show that not all evolution need be adaptive. This being so, we should be pluralists about evolution; but when we are studying adaptation, it is sensible to concentrate on natural **selection**. pag259

The argument so far has been negative: we have ruled out the alternatives to natural **selection**, but we have not made the positive case for natural **selection** itself. We have seen before (Chapter 4) that natural **selection** can explain adaptation, but we can also ask a stronger question: can it explain all known adaptations. pag259

The question is important historically, and it still often rises in popular discussions of evolution. The case against **selection** would run something like this. There is no doubt that natural **selection** explains some adaptations, such as camouflage. However, the adaptation in this case, as well as in other famous examples of natural **selection**, is all simple. In the peppered moth it is just a matter of adjusting external color to the background. pag259

It is very difficult to prove negative statements. Nevertheless, many critics suggested, for various adaptations, that natural **selection** cannot account for them. These types of adaptation can be considered fewer than two headings. pag260

A change in the length of the neckbones would malfunction without an equal change in vein length, and evolution by natural **selection** on one part at a time would be impossible. The example is unconvincing now because of the obvious retort that the lengths of all the parts could be under common genetic control. pag260

The model eye then evolved in the computer, with each new generation formed from the optically superior eyes in the previous generation; changes that made the optics worse were rejected, just as **selection** would reject them in nature. pag261

What had looked like impossibility actually turns out to be possible in a short interval of time. Nilsson and Pelger (1994) used estimates of heritability and strength of **selection** (Section 9.7, p. 236) to calculate how long the change might take; their answer was about 400,000 generations. pag262

The work also illustrates the value of building models to test our intuitions. Darwin himself referred to the evolution of complex organs by natural **selection** as presenting a problem for the imagination, not the reason. Nilsson and Pelger’s computer study supports his remark. pag262

An organ has to be advantageous to its bearer at all stages in its evolution if it is to be produced by natural **selection**. pag262

Or (if the double negative is confusing!), we can conclude that all known adaptations are in principle explicable by natural **selection**. pag262

Natural **selection** has brought into existence creatures that are in many respects marvelously well designed. The designs, however, are generally imperfect, and for a number of reasons. We shall look at several reasons in this chapter . pag272

If some genetic variants in the population produce a better adaptation than others, natural **selection** will increase their frequency. Although this process must always operate in the direction of improvement, it has never reached the final state of perfection. pag272

Natural **selection**, however, takes time, and there will be a period after a major change in the fauna during which the adaptations of fruits will be out of date, and adapted to an earlier form of dispersal agent pag273

Adaptation will be imperfect when natural **selection** cannot operate as fast as the environment of a species changes. (Box 22.1, p. 624, contains further discussion of fruit coevolution.) pag274

A new mutant, with an advantageous effect, may also disrupt other parts of the phenotype and these disruptions will probably be disadvantageous; but if the mutant has a net positive effect on fitness, natural **selection** will favor it. pag276

Selection will then start to act at other loci, to favor genes there that reduce the new mutation's deleterious side effects while maintaining its advantageous main effect. That is, **selection** will make the new mutation fit in with the blowfly's developmental mechanism. The genes at the other loci that restore symmetric development, while preserving the insecticide resistance, are called modifier genes, and the type of **selection** is called canalizing **selection**. pag276

The genes at the other loci that restore symmetric development, while preserving the insecticide resistance, are called modifier genes, and the type of **selection** is called canalizing **selection**. Over time, in the sheep blowfly, the resistance mutation was modified such that it no longer disrupted development (Figure 10.7). pag276

McKenzie was able to show that the modification was caused by genes at loci other than the mutation-carrying locus. (This is important because, just as there is **selection** at other loci to reduce the deleterious side effects of the mutation, so **selection** at that locus will favor other mutations that can produce insecticide resistance without harmful side effects.) It is probably common, given the extent of genetic interaction in development, **selection**, to restore developmental regulation with the new mutation, is therefore likely to be an important evolutionary process. pag276

Developmental constraints have been suggested as an alternative explanation to natural **selection** for two main natural phenomena. One is the persistence of fossil species for long periods of time without showing any change in form (Section 21.5, p. 606). pag277

Large parts of the shell morphospace in Figure 10.9 are not occupied. There are two general hypotheses to explain why these forms do not exist: natural **selection** and constraint. If natural **selection** is responsible, the empty parts of the morphospace are regions of maladaptation. pag277

The absence of these shells would then be no more due to natural **selection** than is the absence of animals that break the law of gravity. pag278

Just as natural **selection** and constraint are hypotheses to explain the absence of any form from nature, so they can both hypothetically explain the forms that are present. Faced with any form of

organism, we can ask whether it exists because it is the only form that organism possibly could have (constraint), or whether **selection** has operated in the past among many genetic variants and the form we now observe was the one that was favored. Pag278-279

How can we test between **selection** and constraint? Maynard Smith and his eight coauthors listed four general possibilities: adaptive prediction, direct measures of **selection**, heritability of characters, and cross-species evidence. pag279

The second test is a direct measure of **selection**. In the case of the shell morphospace, this would mean somehow making the naturally non-existent shells experimentally, and testing how **selection** then worked on them (Section 10.6). We then find out by observation whether there is negative **selection** against these forms. pag279

We can use the third kind of evidence (genetic variability) to see whether allometric relations are embryologically inevitable, or whether they can be altered by **selection**. pag280

Results like Wilkinson's suggest that allometric relations will have been tuned by natural **selection** in the past, to establish a favorable shape in each species. pag281

The attempts so far, as in the example of allometry, have not been finally convincing. In particular cases, we can test between the alternatives of **selection** and constraint. pag281

Evolution by natural **selection** proceeds in small, local steps and each change has to be advantageous in the short term. Unlike a human designer, natural **selection** cannot favor disadvantageous changes now in the knowledge that they will ultimately work out for the best. pag281

As Wright emphasized in his shifting balance model (Section 8.13, p. 216), natural **selection** may climb to a local optimum, where the population may be trapped because no small change is advantageous, though a large change could be. As we saw, **selection** itself (when considered in a fully multidimensional context), or neutral drift, may lead the population away from local peaks; but it also may not. pag282

The fault arose because natural **selection** operates in the short term, with each step taking place as a modification of what is already present. pag282

If they then experienced the same external force of **selection**, each one would still evolve to its nearest peak. The different populations would then evolve different adaptations. pag283

In either case, past evolutionary events can lead to the establishment of forms that cannot be explained by a naive application of the theory of natural **selection**. Adaptation has to be understood historically. pag284

If the character under study is an adaptation then it must exist because of natural **selection**. We are right to persist in looking for the particular reason why natural **selection** favors it. If body size is an adaptation, there will be an adaptive model for it that is correct. However, if the character (or different forms of it) is not favored by natural **selection**, the method breaks down. pag285

Some biologists believe that natural **selection** has fine tuned the details, and established the main forms, of organic diversity. Pag285-286

A character of an organism can have beneficial effects that are not strictly speaking adaptive. Some consequences follow from the laws of physics and chemistry without any need for shaping by natural **selection**. pag286

A character of an organism can have beneficial effects that are not strictly speaking adaptive. Some consequences follow from the laws of physics and chemistry without any need for shaping by natural **selection**. pag286

Even though returning to the sea is a “biological necessity,” natural **selection** in the past has not acted between some types of fish that did return to the sea and some types that did not, with the former surviving and reproducing better. pag286

A character is an adaptation in so far as natural **selection** is maintaining its form in modern populations. Beneficial consequences that are independent of natural **selection** are not adaptations. The point is obvious in practice, but must be borne in mind in conceptual discussion. pag287

Alternatively, we could define adaptations using measurements of reproductive success. If a character is an adaptation, then natural **selection** will work against genetic alternatives. Natural **selection** will act against mutant forms of the eye that produce inferior images. Reeve & Sherman (1993) define an adaptation as that form of a character, among a set of variants that has the highest fitness. pag287

Natural **selection** can theoretically work on a character over millions of years and produce major changes through **selection** coefficients of 0.001 or less. It would be practically impossible to detect this amount of **selection** in a modern population with the normal resources of an evolutionary biologist. Forces that are important in evolution can in some cases be impossible to study directly because they are so small. A direct measurement of reproductive success is most likely to demonstrate that a character is adaptive if the **selection** coefficient is large; but these will tend to be the “obvious” characters in any case. pag287

Likewise, body coloration may be a simple adaptation, brought about by natural **selection**, or it may be non-adaptive and brought about by chance, as may be the case for the red color of the sediment-dwelling worm *Tubifex* (visual factors are not important in the sediment at the bottom of the water column). Again, either natural **selection** is favoring the body coloration or it is not; but if we try to decide whether it is just from looking at the character, the answer may not be clear. pag288

Chapter 9 has further references for canalizing **selection**. Chapter 20 looks at evolutionary development, which probably provides the concepts for future studies of developmental constraint. Galis et al. (2001) discuss the special case of constraints on digit numbers. pag290

The second main section of the chapter asks the more fundamental question of what entity natural **selection** operates on, and describes an argument to suggest that the entity is the gene, though defined in a special sense. pag292

Which, if any, of these levels does natural **selection** act on and produce adaptations for the benefit of? In a fairly superficial analysis, the answer does not matter. If an adaptation benefits an individual organism, it will often also benefit its species at a higher level and, at a lower level, all the parts that make up the individual. pag293

Levels. In some cases, what benefits an organism may not also benefit its species, and in these cases the evolutionary biologist needs to know which level natural **selection** most directly benefits. The question therefore matters when we are studying particular adaptations. pag293

Because the levels of living organization are bound together, if natural **selection** produces an adaptation to benefit one level, many other levels will benefit as a consequence. The question in this chapter is whether natural **selection** really acts to produce adaptations to benefit one level, with benefits at other levels being incidental consequences, or whether it acts to benefit all levels . pag294

The fertility of an sd/+ male is about half that of a normal male. The effect of the lowered fertility on **selection** at the sd locus is complex, and depends on whether the reduction in fertility is more or less than 50% and what effect the reduced fertility has on the number of offspring produced. pag295

Selection at other loci will favor genes that suppress the distorters and restore the status quo. pag295

When **selection** acts in conflicting ways on different genes in the same individual body, it is called intragenomic conflict. The sd/+ fruitfly has intragenomic conflict, because **selection** on the sd gene favors segregation distortion and **selection** on other genes favors restoring normal segregation. Which genes win out can depend on many factors, but the point of the example here is to show what it means for natural **selection** to favor an adaptation that is the interest of a single gene (such as sd) within a body. pag295

The separation of the germ line limits the possibilities for **selection** at the suborganismic level, between cell lines. One cell may mutate and become able to out-reproduce other cell lines and (like a cancer) proliferate through the body. pag296

Any somatic cell line comes to an end with the organism's death. For this reason, cell **selection** is not important in species like ourselves. pag296

In a species in which new offspring can develop from more than one cell lineage, **selection** between cell lines becomes possible. pag296

No **selection** can take place between cell lines if they are all genetically identical. Eventually a mutation may arise in one of the cells. If the mutation increases the cell's rate of reproduction, the cell line will cancerously proliferate at the expense of other cell lines in the organism. pag296

In a Weismannist species, that cell line will die when the organism dies and any **selection** between cell lines will be unimportant. pag296

However, if any cell line in the body has some chance of giving rise to the next organismal generation, the mutant cell line would increase its chance of being in an offspring and be favored by **selection**. Explained in this way, **selection** between cell lines within the body is detrimental to the organism. However, the process could also be advantageous for the organism. Whitham & Slobodchikoff (1981) argued that in plants **selection** between cell lines enables the individual to adapt to local conditions more rapidly than would be possible with strictly Weismannist inheritance. pag296

Buss has developed the idea that cell **selection** can explain certain features of embryology in Weismannist species. pag296

It can hardly be doubted, therefore, that organismal adaptations exist, and natural **selection** can favor them. pag297

Can natural **selection** ever favor altruistic actions that decrease the reproduction of the actor? If we take a strictly organismic view of natural **selection**, it would seem to be impossible. pag298

Natural **selection** would then favor the selfish types, because they receive the benefits but do not pay the costs. pag298

For altruism to evolve, it has to be directed preferentially to other altruists. Suppose, to begin with, that acts of altruism were only ever given to other altruists; what would be the condition for natural **selection** to favor altruism? The answer is that the altruism must take place only in circumstances in which the benefit to the recipient exceeds the cost to the altruist. pag298

Under what condition will natural **selection** favor altruism? The altruist still pays a cost of c for performing the act, and the recipient receives a benefit b . However, the chance that the altruistic gene is in the recipient is r . When rb exceeds c there will be a net increase in the average fitness of the altruists. pag299

The condition for natural **selection** to favor altruism among relatives is that it should be performed if: pag299

This is the theory of kin **selection**. It states that an individual is selected to behave altruistically provided that $rb > c$. The condition itself is called Hamilton's rule, after W.D. Hamilton, who mainly invented the theory of kin **selection**. pag299

Let us use the total figure, for survival to day 60, to calculate whether natural **selection** favors helping. pag300

Either way, natural **selection** favors helping behavior in young Florida scrub jays. The estimates of both b and c are fallible, however, and the test is uncertain. Despite these uncertainties, the test does illustrate how we can attempt a quantitative test of the theory of kin **selection**. pag301

A group adaptation is a property of a group of organisms that benefits the survival and reproduction of the group as a whole. Adaptations produced by kin **selection** asuch as helping in family groups of birds a will satisfy that definition, but we are concerned here with group adaptations that did not evolve by kin **selection**. If any exist, they will have come into existence by **selection** between groups: groups possessing the group adaptation would have gone extinct at a lower rate, and sent out more emigrants, than groups lacking it. pag301

This would trivially be true, for example, of an improvement in the hunting skill of a lion: after the improvement has spread by individual **selection**, all the individuals in the group, and the group as a whole, will be better adapted. pag301

Natural **selection** on individuals does not favor reproductive restraint. An individual that increases its reproduction will automatically be favored relative to individuals that produce fewer offspring. Within a group, if some individuals produce more offspring than others, the former will proliferate. But can individual **selection** within the group be overcome by **selection** between groups? pag301

The question is highly important, both conceptually and historically. It is important historically because vague group **selectionist** thinking a particularly in the form of statements like "adaptation X exists for the good of the species" awas once comm.. pag301

Selection is a weak and unimportant process. There are both theoretical and empirical reasons. pag302

The only obvious exceptions concern genetically related individuals, and can be explained by kin **selection**. Moreover, living things have characteristics that contradict the theory of group **selection**. The 50: 50 sex ratios, which we discuss in Section 12.5 (p. 337), is a case in point. In polygynous species, it is inefficient for the population to produce 50% males, most of whom are not needed. pag302

Many models of group and individual **selection** exist, but they can mainly be reduced to a common form (Figure 11.1). The groups are supposed to occupy “patches” in nature. As before, some patches are occupied by altruistic and others by selfish groups. pag 302

Group **selection**, we conclude, is a weak force. It only works if migration rates are implausibly low and group extinction rates implausibly high. It is also not needed to explain the facts. pag303

The case against group **selection** is presented here in stark terms, but only to make the arguments clear. The matter has not been settled finally, and group **selection** probably operates sometimes. Moreover, group **selection** can have evolutionary consequences even if it never overrides individual **selection**. In Section 23.6 (p. 658) we look at a process called “species **selection**.” Species **selection** operates when different species (or even higher taxa) possess different individual-level adaptations, and their different adaptations have different consequences for the rate of extinction or speciation. pag303

In species **selection**, there is no conflict between **selection** at lower (individual) and higher (species, or even group) levels. In all the species (or groups), individuals act in their own selfish interest. Species **selection** is theoretically uncontroversial, though its empirical importance is open to doubt. The controversy about group **selection** that we looked at above was theoretical as well as empirical. Critics of group **selection** doubt whether group **selection** could be strong enough to cause individuals to sacrifice their own reproductive interests to those of its group.pag303

In nature, group **selection** is rarely likely to override individual **selection**, and to establish individually disadvantageous behavior. In the laboratory, however, conditions can be made extreme enough for it to do so. pag303

Not surprisingly, the population density in the “low” lines decreased relative to the “high” lines (Figure 11.2b). The decrease in the low lines is due to group **selection**. Presumably, within the 37 days of any one cycle, the beetle types with high fecundity were increasing within each colony relative to the less fecund beetles. However, between cycles, Wade’s group **selection** for low fecundity more than out-weighed the individual **selection** and average fecundity declined. The group **selection** was strong enough to work.pag 304

The group **selection** was strong enough to work. In a way, the group selective structure of the experiment is superfluous. We could simply breed from beetles with lower fecundity. Artificial **selection** of this kind would reduce beetle fecundity without their being kept in groups for 37 days. But Wade’s purpose was to illustrate group, not artificial, **selection** and his experiment does so. It has alternating rounds of individual and group **selection** and the experimental group **selection** is strong enough to produce the effect that Wynne-Edwards thought to be common in nature. Box 11.1 shows how the group **selection** design of Wade’s experiment has had a practical application.pag304

The fact that group **selection** can be implemented in an experiment does not mean that group **selection** is important in nature. Biologists doubt group **selection** for theoretical reasons, and because of the kinds of adaptations seen in nature. The experiments are instructive, however. They

show what group **selection** means, and how individual **selection** can decrease the efficiency of a group. Muir's experiment (Box 11.1) also has a commercial interest. pag304

The experiments show how individual and group **selection** can conflict. A selective regime that prevents individual **selection** can improve the average output of the whole group. pag305

Mutations that influence the phenotype of a unit (whether a cell, organism, or group) must be passed on to the offspring of that unit in the next generation; if this happens natural **selection** can act to increase the mutation's frequency. pag305

Muir (1995) found a practical application of the basic experimental set up used by Wade to illustrate group **selection**. pag306

Organisms show heritability in this sense. A finch with an improved beak shape, caused by a genetic change, will on average produce offspring with the improved beak shape. Natural **selection** can work on individual finches. pag306

Thus a group in one generation will only be genetically correlated with the group of its offspring in the next generation when there is practically no migration; then group **selection** works. pag306

The same point can be made about kin **selection** and **selection** among cell lines. Kin **selection** operates because an "offspring" kin group genetically resembles the "parental" kin group. pag306

The same point can be made about kin **selection** and **selection** among cell lines. Kin **selection** operates because an "offspring" kin group genetically resembles the "parental" kin group. Cell **selection**, in Weismannist species, tends not to operate because somatic cells, although they are inherited down a cell line during one organism's brief life, are not passed on from an organism to its offspring; but when they are (in non-Weismannist species), cell **selection** and the evolution of cell line adaptations becomes theoretically more plausible. pag306

We can now give our first answer to the question of what is the unit of **selection**. The general answer is "that entity that shows heritability"; more specifically, it is usually the organism, with some interesting exceptions. This first answer specifies the units in nature that should possess adaptations. pag306

Natural **selection** over the generations adjusts the frequencies of entities at all levels. We have implicitly seen this in the example of the lion hunt. If the lions of one pride become more efficient at hunting, perhaps because of some new behavioral trick, natural **selection** will favor them. pag306

The question in this section is whether natural **selection** directly adjusts the frequency of any of these units a nucleotides, genes, neurons, individual lions, lion prides, lion species? pag307

The answer was most clearly given by Williams in *Adaptation and Natural Selection* (1966) and Dawkins in *The Selfish Gene* (1989a). It is at least implicit in all theoretical population genetics and, indeed, in the previous section of this chapter. For natural **selection** to adjust the frequency of something over the generations, the entity must have a sufficient degree of permanence. You cannot adjust the frequency of an entity between times t_1 and t_2 if between the two times it has ceased to exist. A character that is to increase in frequency under natural **selection** therefore has to be inherited. pag307

We can work through the argument in terms of the example of an improvement in lion hunting skill. (We shall express it in terms of **selection** on a mutation: the same arguments apply when gene

frequencies are being adjusted at a polymorphic locus.) When the improvement first appeared, it was a single genetic mutation pag307

Natural **selection** is starting to work. Now we can ask what natural **selection** is adjusting the frequency of. Is it lions? Lion genomes? Or the mutation? pag307

Natural **selection** cannot work on whole lions because lions die: they are not permanent. Nor can it work on the genome. The mutant lion's offspring inherit only genetic fragments, not a copy of a whole genome, from their parents. Meiotic recombination breaks the genome. pag307

What matters, in the process of natural **selection**, is that some of the lion's offspring inherit the mutation. pag307

However, this long view is of little interest. We are concerned with the timescale of natural **selection**. It takes a few thousand generations for a mutation's frequency to be significantly altered (Section 5.6, p. 107) and, over this time, genes, but not genomes or phenotypes, will be practically unaltered. Genes will then act as units of **selection** and will be permanent enough to have their frequency altered by natural **selection**. pag308

Williams defined the gene to make it almost true by definition that the gene is the unit of **selection**. pag308

It is instead the length of chromosome that has sufficient permanence for natural **selection** to adjust its frequency: longer lengths are broken by recombination and shorter lengths have no more permanence than the gene (for the reason shown in Figure 11.3) pag308

When **selection** is taking place at one locus, a cistron at a neighboring locus will to some extent (depending on the amount of recombination) have its frequency adjusted as a consequence pag308

The random hits of recombination will generate a frequency distribution of genome lengths lasting for different periods of evolutionary time. The average length that survives long enough for natural **selection** to work on has been defined by Williams and Dawkins as the gen. pag309

We must discuss one further matter before considering the significance of the genic unit of **selection**. Critics, such as Gould (2002b), have objected that gene frequencies change between generations only in a passive, "book-keeping" sense. The frequency changes provide a record of evolution, but are not its fundamental cause. True natural **selection**, the critics would say, happens at the level of organismic survival and reproduction. The actual **selection** in the lion example happens when a lion catches, or fails to catch, its prey. The differential hunting success drives the gene frequency changes, and it is a mistake to identify the gene frequency changes as causal. Williams and Dawkins, however, do not deny that whatever ecological processes are causing differential organismic survival produce gene frequency changes within a generation. What they deny is that this ecological interaction of organisms means that natural **selection** directly adjusts the frequencies of organisms over the evolutionary timescale of many generations. pag309

There is an easy philosophical method of deciding whether natural **selection** works on genes or larger phenotypic units. We can consider a phenotypic change such as a new hunting skill, and ask whether natural **selection** can work on it if it is produced genically and if it is produced non-genically. pag309

The thought experiment provides a test case between the organismic, phenotypic and the genic accounts of evolution. In the genic case, we know, natural **selection** favors the improved hunting

type and the gene for it increases in frequency. But what happens in the phenotypic case? The answer is too obvious to labor over. The individual lion with improved hunting ability will survive and produce more offspring than an average lion, but no evolution or natural **selection**, in any interesting sense, will occur. The trait will not be passed on to the next generation. Natural **selection** cannot directly work on organisms. pag310

The change in gene frequency over time, therefore, is not just a passive “bookkeeping” record of evolution. Genes are crucial if natural **selection** is to take place. The need for inheritance, and the fact that acquired characters are not inherited, gives the gene a priority over the organism as a unit of **selection**. Whenever a gene is being selected, it produces a phenotypic change and the frequency of different organismal types will change along with the gene frequency. But the change in organism frequency is a consequence of the change in gene frequency: it is the gene frequency that natural

selection is actually working on and this is why Williams and Dawkins maintain that the gene is the unit of **selection**. pag310

The argument that genes are the units of **selection** provides the fundamental logic that is used to find out. pag310

We can rule a hypothesis about adaptation out before the practical testing stage if it contradicts the theory of gene **selection**. pag310

We have now specified what the unit of **selection** is in two different senses. They have sometimes been confused, but many evolutionary biologists now appreciate the distinction. pag310

We therefore also have to ask which higher level entities should benefit from the natural **selection** of replicating genes. The answer is usually organisms, but in some cases it is a family of genetically related organisms. pag311

Mitochondria are another example, and they enjoy an amazing system of multilevel **selection**, discussed by Rand (2001). (I also discuss **selection** in mitochondria in Ridley (2001).) On kin **selection**, the fundamental works are included in volume 1 of Hamilton’s (1996) collected papers; Dawkins (1989a) is more introductory; Clutton-Brock (2002) is a review; and Woolfenden & Fitzpatrick (1990) is about the Florida scrub jay. Sober & Wilson (1998) is about group **selection**. pag312

Once sex had evolved, natural **selection** favored different sets of adaptations in males and females. The theory of sexual **selection** aims to explain male–female differences. pag313

We are considering only whether natural **selection** favors sexual or asexual reproduction pag314

Natural **selection** can therefore take the population from the state A'B' to AB faster than under asexual reproduction. This argument was first put forward by Fisher and by Muller in the 1930s. pag317

This is the “group **selection**” theory of sex. It accepts that sex is disadvantageous for the individual, because of its 50% cost, but claims that the cost is more than made up for by the reduced extinction rate of populations, or groups, of sexually reproducing organisms. pag318

The main argument for group **selection**, as an explanation for sex, comes from the taxonomic distribution of asexual reproduction. In multicellular life, exclusively asexual reproduction is mainly confined to small twigs of the phylogenetic tree (Figure 12.4).¹
pag318

Either way, according to the group **selection** theory, sexual reproduction prevails despite its cost for the individual because sexually reproducing groups have a lower extinction rate. pag319

The taxonomic distribution of asexuality, therefore, although it is consistent with the group **selectionist** theory of sex, does not confirm it. The same pattern could have arisen if sex had an individual advantage. pag319

There are also arguments against group **selection**. As we saw in Section 11.2.5 (p. 301), biologists are generally suspicious of group **selectionist** theories. When individual and group advantages conflict, individual **selection** is usually more powerful. Adaptations that are disadvantageous for the individual are not expected to evolve even if they do benefit the group. pag319

The reason to be suspicious of group **selection** is that it requires the rate at which asexual females arise in sexual groups to be very low. pag319

Williams (1975) also put forward a specific objection against group **selection** in the case of sex. His objection has come to be called the balance argument. Some species, such as many plants, aphids, sponges, rotifers, and water fleas (Cladocera), can reproduce both sexually or asexually according to the conditions. pag319

The group **selectionist** proposes that sex is disadvantageous to the individual, and only advantageous to the group. pag320

If group **selection** can be ruled out for aphids, it can probably also be ruled out for other species. pag320

In summary, group **selection** will tend to favor sexual over asexual reproduction because sexual populations will have a lower rate of extinction. The taxonomic distribution of asexuality suggests that asexual populations tend to go extinct relatively quickly in evolution. However, biologists doubt whether group **selection** is the reason why sex exists, for two main reasons. One is a general disbelief in group **selection**; the other is Williams' balance argument. Neither of these objections is completely convincing, and group **selection** cannot finally be ruled. pag320

A certain number of deleterious mutations arise every generation, and every individual contains some defective genes. **Selection** acts to remove these deleterious mutations. Here we shall consider how effectively **selection** removes them, depending on whether reproduction is sexual or asexual. The theory that sex exists because it enhances the power of **selection** against deleterious mutation, was proposed by Kondrashov (1988).
pag320

Kondrashov's theory requires two conditions in order for natural **selection** to favor sex despite the 50% cost. We can look at them in turn. pag321

One method is the mutation-accumulation experiment, pioneered by the Japanese geneticist Terumi Mukai. The experimenter attempts to create conditions in which **selection** does not act against mutation. pag321

The best understood example is from wheat and parasitic rusts, and similar **selection** may operate in the human HLA system (Section 8.6, p. 203). pag324

Selection of this sort generates cyclic changes in gene frequency (Figure 12.7). As a genotype increases in frequency, its fitness (after a time lag) decreases. pag325

(In Section 5.13, p. 127, we saw evidence for frequency-dependent **selection** in this system.) The results are all consistent with the parasite theory of sex. However, further work is needed to show that the genetic cycles are of the right type to explain the existence of sex. pag327

For the most part, the characters of organisms are adaptive: they increase the organisms' chances of surviving to reproduce. However, there are some characters that do the opposite, and (as Darwin was well aware) natural **selection** does not explain why these characters exist. If a population contains some types with higher survival than other types, natural **selection** will fix the former and eliminate the latter. pag327-228

Why are these costly characters not eliminated by **selection**? pag328

Darwin's solution was his theory of sexual **selection**. He defined the process by saying that it "depends on the advantage which certain individuals have over other individuals of the same sex and species, in exclusive relation to reproduction." A structure produced by sexual **selection** in males exists not because of the struggle for existence, but because it gives the males that possess it an advantage over other males in the competition for mates. pag328

Darwin's main argument for the importance of sexual **selection** was comparative. Sexual **selection** should operate more powerfully in polygamous than in monogamous species. In a polygynous species, in which several females mate with one male (and other males do not breed at all), a single male can potentially breed with more females than under monogamy; **selection** in favor of adaptations that enable males to gain access to females (whether by male competition or female choice) is proportionally stronger. pag328-329

In polyandrous birds, such as phalaropes, sexual **selection** is reversed: females compete for males, and it is the females that are the larger and more brightly colored sex. There are exceptions, such as monogamous ducks that are sexually dimorphic; Darwin had an additional theory for them. However, the main point is that Darwin's principal evidence for sexual **selection** came from a comparison of large numbers of species that showed that species with brightly colored, large, or dangerously armed males are more often polygynous and species in which males and females are more similar are more often monogamous. pag329

For Darwin, female choice among males was an assumption; he was mainly concerned to show that, if it exists, it can explain extraordinary phenomena like the peacock's tail. He did not have much to say about the prior question of why the female preference should ever evolve to begin with. **Selection** can work on a female preference just like on any other character. If females with one type of preference produce more offspring than females with another, **selection** will favor the more productive preference. pag329

We can spell the problem out more fully in terms of **selection** on a mutant, nonchoosy female. Suppose that peahens do prefer peacocks with dazzling tails, and a mutant female, who does not prefer these males, arises; she might mate at random, or prefer some other sort of male. What does **selection** do to this mutation? The mutant female will produce sons that do not possess the costly character, or at least in a less extreme form. pag329

Suppose that, before some mutant female arose who picked longtailed males, most females picked their mates at random; suppose also that there was at that time a positive correlation between male tail length and survival (Figure 12.9a). **Selection** would then favor a mutant female with a preference for males with longer tails as she would produce sons with longer than average tails, with an associated higher survival. pag330

The original problem was to explain the evolution of a set of apparently deleterious characters. Darwin's solution was that they could be maintained by female choice. He did not, however, explain why females should come to choose males with deleterious characters, nor why the choice would not be lost by natural **selection**. pag331

The choice will be favored by **selection** if the advantage through the superior genes outweighs the cost of the handicap: then the net quality of the choosy female's offspring will be higher than those of the randomly mating female. pag331

A male's genetic quality does not come written on him: it has to be inferred, and if females inferred it from an inexpensive signal, there would be **selection** on males to cheat. If females preferentially mated with males who merely said "I have good genes" (or rather, in a non-human species, something analogous to saying this) and rejected those that said "I have poor genes," mutant males who said the former independently of their true genetic quality would be favored. pag332

Words (and their analogs) are cheap. But if the criterion favored by females is costly, as growing a long and ostentatious tail is, then **selection** will less automatically favor cheats. pag332

If mate choice imposed any cost on a female at all, the randomly mating mutant would spread. Tail length, therefore, must be heritable or **selection** will favor the female who mates at random. pag334

In a population in which some individuals possess good genes and others bad genes, **selection** acts to fix the good genes and once it has done so there will be no variation in genetic quality left. pag335

Several selective forces will be at work in male and female fruitflies. For instance, **selection** favors a male who can accelerate a female's egg production immediately after mating with him, because that male will then fertilize more eggs. pag335-336

Natural **selection** on females favors resistance to the male techniques of accelerating egg production. Females may evolve counterhormones or other methods of restoring the optimal egg production rate. pag336

Sexual **selection**, including intersexual conflict, may also underlie the relatively rapid evolution of genes that are expressed in the reproductive system as a phenomenon noted in Sections 7.8.2 (p. 182) and 14.12 (p. 417). pag336

The theory of sexual **selection** is at a more advanced stage than the theory of why sex exists. The models, such as those of Fisher and Zahavi, may be correct, and some work has been done to test them. pag336

Many other consequences of sexual **selection** are also being investigated. One hot topic is the experimental study of intersexual conflict. The evolutionary forces of intersexual conflict depend on the mating system. pag337

In most species, the sex ratio at the zygote stage is about 50 : 50. Fisher explained the 50 : 50 sex ratio as an equilibrium point: if a population ever comes to deviate from it, natural **selection** will drive it back. pag337

(This is another “group **selection**” argument, see Section 11.2.5, p. 301.) However, imagine what would happen to a population with a persistently female biased sex ratio a one with four females for every one male, for instance. Each male in the population will fertilize on average four females. Pag337-338

The reproductive success of the average female is then higher than that of a male, and natural **selection** will favor mutant females that produce more daughters than sons.pag338

Any population that deviates from the 50 : 50 sex ratio will be shifted back to it by natural **selection**.pag338

This does not mean that **selection** favors any compensating bias at the early stages to produce more of the high-mortality gender.pag339

Natural **selection** can then favour a sex ratio other than 50 : 50, depending on the exact circumstances. pag339

In summary, when one gender of offspring enhance parental reproduction, natural **selection** favors parents who produce more offspring of that gender. When one offspring gender reduces parental reproduction, natural **selection** favors parents who produce less of that gender. Both these predictions have been successfully tested in the Seychelles warbler.pag340

We have looked at the function of sex, sexual **selection**, and the sex ratio, as three related examples of research on adaptation. In each case, the research has advanced to a different stage.pag341

In the case of sexual **selection**, the main theories of female choice have been around for some time. They provide a satisfactory abstract explanation for organs such as the peacock’s tail. The full repertoire of techniques a model building, experiment, comparative methods a are being used.pag341

When we look at organisms today, we are looking at the effects of **selection** in the past. pag352

These genes have not been tried out together and sifted by **selection**, and we have no reason to expect them to interact well. When combined in a single body, they may produce a genetic snarl-up. (Section 14.4, p. 389, further develops the theory of gene interactions within, and between, speciespag352

Natural **selection** will favour organisms who interbreed with other organisms that have a similar set of ecological adaptations. For instance, the ecological adaptation might be the size of the beak, if the beak is adapted to eat seeds found locally. Natural **selection** favors individual birds that interbreed with other birds that have similar beaks. Then they will on average produce offspring that are well adapted to eat the local seeds. Natural **selection** works against birds that interbreed with mates that have very different beaks as their offspring will tend to have maladapted beaks.pag354

It is a form of male competition, and its outcome may well be influenced by female choice. In this case, the “choice” would be effected by the female’s internal reproductive physiology. Section 14.11, p. 413, discusses how sexual **selection** may contribute to speciation, and provides further contexts

for these observations.) pag357

Sexual **selection** is thought to drive speciation, particularly sympatric speciation (Section 14.11, p. 414). The African lake cichlids provide some of the strongest evidence for sympatric speciation (Section 14.10.3, p. 413). Seehausen's experiments, which show that mating preferences are the first kind of isolation to evolve in these fish, fits in with the broad idea that sexual **selection** has contributed to the spectacular radiation of cichlids in East Africa. pag358

Geographic variation in these two species is therefore adaptive: the form of the sparrows differs between regions because natural **selection** favors slightly differing shapes in different regions. pag360

When a new chromosomal fusion mutation arises, it will be selected against because of its disadvantage in heterozygous form. But if it drifts up to a locally high frequency, as may easily happen in a local, small, and perhaps inbreeding, mouse population, natural **selection** will favor it. Natural **selection** favors whichever chromosomal form is locally common (this is an example of positive frequency-dependent **selection**, Section 5.13, p. 127). Natural **selection** alone cannot explain the geographic variation observed by Britton-Davidian et al. Natural **selection** alone would cause all the mice to have the same chromosome numbers. The variation is more likely to be explained by drift, with different individual chromosomal fusions drifting up in frequency in different localities. Natural **selection** may also be at work, depending on the frequency of the chromosomes. But whatever the cause of the pattern in Plate 8, it is a further example of geographic variation. pag361

Geographic variation is probably rarely caused only by drift or only by **selection**. Also, more than one selective factor is likely to operate. In the case of the mouse chromosomes, natural **selection** probably interacts with drift, depending on the chromosomes' frequency. But other kinds of natural **selection** can act, such as meiotic drive (Section 11.2.1, p. 294) and a full account of mouse chromosomal evolution is complex (Nachman & Searle 1995). Moreover, very thorough research is needed to test between **selection** and drift. pag361

Wright (1978) considered it to be the best example of how drift causes differences between local populations (the first stage in Wright's shifting balance theory of evolution see Section 8.13, p. 216). However, a long-term study by Schenck & Bierzychudek (2001) measured the fitness of blue and white flowers and found that **selection** is at work in a complex way that differs from year to year. pag362

Hard work is needed to measure the contributions of drift and **selection** in particular species. But in general, patterns of geographic variation can be explained by some mix of **selection**, as seems to explain body size variation in sparrows, and of drift, as seems to explain chromosomal variation in house mice. pag362

Clines can arise for a number of reasons. In the house sparrows, the reason is likely that natural **selection** favors a slightly different body size along the gradient; sparrows are continuously adapted to an environment that changes continuously in space (Figure 13.6). pag362

Even if the variation within a species is partly due to mutation–**selection** balance (and some individuals are better adapted than others), the environment could change and the currently less fortunate individuals would improve in fitness. pag364

For instance, gene flow (migration) can rapidly unify the gene frequencies of separate populations if **selection** is weak (Section 5.14.4, p. 132). On the other hand, a strong **selection** force can in theory

keep two populations distinct despite gene flow. The relative importance of adaptation to the local ecological conditions and gene flow is an empirical question in cases where the two forces conflict. pag369

Natural **selection** works strongly against the seeds of the surrounding forms when they land on the spoil-tip: the seeds are poisoned. **Selection** also acts against the metal-tolerant forms off the spoil-tips. The reason is less clear, but the detoxification mechanism may cost something to possess. Where the mechanism is not needed the grass is better off without it. pag369

Populations of *A. tenuis* show divergence, in that there are markedly different frequencies of genes for metal tolerance on and off the spoil-tips. The pattern is clearly favored by natural **selection** a but what about gene flow? pag369

In this case, **selection** has been strong enough to overcome gene flow. pag370

There are several possible answers, as we have seen. Different species concepts follow from different ideas about the importance of interbreeding (or gene flow) and natural **selection**. pag377

For criticism, see Coyne et al. (1989). Ritchie & Philips (1998) provide evidence of intraspecific variation in SMRS, in contrast with the theory that stabilizing **selection** acts on SMRS. See also the material on antagonistic sexual **selection** in Section 12.4.7 of this text. pag379

European oaks are a further good case study in ecological versus biological (gene flow) species concepts: see Van Valen (1976) again, and Muir et al. (2000). Other recent studies of **selection** and gene flow include Blondel et al. (1999) on blue tits in Corsica, and Smith et al. (1997) on rainforest biodiversity. pag379

The chapter also looks at the special case of hybrid speciation in plants, at the possibility of speciation between populations that are not geographically separated, and at two current research trends at the influence of sexual **selection** on speciation, and the use of modern genomic techniques to identify genes that cause reproductive isolation pag381

Thus, the populations had diverged under the influence of **selection** to live on different resources in the laboratory. pag384

The mating preference somehow evolves as a correlated response when **selection** favors new adaptations to the environment. pag384

Look at the controls in Dodd's results, for instance (Figure 14.2). No reproductive isolation evolved between populations that were evolving separately but in the same environment. These populations would have evolved apart by drift, but not by **selection**. Reproductive isolation only evolved between lines kept on different foods, and **selection** would have been acting differently between them. pag386

Hitch-hiking means that when natural **selection** favors a gene at one locus, genes at linked loci may also increase in frequency (Section 8.9, p. 210). In Dodd's experiment, natural **selection** increased the frequency of genes coding for appropriate digestive enzymes. pag387

Two copies of a are better than one, and the population will evolve from AABB to AaBB to aaBB; natural **selection** fixes the a allele. This is simple evolution by natural **selection**. In the environmental condition of population 2, a change at the other locus is advantageous. Natural **selection** drives the population from AABB to AABb to AAbb, and fixes the b allele. pag390

It is hard, if not impossible, for a population to cross an adaptive valley. Natural **selection** and random drift are the two main forces of evolution. Natural **selection** almost always acts to drive species toward a peak on an adaptive landscape. Natural **selection** opposes valley crossing as it requires genotypes of lowered fitness to somehow spread through the species. Random drift is only a powerful force when the alternative genotypes are selectively neutral. For drift to drive a population across a valley, it has to work contrary to **selection**, and that is unlikely. pag394

Or that it happens when the action of natural **selection** is temporarily suspended, perhaps when a colonizing population exploits abundant resources in the absence of competitors (the “founder flush” model: see Templeton 1996). pag394-395

Speciation requires the normal action of **selection** and drift to be suspended. The inspiration of these ideas is that speciation is a difficult process, because of the need for valley crossing. This is one view of speciation. pag395

The fitness valley is generated as a consequence of the separate evolution of the two species. In the Dobzhansky–Muller view, speciation happens as an almost automatic consequence of ordinary **selection** and drift within a population, as each population evolves in its own environmental conditions. pag395

So far we have been looking at one of two main theories about how reproductive isolation evolves: that it evolves as a by-product when natural **selection** favors different genetic changes in separately evolving populations. The second theory suggests that natural **selection** can act directly to increase the amount of isolation between two populations. pag399

Reinforcement is one possibility. Natural **selection** may increase the amount of prezygotic isolation. If an AA individual mates with another AA individual, they produce offspring with high fitness. If an AA individual mates with an A'A' individual they produce hybrid AA' offspring who have low fitness. Natural **selection** favours individuals who mate with others who are genetically like themselves a that is, assortative mating.¹ The theory of reinforcement assumes that some postzygotic isolation exists, and argues that prezygotic isolation will increase. Natural **selection** cannot, except in strange circumstances, favor increases in postzygotic isolation. Natural **selection** favors increased prezygotic isolation, because the individuals save themselves from producing inferior hybrid offspring. But an increase in postzygotic isolation means that the fitness of hybrids goes down. The hybrids become more likely to die. Natural **selection** cannot favor genes that make their bearers more likely to die (except in special conditions described in the theory of kin **selection**, Section 11.2.4, p. 298). Indeed the main effect of natural **selection** on postzygotic isolation will be to decrease it, by favoring fitter. pag400

Natural **selection** favors assortative mating. However, other evolutionary forces will also be acting, and may remove the preconditions before reinforcement has increased reproductive isolation to the point of full speciation. pag401

The rarer genotype has an automatic disadvantage, and natural **selection** acts to eliminate it. It may be driven extinct before full assortative mating has evolved. (The precondition for reinforcement is an instance of positive frequency-dependent **selection**: Section 5.13, p. 127.) pag401

Natural **selection** favors assortative mating based on color. The problem is that recombination may generate green AA individuals (and blue A'A' individuals). A blue AA who mates assortatively may now have an A'A' partner, and produce inferior hybrid offspring. pag401

These three objections considerably weaken the theory of reinforcement. But they do not show that it is impossible, and counterarguments can be made. For instance, the preconditions can be stabilized if the two genetic types are a polymorphism that is actively maintained by natural **selection** (by any of the standard mechanisms of Sections 5.11–5.14, pp. 121–33).pag402

Two kinds of evidence have been used to test for reinforcement, one experimental and the other biogeographic. The experimental evidence consists of artificial **selection** experiments, in which the experimenter creates the preconditions for reinforcement. pag402

Natural **selection** favored assortative mating, which duly increased. Many other experiments have obtained similar results. The problem with these experiments, for our purposes here, is that arguably they do not test the theory of reinforcement. Reinforcement is a process that drives speciation. pag402

However, the experiments do have value. They show, for instance, how natural **selection** can increase prezygotic isolation once postzygotic isolation is complete. But they do not provide much of a test of reinforcement. A good test would make the hybrid fitness low, but not zero, with some gene flow continuing during the experiment. pag402

But one experiment is not enough to prove that reinforcement never works. Another species, in some other conditions, might show a different result. However, at present the evidence from artificial **selection** either fails to test, or fails to support, the theory of reinforcement. pag402

One interpretation of reproductive character displacement is that prezygotic isolation has been reinforced in sympatry. When the two species do not encounter each other (that is, allopatrically), natural **selection** will not have favored discrimination against mates from the other species. In sympatry, where interbreeding may produce hybrids of reduced fitness, **selection** will have favored mechanisms to prevent crossbreeding. pag403

Therefore, the biogeographic evidence, like the evidence from artificial **selection**, is currently inconclusive. Evolutionary biologists remain undecided about reinforcement. pag405

Natural **selection** on the hybrid therefore has a kind of positive frequency dependence (Section 5.13, p. 127): when it is rare its fitness is lower because of the difficulty of finding a mate. It may have to reach some threshold of abundance before natural **selection** favors it. (Strictly speaking, this is number, rather than frequency, dependence; but there is frequency-dependent **selection** in at least an informal sense.) pag408

Within one population, natural **selection** will not favor a genetic change that is incompatible with genes at other loci. pag409

The other theory was reinforcement. Reinforcement only occurs in sympatry. Natural **selection** only favors discrimination among potential mates for the range of mates that are present in a particular place. The theory of reinforcement is only weakly tied to the theory of allopatric speciation. Indeed, it is hardly an allopatric theory of speciation at all. pag409

Natural **selection** favors assortative mating. We can therefore imagine a sequence where a stepped cline initially evolves, and then becomes distinct enough to count as a hybrid zone. We are near the border of the origin of a new species. Reinforcement could then finish speciation off, eliminating hybridization from the hybrid zone. pag410

Most models of sympatric speciation suppose that natural **selection** initially establishes a polymorphism, and then **selection** favors prezygotic isolation between the polymorphic forms. “Host shifts” in a fly called *Rhagoletis pomonella* provide a case study that may illustrate part of the process. pag412

Apples and hawthorns differ and **selection** will therefore probably favor different characters in each race; this may be the reason for their divergence. If it is, **selection** may also favor prezygotic isolation and speciation. pag412

We can finish this chapter by looking briefly at two big themes in current, and possibly future, research on speciation. One is the possibility that sexual **selection** is important. pag413

The way natural **selection** acts on mate choice may help explain the evolution of prezygotic isolation in both allopatric and sympatric populations. Consider again those experiments in which some populations of a species are allowed to evolve in two environmental conditions, such as a diet of maltose or of starch (see Figure 14.2). pag414

Now let us think some more about how natural **selection** will work in each experimental population. On a starch medium, **selection** favors individuals who can eat, digest, and thrive on starch. But it also favors female flies who choose as mates those males that are better than average at living on a starch die. pag414

Natural **selection** works on mate choice mechanisms as well as ecological adaptation, and the two may become associated. pag415

But sexual **selection** can help to strengthen the association, making sympatric speciation more plausible. pag415

These two arguments are only two of several ways in which sexual **selection** has recently been suggested to drive speciation. (Schluter (2000, p. 195) gives a table with six or so additional ideas. For instance, evolutionary conflict between males and females (Section 12.4.7, p. 336) may contribute to speciation.) Most of the arguments are hypothetical. Sexual **selection** has not yet been shown to drive the evolution of prezygotic isolation in any case of speciation, though good suggestive evidence exists. We do not know that sexual **selection** is a general force of speciation. But much research on this topic is being done. pag415

The impressive evidence that we now have from artificial **selection** experiments (Section 14.3.1) plugs one hole in Darwin’s case. Darwin had no evidence that reproductive isolation evolved between domestic varieties that had been selected apart. pag417

Finally, some other criteria can sometimes be useful. Convergence is caused by natural **selection**, when organisms in different evolutionary lineages face similar functional requirements (such as flying in birds and bats). We have grounds for suspecting that a shared morphological structure may be homoplasious when the species that share it clearly need it for their way of life. pag430

Nor can we usually assess the reliability of different pieces of molecular evidence by thinking about how natural **selection** could have acted on them. When morphologists examine a similarity between the organs of two species, they keep a look out for functional convergences such as the evolution of wings in species that fly. pag438

Each change requires a gene (or set of genes) to arise by mutation and then to be substituted, either by drift if the change is neutral or by **selection**; both these processes are improbable. It is much more likely that the same character would have been continuously passed on, in much the same form, from ancestor to descendant by simple inheritance. We know that this is plausible because it happens every time a parent produces an offspring as the parental characters are passed on. pag445

The initial evolution of each of these characters required improbable mutations, and natural **selection** operating over millions of generations. It is evolutionarily improbable to the point of near impossibility that the same changes would have evolved independently in the two lineages after their common ancestor. pag446

But why should evolution proceed in this form? The question has an important place in the history of Darwin's thinking. He thought up natural **selection** in the late 1830s, as a natural explanation for adaptation and evolution. pag487-488

While the members of two populations interbreed, natural **selection** favors genetic changes that are advantageous in both populations. The two populations are kept relatively similar. pag489

The small populations in the different refuges would have evolved genetic differences, either by **selection** or drift. The populations in Spain, Italy, and the Balkans diverged. Then when the ice cap retreated north, all three populations expanded north too. This has had two detectable consequences. pag499

This reduction in carbon dioxide set up a force of **selection** in favor of leaves and the evolution of leaves, and more powerful photosynthesis, further reduced the carbon dioxide levels. pag539

It refers to changes in gene frequencies within populations, under the influence of natural **selection** and random drift. Macroevolution refers to the topics we are looking at in Part 5 of the book. It refers to the origin of higher taxa, such as the evolution of mammal-like reptiles into mammals, fish into tetrapods, and green algae into vascular plants. pag550

These are surely adaptive changes, which would have been brought about by natural **selection**. pag551

The general evolutionary model suggested by the mammal-like reptiles, therefore, is one of cumulative action of natural **selection** over a long (100 million year) period. pag551

In these examples, macroevolution proceeds by the same process as natural **selection** and adaptive improvement as has been observed within species and at speciation; but the process is operating over a much longer period. pag551

At any one time, natural **selection** will be favoring a variety of adaptations in different lineages as tropical adaptations in tropical species, polar adaptations in polar species. Something about the polar adaptation makes them more likely to contribute to macroevolutionary change. That something, whatever it is, cannot be seen simply by studying microevolution. pag552

In this chapter, we have seen that the origin of higher taxa can at least be mainly understood as the evolution of adaptation by natural **selection** over the long term. pag552

Genomes, as a whole or in part, change size during evolution by means of duplications and deletions (Section 2.5, p. 30). A duplication or deletion will initially be rare in the population; it may arise as a unique mutation. Its frequency may then increase by natural **selection** or random drift. pag559

A gene loss originates as a deletion mutation, which may then spread by drift or **selection**. pag562

The resources are provided by the host, and natural **selection** on some of the genes in intracellular bacteria will be relaxed. Genes that are needed in a free-living bacterium to provide the resources that are present in the host cell are not needed in an intracellular bacterium. pag562

Natural **selection** may favor gene reduction for this reason. (Box 19.1 discusses a medically interesting example. Yet another dramatic example of gene loss in an intracellular bacterium is provided by mitochondria. We look at mitochondria in the next section.)pag562

Natural **selection** discriminates more against fruitflies with non-coding DNA than against crickets with non-coding DNA. Why this should be is a question for the future. pag562

Natural **selection** can increase its frequency to 100%. Every individual will then have a chromosomal pair with the same gene on each chromosome. If a superior version of a gene arises on an X (or on a Y) chromosome, natural **selection** can only increase its frequency until it is present in every X (or Y) chromosome in the population. pag565

Are the rates of change seen in the fossil record consistent with the mechanisms of evolutionary change studied by population geneticists? Population genetics identifies two main mechanisms of evolution, natural **selection** and random drift, though drift is arguably unimportant in morphological evolution (Section 7.3, p. 165). pag593-594

However, we can at least find out whether the results of research in the two areas are consistent. We can first ask whether there is any contradiction between the rates of evolution observed in population genetics work, such as artificial **selection** experiments, and those observed in fossils. If, for example, the fossil rates are significantly higher, it would suggest that **selection** alone cannot be the only cause of evolution. Some other more rapid factor would be needed. In fact, it turns out, the rates of evolution in artificial **selection** experiments are far higher than those measured in fossils. Evolution under artificial **selection** has proceeded about five orders of magnitude faster than in the fossil record (Table 21.1). pag594

Strictly speaking, this does not confirm that the fossil changes were driven by **selection** and (perhaps) drift. However, it does show that the observations are consistent. For this reason, and because no other mechanisms of evolution are known, no one seriously doubts that the microevolutionary processes of Chapters 4–9, 14 and 15 are even if operating indirectly (tooth sizes might increase because of **selection** for larger body size, for instance) ultimately underlie the observed rates of evolution over geological time periods. pag594

The same point is that rates of evolution over different time periods are consistent and can be made by another argument. We saw (Section 9.1, p. 223) how natural **selection** operates on the beaks of Darwin's finches. The evidence there was for natural **selection** within a species. pag595

In 1976–77 (and subsequently), the Grants measured the strength of **selection** on the finches' beaks, and its evolutionary results (Figure 9.9, p. 241). Today, 14 different finch species occupy the

Galápagos (Figure 21.2). The species mainly differ in their beak and body proportions. What we can do is calculate whether the kind of **selection** observed in the short term would be enough to account for the origin of all the finches in the Galápagos in the time available. pag595

If the extrapolation is correct, the reason for the speciation in the finches was the same process as has been observed in the present a natural **selection** for changes in beak shape, which were probably in turn due to changes in food types through time and between islands. Although the finches have speciated rapidly, no peculiar mechanism of evolution is needed to account for it. Arguments of this general kind are common in the theory of evolution. We met a similar argument in Section 18.6.2 (p. 542), where natural **selection** over long periods was used to explain the major evolutionary transition from the mammals to the reptiles. pag596

In the previous section, we considered the rate of evolution during a single burst of evolutionary change. Now we need to turn to the fluctuating **selection** pressure over several consecutive years (Section 9.1, p. 223). pag597

Other factors may be contributing. For instance, the cases of rapid evolution over short time intervals are for artificial **selection** experiments (dataset I) and natural ecological colonizations (dataset II); it may be that these are extraordinary events and have higher than average **selection** intensities. (Alternatively, however, it might be argued that the rates are high only because the measurement interval is short enough to catch evolution in its unidirectional phase, and not because the intensity of **selection** is peculiar. Opinions differ about how representative the **selection** intensities in datasets I and II are of those in the lineages making up datasets III and IV.) pag598

Between speciation events, species may have a low rate of evolutionary change a a condition Eldredge and Gould called stasis. In theory, the absence of evolutionary change in a species can be explained by stabilizing **selection** (Section 4.4, p. 76) or constraint (Section 10.7, p. 272). pag600

Stabilizing **selection**, by contrast, is a well documented fact and is highly plausible in theory. Stabilizing **selection**, therefore, is the most likely (if not universally accepted) explanation for stasis in the fossil record. The theory of punctuated equilibrium holds that stasis is the normal condition within a species. Stasis breaks down only when speciation occurs. pag600

Simple natural **selection** cannot then drive evolution from one species to the other. Some special circumstances, or evolutionary processes, will be required, and evolution may proceed by a rapid “peak shift.” pag601

Their stability may be due to stabilizing **selection** or absence of genetic variation. pag608

Natural **selection** probably favored mutually adapted changes in each species, after the ancestors of the two species had become associated. pag615

This kind of reciprocal influence is what is meant by coevolution: each species exerts **selection** pressures on, and evolves in response to, the other species. The two lineages evolve together (Figure 22.2). pag615

In turn, natural **selection** on the plants favors the evolution of improved insecticides. Plant–insect coevolution should therefore consist of cycles, as plant groups are drawn into, and removed from, the diets of insect groups, and the insects evolutionarily “move” between plant types according to their biochemical abilities. pag617

Once insect pollination had evolved, natural **selection** could favor increasingly specialized pollinator relations. In any one flower species, natural **selection** favors those flowers whose pollen is transported only to other flowers of the same species. If the insect flies to another flower species, the pollen is more likely to be wasted. pag617

As natural **selection** favors specialized pollinator relationships, it will tend to increase the diversity of both plants and insects. Plants that are pollinated by a single insect species have an advantage, because less of their pollen is wasted. pag618

Therefore, both parasitic virulence and host resistance can evolve. Natural **selection** will clearly always favor increased resistance in hosts, but how will it operate on virulence in parasites? pag625

One idea about how natural **selection** will work on virulence is that it will usually act to reduce it. Parasites depend on their hosts, and if they kill their hosts they will soon be dead too. pag627

The objection to this argument, and the reason why it is almost universally rejected by evolutionary biologists, is that it is group **selectionist** (Section 11.2.5, p. 301). Although a parasite species has a long-term interest in not destroying the resource it lives off, natural **selection** on individual parasites will favor those parasites that reproduce themselves in the greatest numbers over those that restrain themselves in the interest of preserving their hosts. pag627

Natural **selection** will favor individual parasites that can consume as much of the host as possible, as fast as possible, before any of the other parasites take advantage of the resource. Virulence will increase. If an individual restrains itself to preserve the host, other parasites will step in to take it over. pag627

Herre's results are shown in Figure 22.7 and show the predicted relation. The virulence of the parasite appears to have been tuned by natural **selection** to the habits of the host. pag628

The example here illustrates only one way in which natural **selection** works on virulence. In other cases virulence may not depend on the rate at which a parasite grows in, and uses up, its host. For other kinds of virulence, other theories may be needed. Even when virulence does depend on the parasite's growth rate, kin **selection** and vertical as opposed to horizontal transmission are just two of the evolutionary factors that have been hypothesized to influence it. pag628

He suggests that natural **selection** has favored higher intelligence both in the prey, to escape predators, and in predators, to catch prey. pag634

The analogy for running is coevolutionary change. In the Red Queen mode of coevolution, natural **selection** continually operates on each species to keep up with improvements made by competing species; each species' environment deteriorates as its competitors evolve new adaptations. pag639

This increase will be experienced by its competitors as an equivalent decrease in the resources available to them. The **selection** pressure on them to improve will increase, by an amount proportional to the loss in resources caused by the competitor's improvement. pag639

The first is species **selection**; the second is evolutionary replacement; and the third is the history of biological diversity on the global scale over geological time. pag643

Natural **selection** could have been favoring direct development within the majority of lineages. Hansen "suggested" this was not true (though he gave no evidence). The period was a time of

global cooling, which might favor direct development, given the latitudinal trend mentioned earlier.
pag662

The trend toward increasing numbers of snail species with direct development is an example of what is sometimes called species **selection**. Species **selection** is a higher level analog of normal natural **selection** within a population. Species **selection** means, other things being equal, that those kinds of species that have lower extinction and higher speciation rates will tend to increase in frequency over evolutionary time. pag665

The key question, for determining whether a trend is caused by species **selection**, is whether natural **selection** within a species is driving evolution in the direction of the trend. Consider a trend toward increasing body size (Figure 23.10). If natural **selection** within each species is stabilizing, but species in which body size is larger have lower extinction rates, then the trend to larger body size is driven by species **selection**. If natural **selection** within each species favors larger body size, then the trend is probably driven by conventional natural **selection**. The question is difficult to study. However, Alroy (1998) studied it for a trend to increasing body size in North American fossil land mammals. He found that the trend, on average, could be accounted for by increases within each lineage suggesting that species **selection** is at most a minor factor in this case. pag665

Species **selection** should not be confused with group **selection** (Section 11.2.5, p. 303). Group **selection** aims to explain why individuals sacrifice themselves for the good of the group (or species) they belong to, and we have seen that it is difficult for adaptations of this sort to arise. pag665-666

In species **selection**, there is no question of individuals using a disadvantageous developmental mode in order to boost the speciation rate of their taxonomic groups.
pag666

Direct and planktonic development are favored by natural **selection** in different taxonomic groups for good ecological reasons within each species: but they can then have different long-term consequences for radiation and extinction. We have no reason to suppose that what is favored by the short-term process of natural **selection** will always be the same as that which allows species to last a long time or split at a high rate. Natural **selection** may favor adaptations within some species that result in reduced long-term survival and adaptations that increase it in others. pag666

Species **selection** is another example of a reason why macroevolution cannot simply be extrapolated from microevolution (Section 18.8, p. 550). Within a species natural **selection** favors one character in one species and another in a different species; but species **selection** over long periods may cause the species with one of the characters to proliferate, because of the character's consequences for speciation or extinction rates. This does not mean that the long-term process contradicts, or is incompatible with, the short-term process, only that we cannot understand the long-term evolutionary pattern by studying natural **selection** in the short-term alone and extrapolating it.
pag666

A similar conclusion can be drawn from the argument about niches. Again, macroevolution cannot simply be predicted from microevolution. A microevolutionary study would reveal how natural **selection** was favoring various characters in the stickleback populations, according to the aquatic environments they were occupying. The key to macroevolution is the persistency of the niches over time, and that is irrelevant to the short-term process of natural **selection** and to investigations of it. (Natural **selection** does not favor one adaptation over another because it allows the organisms to occupy a longer lasting niche.) pag666

In contrast, in the Cretaceous–Tertiary mass extinction the difference disappeared. The conditions had altered and the form of species **selection** altered too. pag667

The main point of these examples is that species **selection** can be studied in mass extinctions, and that the form of species **selection** may change during mass extinctions from other times. However, we can also notice that the results provide an independent source of evidence that mass extinctions were real rather than artifactual events. pag668

Which taxa do survive, and which go extinct, in the exceptional circumstances of mass extinctions, may be largely a matter of luck, and have little to do with the microevolutionary process of adaptation and natural **selection**. Thus, there could be distinct “macroevolutionary regimes” during, and between, mass extinctions. In this set of ideas, mass extinctions are the key to understanding much of evolutionary history.
pag677

EVO DEVO

The other two ways in which molecular genetics is being used in macroevolutionary research are more recent. I have added chapters on evolutionary genomics (Chapter 19) and “**evo-devo**” (Chapter 20). Pág prefacio 23

The emerging subject of “**evo-devo**” (Chapter 20) is documenting many examples of molecular cooption. In embryonic development, certain regulatory genes code for subroutines that can be useful in many circumstances. Pág 265

Homology has been much discussed recently, mainly because of the astonishing discoveries in “**evo-devo**.” Pág 468 Chapters 19 and 20 are about two emerging subdisciplines of evolutionary biology: evolutionary genomics and “**evo-devo**.” Pág 521

Evo-devo is concerned with how developmental processes change in evolution, and can cause changes in morphology pag 522

In this chapter, we look at evolutionary genomics, which has grown out of whole-genome sequencing. In the next chapter we look at “**evo-devo**,” which exploits our ability to identify the individual genes that control development. Pág 557

King & Wilson (1975) provide a classic view on regulatory genes as discussed in the **evo-devo** section of this chapter. Pag 570

Evolutionary developmental biology, now often known as “**evo-devo**,” is the study of the relation between evolution and development pag 572

Many genes that control development have now been identified, and molecular techniques can be used to study how those genes have changed between species. The new field is often called by the informal term “**evo-devo**.” Pag 573

The new field is often called by the informal term “**evo-devo**.” In this chapter we shall look briefly at some older theories about developmental change and morphological evolution. We then look in more detail at some examples of modern “**evo-devo**” research pag 573

We can finish with some general reflections that apply to both this and the previous

chapter. The two chapters have not had space for a full survey of either evolutionary genomics or **evo-devo**. Pág 587

Evolutionary genomics and **evo-devo** are two ways in which genetics is now being used to answer macroevolutionary questions. Pág 587

In the case of **evo-devo**, biologists have always realized that morphological evolution must be driven by changes in development. Pág 587

Understanding the major transitions is largely a matter of understanding evolutionary genomics and **evo-devo**. The advance of these two subjects should give us some insights into the grandest questions of macroevolution. Pág 587

General developmental biology texts, such as Gilbert (2000) and Wolpert (2002) contain chapters on evolution, as well as developmental biology background. Wilkins (2001), Carroll et al. (2001), and Hall (1998) are texts more specifically on **evo-devo**. Pág 588

Proceedings of the National Academy of Sciences (2000), vol. 97 (9), pp. 4424–540 contains the proceedings from a conference on **evo-devo**. Gerhart & Kirschner (1997) is a stimulating book, more about the evolution of cells, but containing much relevant material for this chapter. Pág 588

Meyerowitz (2002) gives an **evo-devo** comparison of plants and animals. Pág 588

The identification of genes that influence development is a major area of modern biology, and its methods can be applied to study the relations of development and evolution, a field known as “**evo-devo**.” Pág 588

DESENVOLVIMENTO

Two new chapters a one on evolutionary genomics and one on evolution and **development** bring state-of-the-art information to the coverage of evolutionary study
Prefacio xxv

The chapter first defines biological evolution, and contrasts it with some related but different concepts. It then discusses, historically, the rise of modern evolutionary biology: we consider Darwin’s main precursors; Darwin’s own contribution; how Darwin’s ideas were received; and the **development** of the modern “synthetic theory” of evolution. Pág 3

Developmental change within the life of an organism is not evolution in the strict sense, and the definition referred to evolution as a “change between generations” in order to exclude **developmental** change. A change in the composition of an ecosystem, which is made up of a number of species, would also not normally be counted as evolution. Pág 4

However, the theory does not require any conscious striving on the part of the organism an only some flexibility in individual **development** and the inheritance of acquired characters. Pág 8

Alternative splicing can be illustrated by the gene slo, which works in the **development** of our acoustic sensory system. Pág 24

Not only are there discrete genes that encode discrete proteins, but the genes are also preserved during **development** and passed on unaltered to the next generation. In a blending mechanism, the “genes” are not preserved.Pag 39

There is a slippery slope from interindividual variation all the way up to the difference between two species. Small individual differences, we know, arise by the ordinary processes of reproduction and **development**: we can see that each individual is not separately created.Pag 52

Indeed, population geneticists have constructed models of all the complications listed in the previous paragraph, and those models are all **developments** within the general method we have been studyingPag 121

We see how certain details of molecular evolution have led to the **development** of the “nearly neutral” theory. We then look at the relation between functional constraint on molecules and their rate of evolutionPag 155

One is the **development** of the “nearly neutral” theory of molecular evolution. Kimura’s original theory considered only purely neutral mutations, with a selection coefficient of zero.Pag 158-159

Research on this topic can be followed in Trends in Ecology and Evolution, Trends in Genetics, Bioessays, and the December special issue each year of Current Opinion in Genetics and **Development**.Pag 192

They might be unconvinced by the evidence of Figure 8.5, perhaps calling it “limited,” or “for a single species.” The amount of interaction between loci that must go on during the **development** of a complex, organic body is so high that they would expect epistatic fitness interactions to be common. Such is the assumption of the school of thought that follows Wright, whose ideas we shall discuss at the end of the chapter.Pag 209-210

As we saw above, **developmental** interactions among genes do not automatically generate epistatic fitness interactions among loci. The extent to which undoubted **developmental** interaction will produce a multiply peaked fitness surface is therefore open to question; but the possibility is plausible. (Wright called the genes that interact favorably to produce an adaptive peak an “interaction system.”)Pag 216

The extent to which undoubted **developmental** interaction will produce a multiply peaked fitness surface is therefore open to question; but the possibility is plausible. (Wright called the genes that interact favorably to produce an adaptive peak an “interaction system.”)Pag 216

The value of a real character will usually be influenced by the individual’s environment as well as its genotype. If the character under study is something to do with size, for example, it will probably be influenced by how much food the individual found during its **development**, and how many diseases it has sufferedPag 229

Adaptations may be out of date or may be constrained by genetics, **developmental** mechanisms, historic origins, or trade-offs between multiple functions.Pag 255

Macgregor and Horner carried out breeding experiments, in which they crossed two normal individuals, and counted the proportion of eggs that survived. In every case, approximately half the offspring died during **development**.Pag 274

A nine-penned discussion (Maynard Smith et al. 1985) of **developmental** constraints gave the following definition: “a **developmental** constraint is a bias on the production of variant phenotypes or a limitation on phenotypic variability caused by the structure, character, composition, or dynamics of the **developmental** system.”Pag 275

The idea is that different groups of living things that evolved distinct **developmental** mechanisms and that the way an organism develops will influence the kinds of mutation it is likely to generate.Pag 275

A plant, for example, may be likely to mutate to a new form with more branches than would a vertebrate, because it is easier to produce that kind of change in the **development** of a plant (indeed it is not even clear what a new “branch” would mean in the vertebrate aperhaps it might be extra legs, or having two heads). The rates of different kinds of mutation a or of “production of variant phenotypes” in the quoted definition atherefore differs between plants and vertebrates.Pag 275

Developmental constraints can arise for a number of reasons. Pleiotropy is an example. A gene may influence the phenotype of more than one part of the bodyPag 275

A **developmental** constraint exists whenever there is a tendency for mutants (in this example) to affect both legs and the tendency is due to the action of some **developmental** mechanism.Pag 275

The genes divide up the body in a different way from the human observer. Genes influence **developmental** processes, and a change in **development** will often change more than one part of the phenotype. Much the same reasoning lies behind a second sort of **developmental** constraint. New mutations often disrupt the **development** of the organism.Pag 276

In a species with bilateral symmetry, any deviation from that symmetry in an individual is a measure of how well regulated its **development** was. Mutations can therefore cause **developmental** asymmetry.Pag 276

When the resistance mutation first appears, it produces **developmental** asymmetry as a by-product. Presumably, the disruption of **development** is deleterious, though not so deleterious that the mutation is selected against. The advantage in insecticide resistance more than makes up for a little **developmental** disruption. ThePag 276

The advantage in insecticide resistance more than makes up for a little **developmental** disruption. The mutation therefore increases in frequency.Pag 276

That is, selection will make the new mutation fit in with the blowfly’s **developmental** mechanism. The genes at the other loci that restore symmetric **development**, while preserving the insecticide resistance, are called modifier genes, and the type of selection is called canalizing selection.Pag 276

The genes at the other loci that restore symmetric **development**, while preserving the insecticide resistance, are called modifier genes, and the type of selection is called canalizing selection. Over time, in the sheep blowfly, the resistance mutation was modified such that it no longer disrupted **development** (Figure 10.7).Pag 276

It is probably common, given the extent of genetic interaction in **development**, for new mutations to disrupt the existing **developmental** pattern. Canalizing selection, to restore **developmental** regulation with the new mutation, is therefore likely to be an important evolutionary process.Pag 276

It is probably common, given the extent of genetic interaction in **development**, for new mutations to disrupt the existing **developmental** pattern. Canalizing selection, to restore **developmental** regulation with the new mutation, is therefore likely to be an important evolutionary process. Pag 276

Another sort of **developmental** constraint can be seen in the “quantum” growth mechanism of arthropods. Arthropods grow by molting their exoskeleton and then growing a new, larger one. Pag 276

The explanation for the quantum jumps is a **developmental** constraint: growth, by molting, is dangerous and to grow with a smooth curve would require frequent risky molts. It is better to molt more rarely and grow in jumps. Pag 277

Constraints have been suggested as an alternative explanation to natural selection for two main natural phenomena. One is the persistence of fossil species for long periods of time without showing any change in form (Section 21.5, p. 606). The other is the variety of forms to be found in the world pag 277

If the constraint was **developmental**, it would mean that for some reason it is **developmentally** impossible (or at least unlikely) for these kinds of shells to grow. The non-existent shells would be embryological analogies for animals that disobey the law of gravity as they are shells that break the (unknown) laws of embryology. pag 278

If a theory of shell adaptation predicted accurately and successfully the relation between shell form and environment which forms should be present, and which absent, in various conditions a then, in the absence of an equally exact embryological theory, that would count in favor of adaptation and against **developmental** constraint. pag 279

As it happens, this kind of evidence suggests that the gaps in the shell morphospace are not caused by **developmental** constraint. pag 279

Finally, cross-species evidence may be useful. It has particularly been used for pleiotropic **developmental** constraints. When more than one character is measured, and the values for the two characters in different organisms are plotted against each other, a relation is nearly always found. pag 279

Some kinds of evidence are more persuasive than others. Allometric relations, in particular, are not strong evidence of **developmental** constraint pag 280

On **developmental** constraint, Maynard Smith et al. (1985) and Gould (2002b) are major reviews. McKenzie & Batterham (1994) and McKenzie (1996) discuss the insecticide resistance example (see also the further reading in Chapter 5, p. 135). pag 290

On **developmental** stability in general, see Lens et al. (2002). Harvey & Pagel (1991) contains an account of, and references to, recent work on allometry. Chapter 9 has further references for canalizing selection. Chapter 20 looks at evolutionary **development**, which probably provides the concepts for future studies of **developmental** constraint. Galis et al. (2001) discuss the special case of constraints on digit numbers.

pag 290

However, Buss (1987) pointed out that Weismannist **development** is relatively exceptional among multicellular organisms (Table 11.1). We tend to think of it as usual because vertebrates, as well as the more familiar invertebrates like arthropods, develop in a Weismannist manner pag296

The case we discussed above was genic: the advantageous new hunting behavior was caused by a genetic mutation. Now suppose that the same advantageous phenotypic change was caused by a non-heritable phenotypic change instead, such as individual learning or some **developmental** accident in the lion's nervous system. The thought experiment provides a test case between the organismic, phenotypic and the genic accounts of evolution. Pag309-310

Either reinforcement has not operated when it might have been expected, or, alternatively, the differences in behavior and **development** time in the field may be enough to reduce interbreeding to the level natural selection favors. pag412

They looked into *Odysseus* some more. *Odysseus* contains a "homeobox," a sequence found in genes that regulate **development** (Section 20.6, p. 582). It is expressed in the **development** of the male reproductive system. The sterility of *D. mauritiana* × *simulans* hybrids may be caused by an incompatibility between the *mauritiana* form of the *Odysseus* gene and a *simulans* gene that is also expressed in the male reproductive system. pag416

Third, the character is likely to have the same embryonic **development** in different groups. A character that looks similar in the adult forms, but develops by a different series of stages, is unlikely to be homologous. pag430

A homology can be recognized as a character that has fundamentally the same structure, relations with surrounding parts, and **development**, in a set of species. Once the homologies are (often tentatively) identified, they can be retained in the list of evidence used to infer the phylogeny. The homoplasies are discarded. pag430

Amniotes are the group made up of reptiles, birds, and mammals; all these animals possess an egg membrane, called the amnion, during their **development** pag434

At one extreme, non-independence is obvious; no one would think of treating the right leg and the left leg as two pieces of evidence. But less obvious correlations can also arise as a consequence of **developmental** processes, which make the recognition of independence tricky. pag438

In a way, it is the DNA equivalent of the morphological history we looked at in Chapter 18. Evo-devo is concerned with how **developmental** processes change in evolution, and can cause changes in morphology. Pag521-522

"Multicellular" life is used to refer not simply to the presence of more than one cell in an organism, but to more than one kind of cell a that is, to cell differentiation. Life forms with more than one kind of cell have at least a rudimentary **development**. They develop from a single-celled zygote to an adult with specialized cell types. The origin of **development** is an important step in the evolution of life. Life forms consisting of rows or mats made up of many identical cells had existed early in lifepag533

They develop from a single-celled zygote to an adult with specialized cell types. The origin of **development** is an important step in the evolution of life. Life forms consisting of rows or mats made up of many identical cells had existed early in life. Schopf pag533

But multicellular life, in the sense of life with work **development** and cell differentiation, evolved much later. With only minor exceptions, all life forms with cell differentiation are eukaryotic. pag535

Changes in social and cultural behavior. The main way we differ from other apes is in our social and cultural lives. This **development** can be followed only indirectly in fossils. Sexual dimorphism, for example, is probably related to the breeding system. pag546

In this chapter, we look at evolutionary genomics, which has grown out of whole-genome sequencing. In the next chapter we look at “evo-devo,” which exploits our ability to identify the individual genes that control **development**. pag557

These “animal” genes include the genes such as Hox genes that control **development**. We look at these genes further in Chapter 20. Another 22% of our genes are shared only with vertebrates. pag559

Evolutionary **developmental** biology, now often known as “evo-devo,” is the study of the relation between evolution and **development**. The relation between evolution and **development** has been the subject of research for many years, and the chapter begins by looking at some classic ideas. pag573

The origin of a set of genes controlling **development** may have opened up new and more flexible ways in which evolution could occur: life may have become more “evolvable.” pag573

If the descendant species has longer legs, it is because the **developmental** process that produces legs has been accelerated, or extended over time. Evolutionary changes in **development**, and **developmental** genetics, are the mechanism of all (or almost all) evolutionary change in morphology. We need to understand **developmental** evolution in order to understand morphological evolution. The same need not be said of molecular or chromosomal evolution: we do not need to study **development** in order to study molecular and chromosomal evolution. Some other kinds of evolution, such as behavioral evolution, can also have a **developmental** basis. But this chapter concentrates on the **developmental** basis of morphological evolution. pag573

Biologists have recognized since the nineteenth century that **development** is the key to understanding morphological evolution. pag573

In the past 10–15 years, a new field of research has grown up. Many genes that control **development** have now been identified, and molecular techniques can be used to study how those genes have changed between species. The new field is often called by the informal term “evo-devo.” pag573

The aim of all the research, from the nineteenth century to today, is to use a knowledge of **development** to explain how morphological evolution proceeds. pag573

According to the theory of recapitulation, the stages of an organism’s **development** correspond to the species’ phylogenetic history: in a phrase, “ontogeny recapitulates phylogeny.” Each stage in **development** corresponds to (that is, “recapitulates”) an ancestral stage in the evolutionary history of the species. pag573

Each stage in **development** corresponds to (that is, “recapitulates”) an ancestral stage in the evolutionary history of the species. The transitory appearance of structures resembling gill slits in the **development** of humans, and other mammals, is a striking example. Mammals evolved from an ancestral fish stage and their embryonic gill slits recapitulate the piscine ancestry. Pag 573-574

During the **development** of an individual, evolutionarily advanced fish species, such as the flatfish *Pleuronectes*, the tail has a diphyercal stage in the larva. pag574

Thus evolution has proceeded by adding on successive new stages to the end of **development**. pag574

The second kind of exception arises when the members of a species evolve to reproduce at an earlier **developmental** stage. We need to distinguish the rate of reproductive **development** from the rate of somatic **development**. pag575

Somatic **development** proceeds through a series of stages, from egg to adult. If the organism becomes reproductively mature at an earlier stage, then its **development** will not fully recapitulate its ancestry. Its ancestral adult form has been lost. Reproduction in what was ancestrally a juvenile form is called pedomorphosis. Pedomorphosis can arise in two ways (Figure 20.3). One is neoteny, where somatic **development** slows down in absolute time, while reproduction **development** proceeds at the same rate. The other is progenesis, where reproductive **development** accelerates while somatic **development** proceeds at a constant rate. pag575

If the organism becomes reproductively mature at an earlier stage, then its **development** will not fully recapitulate its ancestry. Its ancestral adult form has been lost. pag575

One is neoteny, where somatic **development** slows down in absolute time, while reproduction **development** proceeds at the same rate. The other is progenesis, where reproductive **development** accelerates while somatic **development** proceeds at a constant rate. pag575

This strongly suggests that the timing of reproduction has moved earlier in **development** during the axolotl's evolution. Otherwise there would be no reason for it to possess all the unexpressed adaptive information of the terrestrial adult. pag575

Its time of reproduction has therefore probably stayed roughly constant, while somatic **development** has slowed down. The axolotl is an example of neoteny. Humans have also been argued to be neotenous. As adults, we are morphologically similar to the juvenile forms of great apes. pag576

Our somatic **development** has not simply slowed down while reproductive **development** has stayed the same. What might have happened was that our somatic **development** slowed down even more than our reproductive **development**. pag576

In summary, Haeckel and others initially suggested that evolution almost always proceeds in one mode. Changes are made only in the adult, and new stages are added on to the end of the existing **developmental** sequence. Through the 1920s, biologists come to accept a broader view. Evolution does often proceed by terminal addition and recapitulation results. But other **developmental** stages can also be modified, and the timing of reproductive and somatic **development** may be altered in any way a some of which result in recapitulation, and others which result in pedomorphosis (Table 20.1). pag576

Heterochrony refers to all cases in which the timing or rate of one **developmental** process in the body changes during evolution relative to the rate of another **developmental** process. In progenesis, neoteny, and so on (Table 20.1) the rate of reproductive **development** is sped up or slowed down relative to the rate of somatic **development**. pag577

Heterochrony is a more general concept, however. It also refers to changes in the **development** of one somatic cell line relative to another. Consider, for example, a D'Arcy Thompson transformation (Figure 20.4). D'Arcy Thompson (1942) found that related species superficially looking very different could in some cases be represented as simple Cartesian transformations of one another. pag577

Evolutionary changes in morphology are often produced by changes in the relative rates of different **developmental** processes: that is by heterochrony. Heterochrony also explains evolutionary changes in allometry, which we looked at in Section 10.7.3, (p. 279). pag577

A long list of genes that operate during **development** is now known, and the list is rapidly expanding. pag579

However, other **developmental** genes, such as the genes in fruitflies called hedgehog, notch, and wingless, are signaling proteins, and most of the points of principle that we look at for transcription factors would also apply for signaling proteins. pag580

All animals seem to use much the same set of genes to control **development**. For example, the Hox genes were first studied in fruitflies. After the genes were cloned it was possible to look for them in other species too, and they were duly found in every other animal taxon. pag580

Then, during **development**, specific sets of genes are switched on to cause the correct structures to develop in each region of the body. The genes for building a head have to be switched on at the top of the body, for example pag580

The finding that all animals use much the same set of **developmental** genes might not have been predicted. The main groups of animals are the Protostoma and Deuterostoma (Figure 18.5, p. 536) and were initially defined by basic differences in how the animals develop. pag580

And so on. It might have been expected that these deep differences in **development** would reflect different genes regulating **development**. But in fact the same set of genes is at work in both taxa. The genes that regulate **development** presumably evolved once, when animals with **development** first originated, and has been conserved ever since.² pag580

The ey gene could be shown to cause eye **development** in fruitflies; because if the gene is switched on in inappropriate parts of the body, such as a leg, it induces the **development** of an “ectopic” eye.³ Then genetic tricks were used to introduce the fruitfly ey gene into mice. These mice grew up with fly-type compound eyes. It seems that the same gene is used in both mice and fruitflies to cause eye **development**. If the insect and vertebrate eyes have evolved independently, we would hardly expect them to have hit on the same gene to act as the master gene of eye **development**.. pag581

The evolution of eyes in the two taxa would have been easier if they already possessed the **developmental** genetic machinery for specifying something about eye **development**. pag581

It would be less remarkable if mice and fruitflies have homologous genes for controlling **development** in a particular region of the head, than if they have homologous genes for developing eyes. At some level, homology must exist between mice and fruitfly eyes; the question is whether the homology is at the level of eyes, or head regions. pag581

Are changes in the **developmental** genes associated with major evolutionary changes in the history of life? The Hox genes are the most hopeful gene set for answering this question at present.. pag582

More is known for the Hox genes about which genes are present in which animal taxa than is known for any of the other genes associated with **development**. pag582

So also were some other sets of genes that operate in **development**. This increase in gene numbers may have contributed to the evolution of vertebrates. pag582

The Hoxc6 gene is probably part of the control system that switches on the **development** of thoracic, rather than cervical, vertebrae. Thus, an evolutionary change in the morphology of the spine was probably partly produced, at a genetic level, by a change in the spatial expression of the Hoxc6 gene in the embryo. Vertebrates develop in an anterior–posterior direction, with the head being specified first. A delay in switching on hox6c could cause the cervical–thoracic boundary to be shifted to the posterior, down the spine. pag584

Here we can see a genetic example, in which a change in the timing of a **developmental** genetic process leads to evolutionary change in morphology. pag585

In summary, we have seen three **developmental** mechanisms that are thought to have contributed to evolutionary changes in morphology. One is the change in the spatial expression of genes. A second is the change in which genes are switched on or off by transcription factors that have not themselves changed; this is achieved by changes in enhancers. A third is the change in transcription factors, such that they change their interactions with enhancers. pag585

In the case of evo-devo, biologists have always realized that morphological evolution must be driven by changes in **development**. They had concepts, such as heterochrony, for thinking about the **development** basis of evolution. The modern **developmental** genetic work provides a new way of thinking about these long-established problems. pag587

They had concepts, such as heterochrony, for thinking about the **development** basis of evolution. The modern **developmental** genetic work provides a new way of thinking about these long-established problems. The modern work is more concrete than the earlier work, because it builds on knowledge of individual genes and the **developmental** processes that they influence. pag587

On the origin of Hox genes see also the material on duplications in the genomics section of this chapter. Slack et al. (1993) discuss a further topic the “phylotypic stage.” They suggest: (i) that all animals are more similar at a certain **developmental** stage than earlier or later in **development**; (ii) the stage of maximum similarity is the stage at which Hox genes are expressed; and (iii) animals can be taxonomically defined by the possession of the phylotypic stage. pag589

Carroll et al. (2001) give references for the examples in which gene expression in **development** is associated with morphological evolution. On butterfly spots, see also the general review by McMillan et al. (2002) and the particular contributions of Beldade et al. (2002a, 2002b), the second paper particularly connects with another classic theme, that of **developmental** constraints on evolution a discussed in this text in Chapter 10. pag589

It also helps to know whether any changes in a population are genetic. In some species, individuals can grow up with distinct forms, depending on the environmental conditions in which they develop. These changes in **development** are called “ecophenotypic switches.” pag602

The evolution of fruit manufacture in plants, and of fruit exploitation in vertebrates, insects, and fungi, required special genes coding for appropriate **developmental** and metabolic circuits. pag624

Different mollusks grow up in different ways. In gastropod snails, planktonic and direct **developments** are two of the main types of **development**. With planktonic **development**, the egg is released into the surface waters of the ocean and develops into a larval form which disperses among, and feeds on, the microscopic organisms (called “plankton”) that float near the ocean surface. pag660

After a while, the larva settles and metamorphoses into an adult snail. With direct **development**, the eggs and young grow up near or (to begin with) inside the parental snail. Various ecological trends are known among modern forms, such as that planktonic **development** are commoner among shallow- than deep water species, and commoner among tropical species than polar species. These results suggest that the mode of **development** in a species is an adaptation to the local ecological conditions.

Pag 660-661

Hansen (1978, 1983) looked at the relation between larval type and speciation rate. He predicted that snails with direct **development** will speciate more rapidly than species with planktonic larvae, because the species with non-planktonic **development** will be more likely to be geographically localized and isolated, which makes allopatric speciation easier. Planktonic **development** increases gene flow and makes allopatric speciation less probable. pag662

Two alternatives are left. Natural selection could have been favoring direct **development** within the majority of lineages. Hansen “suggested” this was not true (though he gave no evidence). The period was a time of global cooling, which might favor direct **development**, given the latitudinal trend mentioned earlier. pag662

They show that, in a group of modern snails, species with planktonic **development** have repeatedly evolved from ancestral species with direct **development**. pag664

For the trend in Figure 23.9 to be driven by differences in speciation rate, it is important that the ancestor–descendant lines of species tend to retain the same mode of **development**. (In technical language, heritability is required at the level of species.) Duda and Palumbi’s result for modern species suggests that the expanding group of species with direct **development** may not have been a clade with a constant mode of **development**. Species with direct **development** may have arisen from ancestors with planktonic **development**. Currently it is uncertain whether, as Hansen originally argued, the decline in planktonically developing forms in the early Tertiary occurred because they had a low speciation rate. pag664

The influence, if real, is a straight consequence of the character itself: species in which there is direct **development** are more likely to split, in the process of allopatric speciation, than species in which there is planktonic **development**. pag664

The trend toward increasing numbers of snail species with direct **development** is an example of what is sometimes called species selection. pag665

In species selection, there is no question of individuals using a disadvantageous **developmental** mode in order to boost the speciation rate of their taxonomic groups. Direct and planktonic **developments** are favored by natural selection in different taxonomic groups for good ecological

reasons within each species: but they can then have different long-term consequences for radiation and extinction. pag666

ESPECIACÃO

From population genetics, the modern synthesis spread into other areas of evolutionary biology. The question of how one species splits into two a the event is called **speciation** a was an early example. Pag.16

Before the modern synthesis had penetrated the subject, **speciation** had often been explained by macromutations or the inheritance of acquired characters. Pag 16-17

Richard Goldschmidt (1878–1958), most famously in his book on *The Material Basis of Evolution* (1940), argued that **speciation** was produced by macromutations, not the selection of small variants. Pág 17

Polyploid hybridization is also important in natural plant evolution. Section 14.7 (p. 405) discusses hybrid **speciation** in plants further, and we shall meet there the example of *Tragopogon* in the Washington–Idaho region. In these plants, two new species have originated in the past century by natural hybridization and polyploidy. Pág 53

For the salamanders (*Ensatina*) in California, we saw the smooth continuum of increasing difference, from the variation between individual salamanders in a region, to interregional variation, to **speciation**. Pag 54

Disruptive selection is of particular theoretical interest, both because it can increase the genetic diversity of a population (by frequency-dependent selection a Section 5.13, p. 127) and because it can promote **speciation** (Chapter 14). Pag 80-81

The dN/dS ratio is found to be larger between species rather than within. If that were true equally for all sites in the genome, the result could be explained either by positive selection for change or by the nearly neutral theory (with a population bottleneck during **speciation**). Pag 185

Everything is included: multiple loci, fitness interactions, selection within and between populations, drift, and migration. (The theory of adaptive peaks is also relevant to **speciation**: Section 14.4.4, p. 394.) pág 217

Species selection operates when different species (or even higher taxa) possess different individual-level adaptations, and their different adaptations have different consequences for the rate of extinction or **speciation**. Pag 303 Taxa with lower extinction, or higher **speciation**, rates tend to proliferate. Much the same could be true of groups within a species. Pag 303

(Chapter 14) has probably often occurred when two populations have evolved independently, and accumulated incompatible genetic differences. Pág 343

Finally, the theory of **speciation**, as well as classification and phylogenetic reconstruction are all needed in evolutionary biogeography (Chapter 17) a the use of evolutionary theory to understand the geographic distribution of species. Pag 346

(The theory of **speciation** (Chapter 14) suggests some further reasons why discrete species evolve on continuous resources. Also, Section 13.7.2 discusses further evidence that ecological factors influence the array of phenetic forms in a species.) pag 353

It is a form of male competition, and its outcome may well be influenced by female choice. In this case, the “choice” would be effected by the female’s internal reproductive physiology. Section 14.11, p. 413, discusses how sexual selection may contribute to **speciation**, and provides further contexts for these observations.) pág 357

The other interest is in relation to **speciation**, and illustrates a similar point to the study of flour beetles. Mate preference, like sperm competition, is a form of sexual selection. Sexual selection is thought to drive **speciation**, particularly sympatric **speciation** (Section 14.11, p. 414). Pág 358

The African lake cichlids provide some of the strongest evidence for sympatric **speciation** (Section 14.10.3, p. 413). Seehausen’s experiments, which show that mating preferences are the first kind of isolation to evolve in these fish, fits in with the broad idea that sexual selection has contributed to the spectacular radiation of cichlids in East Africa. Pág 358

These experiments can reveal what isolating barriers are at work in the early stages of **speciation**. We return to this topic in Chapter 14. pag 359

The ecological and genetic explanations of hybrid fitness are discussed in Schluter (2000) and many of the papers about reinforcement, hybrid **speciation** in plants, and the Dobzhansky–Muller theory that are referred to in Chapter 14. pag 359

*This chapter begins by showing that we have extensive evidence for, and a good theoretical understanding of, the “by-product” theory of **speciation** pag 381*

*The chapter also looks at the special case of hybrid **speciation** in plants, at the possibility of **speciation** between populations that are not geographically separated, and at two current research trends: the influence of sexual selection on **speciation**, and the use of modern genomic techniques to identify genes that cause reproductive isolation. Pág 381*

However, many species do differ by being reproductively isolated, and even if the evolution of reproductive isolation is not always the crucial event in **speciation**, it is certainly the key event in research on **speciation**. The topic of this chapter is the evolution of reproductive isolation. Pag 382

Some of the theories of **speciation** apply only to prezygotic isolation, some only to postzygotic isolation, and some to both. Pag 382

If a new species evolves in geographic isolation from its ancestor, the process is called *allopatric **speciation***. Pag 382

If the new species evolves in a geographically contiguous population, it is called *parapatric **speciation***. If the new species evolves within the geographic range of its ancestor, it is called *sympatric **speciation*** (Figure 14.1 pag 382

The distinctions between these three kinds of **speciation** can blur, but we shall begin the chapter with the most important of the three processes: allopatric **speciation**. Almost all biologists accept that allopatric **speciation** occurs. The importance of parapatric and sympatric **speciation** are more in doubt, and we shall come on to them later. Pág 382

In allopatric **speciation**, new species evolve when one (or more) population of a species becomes separated from the other populations of the species, in the manner of

Figure 14.1a. pág 382

In the theory of allopatric **speciation**, the cessation of gene flow between allopatric populations leads, over time, to the evolution of intrinsic isolating barriers between the populations. Let us see what happens to the reproductive isolation between these populations over evolutionary time. Pag 383

The theory of allopatric **speciation** suggests that two such populations will also, at least sometimes, evolve some degree of reproductive isolation in consequence. Pag 384

Two other results of the experiments are worth noticing. One is that they suggest, though they do not prove, that **speciation** normally requires natural selection; genetic drift alone is not enough. Look at the controls in Dodd's results, for instance (Figure 14.2). pág 386

Templeton (1996), however, has argued that this experimental design is inappropriate for testing the influence of drift in **speciation**. Secondly, experiments have usually measured the evolution of prezygotic, not postzygotic, isolation. Pag 386

Postzygotic isolation would probably evolve by the same process in experimental populations, but this has not been properly shown. In conclusion for the experiments on allopatric **speciation**, we have strong evidence that prezygotic isolation tends to evolve in populations that are kept separately, in different conditions, for many generations. Pág 386

In the other 24 species the problems in the hybrid were due to epistatic interactions at multiple loci. It is a well supported generalization about **speciation**, that postzygotic isolation is due to multilocus gene interactions. Pág 391

Biologists are beginning to explore its rich implications for the genetic changes that cause **speciation**, and these two subtle predictions are examples of the kinds of hypotheses being tested now. Pag 392

We can now look at a more general version of that argument, and use it to explore a general question about **speciation**. Is **speciation** an "easy" evolutionary process that follows almost automatically from normal evolutionary change, or is it an evolutionarily "difficult" process that requires extraordinary mechanisms? Pág 394

The problem in **speciation** is that it seems to require "valley crossing." For species 1 to evolve into species 2, or vice versa, the population has to pass through a disadvantageous phase pag 394

Therefore, if **speciation** requires valley crossing, **speciation** is a difficult evolutionary process and will not normally happen; it will require some special conditions. Pag 394

For instance, evolutionists have argued that **speciation** happens in small stressed populations where a "genetic revolution" occurs (Mayr 1963, 1976). Or that it happens by a special process of "peak shifts." Pag 394

requires the normal action of selection and drift to be suspended. The inspiration of these ideas is that **speciation** is a difficult process, because of the need for valley crossing. This is one view of **speciation**. Pág 395

The Dobzhansky–Muller model offers a different view of **speciation**. It has no valley crossing. The fitness valley is generated as a consequence of the separate evolution of the two species. In the

Dobzhansky–Muller view, **speciation** happens as an almost automatic consequence of ordinary selection and drift within a population, as each population evolves in its own environmental conditions. **Speciation** does not require special conditions, in which normal evolutionary processes are suspended. Pág 395

Speciation instead is an almost automatic consequence of evolutionary change. The special mechanisms proposed in the alternative, valley crossing, view are little supported or unsupported by facts and are at best questionable in theory (Turelli *et al.* 2001a). pág 395

That could change in the future, but many evolutionists currently prefer the view that **speciation** is an evolutionarily “easy” process, requiring no more than the most commonplace of evolutionary mechanisms. Pag 395

Meanwhile, the Dobzhansky–Muller theory has been extensively tested and supported and has almost undoubtedly contributed to **speciation**, but only limited work has been done on the ecological theory so its contribution is more uncertain. Pag 396

However, we now know that in fact most **speciation** events do go through a “Haldane rule” phase. Coyne & Orr (1989) quantified this fact as follows. Pág 396

Thus if we cross two members of a species their offspring will have high fitness, and $I \approx 0$. If we cross individuals from two different species, usually the hybrid fitness is zero, and $I \approx 1$. The isolation (I) increases from 0 to 1 during **speciation**. Pág 396

Now it might be thought that during **speciation**, the degrees of isolation would increase in some fashion from 0 to 1 (Figure 14.8a). But Coyne & Orr (1989) found that of 43 *Drosophila* species pairs with intermediate degrees of isolation ($0 < I < 1$), 37 showed a sex difference and fitted Haldane’s rule. Pag 397

It is a normal fact about **speciation**, at least in fruitflies, that low male hybrid fitness evolves earlier than low female fitness. The true course of **speciation** looks something like Figure 14.8b. Haldane’s rule is a general property of **speciation**, not a curiosity. Pag 397

The true course of **speciation** looks something like Figure 14.8b. Haldane’s rule is a general property of **speciation**, not a curiosity. Pag 397

Haldane’s rule is a big generalization about **speciation**. Whatever the explanation is for the rule, we can conclude that **speciation** often proceeds in the manner of rule in at least some cases. Pag 398-99

Haldane’s rule has proved to be an excellent route to understanding the genetic changes that cause **speciation**, or at least that cause postzygotic isolation. Pag 398

Thus, the Dobzhansky–Muller theory not only explains the multilocus, epistatic genetic control of postzygotic isolation, it also helps to explain a general sex difference in the time course of **speciation**. Pág 399

We have abundant evidence, from experiments and biogeographic observations that **speciation** evolves as a by-product when two geographically separate populations evolve apart. For prezygotic isolation, we have some hypotheses, but few research results, on the genetic changes that underlie it. Pag 399

We can conclude the chapter so far by saying that there are two solid results in the study of **speciation**: reproductive isolation evolves as a by-product of allopatric divergence, and postzygotic isolation is caused by epistatic interactions among multiple genetic loci. Pag 399

These generalizations are worth keeping in mind as we move on. We are now going to turn to some less solid, more controversial areas of research on **speciation** pag 399

If we concentrated on these controversial areas alone, it might appear that little is known about **speciation** and that it is a permanently confused area of evolutionary biology pag 399

(We shall meet some other ways in which the same basic set up can arise, in Sections 14.9 and 14.10, when we look at parapatric and sympatric **speciation**.) What will be the next evolutionary step? Pág 400

How important is reinforcement in **speciation**? The initial condition for it looks simple, and probably arises quite often. All we need is the evolution of two genetic forms between which crosses are disadvantageous. Pag 400

We might therefore expect reinforcement to occur quite often during **speciation**, as a supplement to the “by-product” theory we have looked at. Pag 400

Natural selection favors assortative mating. However, other evolutionary forces will also be acting, and may remove the preconditions before reinforcement has increased reproductive isolation to the point of full **speciation**. Pág 401

The rate of blurring will depend on the fitnesses of the different gene combinations. Again, the precondition for reinforcement may disappear before **speciation** takes place. Pág 401

Reinforcement is a process that drives **speciation**. But the experimenter made hybrid fitness zero, meaning that **speciation** was effectively complete. Gene flow between the lines was experimentally prevented. Rice & Hostert (1993) called experiments of this kind “destroy the hybrids” experiments. Pag 402

Of the two processes that can drive the evolution of reproductive isolation a (i) divergence with isolation as a by-product, and (ii) reinforcement the first is well documented and is almost certainly important in **speciation**, but the second is not well documented and its influence in **speciation** is indeterminate. Pág 405

Many cases of hybrid **speciation** in plants probably involve a number of generations of introgression, rather than an instantaneous **speciation** event. Pag 406

Rieseberg & Wendel (1993) reviewed introgressive **speciation** in plants: they listed 155 cases in which it had been suggested, and they judged that the evidence for introgression was good in 65 of them. Pág 406

This problem is probably the reason why hybrid **speciation** has been much commoner in some groups of plants than others. A new hybrid can more easily cross the difficult transition stage, in which it is rare, if it has alternative reproductive options besides sexual cross-fertilization. Pág 408

Stebbins (1950) has shown that hybrid **speciation** is commoner in groups in which asexual reproduction or self-fertilization are possible. *Iris nelsonii*, for example, can reproduce asexually by

rhizome runners, in addition to sexual cross-fertilization via pollen that is carried by bumblebees
pag 408

Hybrid **speciation** is a distinctive contribution to evolutionary biology that has come from the study of plants. Hybrid **speciation** is probably commoner in plants than in animals (though animal examples do exist, as Arnold's (1997) book shows). It is certainly much better understood in plants than in animals, and practically all our understanding of the process has come from plants. Pag 408

What is the relation between these theories and the allopatric, parapatric, and sympatric theories of **speciation** (see Figure 14.1)? Both prezygotic and postzygotic isolation can evolve as by-products of divergence. Pag 408
Postzygotic isolation evolves according to the Dobzhansky–Muller theory, and that theory is closely tied to the allopatric theory of **speciation**. Pág 408

This theory is less strongly tied to the theory of allopatric **speciation**.
The process can indeed occur between populations that are separately evolving in different places. But adaptive divergence can also occur within one population, as we shall see, and that at least raises the possibility that **speciation** could occur nonallopatrically. Pág 409

The theory of reinforcement is only weakly tied to the theory of allopatric **speciation**. Indeed, it is hardly an allopatric 'theory of **speciation** at all. Reinforcement was only used in the allopatric theory to "finish off **speciation** that was incomplete in allopatry. Pag409

Thus, in the theories we have met so far, **speciation** in non-allopatric populations is relatively unlikely. One well supported theory, the Dobzhansky–Muller theory, is allopatric. Reinforcement is a sympatric process, but (as we saw) little supported by evidence and problematic in theory. Pag 409

However, non-allopatric **speciation** has not been ruled out, and in the next two sections we shall look some more at whether **speciation** could occur parapatrically or sympatrically. Pag 409

In parapatric **speciation**, the new species evolve from contiguous populations, rather than completely separate ones, as in allopatric **speciation** (see Figure 14.1). The full process could occur as follows. Pag 409 The fact that the crows interbreed in the hybrid zone means that **speciation** between them is incomplete. We shall meet some more examples of hybrid zones in Section 17.4 (p. 497). Pág 410

The conditions in a hybrid zone (or a stepped cline) are particularly ripe for **speciation** if it is a *tension zone*. A tension zone exists when the hybrids between the forms on either side of the boundary are selectively disadvantageous. Pag 410

Reinforcement could then finish **speciation** off, eliminating hybridization from the hybrid zone. That sequence of events constitutes parapatric **speciation**. Pag 410

The strong point of the theory of parapatric **speciation** is that the environment "stabilizes" the preconditions for reinforcement. We saw that these conditions are liable to autodestruct, as the two forms interbreed, or as one eliminates the other. But if the environment varies in space, the clinal variation will be maintained. Parapatric **speciation** could work, in theory. Pag 410

The theory of parapatric **speciation** has two main weak points in the evidence. One is the evolutionary history of hybrid zones. Hybrid zones can be "primary" or "secondary." Pag 411

Real hybrid zones only illustrate a stage in parapatric **speciation** if they are primary. The abundance of hybrid zones in nature would only be evidence that parapatric **speciation** is a plausible process if those hybrid zones are mainly primary. Pag 411

The abundance of hybrid zones in nature would only be evidence that parapatric **speciation** is a plausible process if those hybrid zones are mainly primary. If most hybrid zones are secondary, the difference between the forms evolved allopatrically not parapatrically. Pág 411

Hooded and carrion crows, for instance, have met up after their ranges expanded following the most recent ice age. Indeed, range expansion following the ice age is a common explanation of hybrid zones (Section 17.4, p. 497). Hybrid zones provide little support for the theory of parapatric **speciation**. Pág 411

Thus, the process of parapatric **speciation** is possible in theory. The theory solves one key problem in reinforcement. Most (but not all) stages of parapatric **speciation** can be illustrated by evidence. Pág 411

Thus, the process of parapatric **speciation** is possible in theory. The theory solves one key problem in reinforcement. Most (but not all) stages of parapatric **speciation** can be illustrated by evidence. Pág 411

Parapatric **speciation** cannot be ruled out, and probably operates in some cases. But the case that it is important has still to be made. Pag 411

In sympatric **speciation**, a species splits into two without any separation of the ancestral species' geographic range (see Figure 14.1). Sympatric **speciation** has been a source of recurrent controversy for a century or so. Mayr pag 411

In the theory of parapatric **speciation**, the initial stage in **speciation** is a spatial polymorphism (or stepped cline). In sympatric **speciation**, the initial stage is a polymorphism that does not depend on space within a population. For instance, two forms of a species may be adapted to eat different foods pag 411

Most models of sympatric **speciation** suppose that natural selection initially establishes a polymorphism, and then selection favors prezygotic isolation between the polymorphic forms. "Host shifts" in a fly called *Rhagoletis pomonella* provide a case study that may illustrate part of the process. Pag 412

These moves to new food plants are called *host shifts*. In the host shift of *R. pomonella*, **speciation** may be happening before our eyes. Pág 412

Apples and hawthorns differ and selection will therefore probably favor different characters in each race; this may be the reason for their divergence. If it is, selection may also favor prezygotic isolation and **speciation**. Pag 412

Once again, the evidence for reinforcement is the weak point in a theory of **speciation**. Pág 412

However, it is not a full example of sympatric **speciation** because the races have not fully speciated. Indeed, we do not know whether they will, or whether the current situation, with incomplete **speciation**, is stable. Pag 412

How general a process is sympatric **speciation** by host shifts? A definite answer cannot be given as it has not even been confirmed that sympatric **speciation** ever does take place by host shifts. Pág 413

If phytophagous insect species consisted of an occasional odd species scattered through the phylogeny of insects, and feeding on unrelated kinds of food plants, the process would probably have not been operating; but the existence of whole large taxa of host plant-specific phytophages does suggest that **speciation** by host shifts could have contributed to their diversification. Pag 413

Direct attempts to test the theory of sympatric **speciation**, such as in *Rhagoletis pomonella*, are only one way to test whether sympatric **speciation** occurs. Pag 413

Recently, a new kind of evidence has been put forward for sympatric **speciation**. The evidence suggests that sympatric **speciation** occurs, but tells us nothing about how it occurs. Pag 413

As we saw (Section 13.3.3, p. 357), many species of cichlid fish have evolved in the East African lakes. Did they originate by sympatric, or allopatric, **speciation**? Pág 413

Figure 14.14 shows the argument. If a new species arises by allopatric **speciation**, its nearest relative will usually live in a different geographic area, such as in a nearby lake or river. If the species evolved sympatrically, the nearest related species will usually live in the same lake. I pág 413

In the case of a number of fish species, including the African cichlids, the phylogenetic evidence supports sympatric **speciation**. Similar studies for other taxa usually suggest allopatric **speciation** (Barraclough & Vogler 2001). Pag 413

the case of a number of fish species, including the African cichlids, the phylogenetic evidence supports sympatric **speciation**. Similar studies for other taxa usually suggest allopatric **speciation** (Barraclough & Vogler 2001). Pag 413

In conclusion, few biologists would rule out non-allopatric mechanisms of **speciation**. **Speciation** probably occurs non-allopatrically, though it may only be rare. Sympatric and parapatric **speciation** are more controversial theories than allopatric **speciation**, except for special cases such as hybrid **speciation** in plants, because they are not supported by such an impressive range of evidence. Pag 413

We can finish this chapter by looking briefly at two big themes in current, and possibly future, research on **speciation**. Pág 413

Sexual selection is discussed in Section 12.4 (p. 327) and has two main components: male competition and female choice. The mechanisms that females use to choose mates may influence **speciation** because they can contribute to, or even wholly determine, prezygotic isolation. pag 414

A similar association arises in some recent models of sympatric **speciation** (Dieckmann & Doebeli 1999; Higashi *et al.* 1999; Kondrashov & Kondrashov 1999). Pag 415

But sexual selection can help to strengthen the association, making sympatric **speciation** more plausible. Pág 415

These two arguments are only two of several ways in which sexual selection has recently been suggested to drive **speciation**. Pag 415

For instance, evolutionary conflict between males and females (Section 12.4.7, p. 336) may contribute to **speciation**.) pag 415

Sexual selection has not yet been shown to drive the evolution of prezygotic isolation in any case of **speciation**, though good suggestive evidence exists. We do not know that sexual selection is a general force of **speciation**. But much research on this topic is being done. Pag 415

But research of this sort may provide one way forward in studying **speciation**. If we can identify genes that cause prezygotic isolation, we can see what (if anything) their pleiotropic, and hitch-hiked, effects are. Pag 415

Our understanding of **speciation** should improve as we move from abstract theory to concrete examples. Moreover, modern genetics has powerful techniques for identifying genes at techniques that were not available before the “genomics” era. Pag 415

We can fit these observations in with a general idea about **speciation**: the idea of “**speciation** genes.” **Speciation** genes can be defined as genes that differ between a pair of species, and cause reproductive isolation between them. Pag 416

(A more demanding definition would be that **speciation** genes are genes that differ between a pair of species and drove **speciation** between them. However, empirical research can usually only show that a gene causes reproductive isolation and we remain uncertain whether the gene also drove **speciation**.) pag 416

Biologists discuss various hypotheses about **speciation** genes. We can distinguish a strong and weak claim. The strong claim would be that some genes in the genome may be particularly likely to drive **speciation**. Pag 416

That is, we can look at the genome in advance of **speciation** and say “if gene *X* changes, **speciation** will follow.” For instance, changes in the genes concerned with courtship or mate choice might be more likely to drive **speciation** than changes in other genes. If true, genes that influence courtship and mate choice would be “**speciation** genes. Pag 416

Other possible examples include genes on the X chromosome, or genes such as the segregation distorter genes (Section 11.2, p. 294), or chromosomal mutation. But none of these kinds of genes have been shown to drive **speciation** in general, and the strong claim about **speciation** genes may well be false. Pag 416

Alternatively, changes in almost any gene might be able to drive **speciation**. Then we can talk about **speciation** genes in a weaker sense simply to refer to the genes that happen to cause reproductive isolation in a particular pair of species. Pag 416

However, the genes that drive **speciation** will be the genes that have changed in evolution. An unchanging, conserved gene cannot cause isolation between two species. The genes driving **speciation** will be the first genes to change that is, the genes that evolve fastest. Pag 417

The genes driving **speciation** will be the first genes to change that is, the genes that evolve fastest. Maybe they will be genes like *Odysseus*, which does not normally evolve fast but happened to in one population. Pag 417

One gene may have an evolutionary spurt in one lineage, and cause **speciation** there. Another gene may spurt in another lineage, and cause **speciation** there. The “**speciation** genes” will be those that happened to evolve fast in a particular lineage. pag 417

The “**speciation** genes” will be those that happened to evolve fast in a particular lineage. Or it could be that some genes in the genome evolve faster than average in all life forms. Then, these fast evolving genes may be the **speciation** genes. One suggestion of this sort is that genes expressed in the reproductive system may evolve faster than other genes (see Swanson & Vacquier (2002) for the facts). Then **speciation** will more often be caused by evolution in the genes of the reproductive system than in genes of (for example) the nervous or digestive system. Pág 417

These ideas about **speciation** genes are currently conjectural. However, they are an example of the kind of general idea about **speciation** that we should be able to investigate as modern genetic techniques are used to identify the genes that are causing reproductive isolation in particular species. Pág 417

He devoted a chapter to arguing the point. He was less interested in the geographic circumstances of **speciation**, but argued for something like what we would now call sympatric **speciation** rather than allopatric **speciation**. Competition between forms within an area would force them to diverge, he reasoned. Pag 417

Associated with this was a second claim, that speciating populations tend to be small and that genetic drift is particularly important in **speciation**. Thirdly, Dobzhansky and others argued that reinforcement also contributes to **speciation**. (pag 417

Now, 50 or more years later, the allopatric theory of **speciation** still stands up. Many biologists would allow some contribution from sympatric **speciation**, but most accept that allopatric **speciation** is the main process. In this respect, biologists now agree with the modern synthesis rather than Darwin. Pág 418

The second claim, that **speciation** is often powered by genetic drift now has few supporters. It is the least important of the five claims listed above, and may not have been strongly believed in even during the period from the 1930s to the 1950s. In the 1920s, biologists often suggested that the characters that differ between species are non-adaptive. Pag 418

This partly inspired “non-adaptive” theories of **speciation**, but few biologists now argue that species differences are nonadaptive.

The experimental evidence and theory of **speciation** suggest the genetic drift is not all that important in **speciation**. **Speciation** is probably more often a by-product of normal adaptive divergence between populations. pag 418

The theory of reinforcement has had its ups and downs. Reinforcement continues to tantalize biologists, but a compelling case for its importance has yet to be made. The theory of hybrid **speciation** in plants, by contrast, has held up well. New genetic techniques have enabled biologists to trace the ancestry of modern species, providing a detailed description of hybrid **speciation**. Pag 418

The Dobzhansky–Muller theory looks as if it may continue to inspire research as the techniques of modern genomics are imported into the study of **speciation** pag 418

The recent research monographs by Arnold (1997), Levin (2000), and Schluter (2000) contain much material about **speciation**, as does the conference proceedings edited by Magurran & May (1999).

The special issue of *Genetica* (2001), vol. 112/113 contains several papers on **speciation**; it was also issued as a separate book (Hendry & Kinnison 2001). Also see the supplement (edited by Via) to vol. 159 of *American Naturalist* (2002); it is a special issue on the ecological genetics of **speciation**. Pág 420

(Wolbachias are worth looking into in their own right for dramatic experiments, such as Breeuwer and Werren's, in which antibiotic treatment "cures" **speciation**. Werren (1997) is a review.) Pág 420

Two other excellent case studies in the genetics of **speciation** are the work of Schemske & Bradshaw (1999) on monkey flowers, in which genes influence flower coloration, which influences pollinators, and of Rieseberg on sunflowers (see the hybrid **speciation** references given below). Pág 420

Rieseberg also has a piece in the special issue of *Trends in Ecology and Evolution* (2001) that introduces the role of chromosomal change in **speciation** which is a further big historic theme in the **speciation** literature. Noor *et al.* (2001) is a recent study of a pair of *Drosophila* species in which a chromosomal inversion influences reproductive isolation. Pág 420

On hybrid **speciation**, see Arnold (1997), Rieseberg (1997, 2001), and Rieseberg & Wendel (1993). Soltis & Soltis (1999), Ramsey & Schemske (1998), and Leitch & Bennett (1997) discuss polyploidy in plants, a closely related topic. Pag 421

Grant (1981) is a classic and covers plant **speciation** in general. See also general books on plant evolution, such as Niklas (1997). Arnold (1997) and Dowling & Secor (1997) discuss evidence for animals too. Pág 421

On parapatric **speciation** see Endler (1977), which includes an important discussion of the biogeographic evidence for hybrid zones. Harrison (1993) is a multiauthor book about hybrid zones. See also Chapter 17 of this text, and the Hewitt references in it. On the European crows, see Cook (1975). Pág 421

On sympatric **speciation**, Mayr (1942, 1963) is the classic critic, though see Mayr (2001) for his current view. Guy Bush has inspired much work, and the book edited by Howard & Berlocher (1998) was a *Festschrift* for Bush: it includes several papers on host shifts and *Rhagoletis*, as well as on other topics in sympatric **speciation**. Pag 421

The issues of *Nature* (1996), vol. 382, p. 298, and of *Science* for September 13, 1996 have news features on a conference again mainly about Bush's work. Via (2001) reviews sympatric **speciation**, and Barraclough & Nee (2001) discuss the use of phylogenetic evidence, in the special issue of *Trends in Ecology and Evolution*. For the cichlids see Stiassny & Meyer (1999) and Fryer (2001). Pág 421

The classic treatises on **speciation** by Mayr (1942, 1963) and Dobzhansky (1970) remain good, if dated, introductions. See Mayr (2001, and Mayr & Ashlock 1991) for his more recent ideas; Coyne (1994) discusses **speciation**, particularly in relation to Mayr's ideas. The multiauthor book edited by Otte & Endler (1989) is becoming dated, but introduces many themes in **speciation**. Pag 421

The branching events can be either geneduplications or **speciation** events.⁶ The species tree is the phylogeny in the sense of the present chapter. The branching events correspond to **speciation** in the past. Pag 457

Ting *et al.* (2000) avoid one confusion between gene and species trees in an interesting way. They use the “**speciation**” gene *Odysseus*, which we met in Section 14.12. It should be invulnerable to the lineage sorting problem, if it caused **speciation**, making it a reliable indicator of phylogeny. Pag 469

Here we concentrate on the other two problems. (Other problems can arise when evolution is non-hierarchical, for instance because of hybrid **speciation** (Section 14.7, p. 405) or horizontal gene transfer (Figure 15.19, p. 456).) pág 483

Other factors probably also contribute to causing divergence. For instance, **speciation** is often allopatric and each pair of sister species becomes increasingly isolated over time by the Dobzhansky–Muller process (Section 14.4, p. 389). Pag 489

The two gene pools have evolutionarily “escaped” from each another and are free to diverge further. Our modern genetic understanding of **speciation** has added to Darwin’s explanation for divergence. Pág 489

The genetic changes in the fragmented refugial populations were not probably enough to produce full **speciation**. The European hedgehogs, for instance, are currently divided into two species. Pág 499

Haffer suggested that the fragmentation of ranges accelerated the process of allopatric **speciation**, creating what was called a “**speciation pump**” that contributed to modern biodiversity. Pag 499

Haffer stimulated research, but the results of that research have not supported his ideas. Evidence from molecular clocks, for instance, suggests that the **speciation** events that produced many modern species are too old to fit Haffer’s hypothesis, nor do **speciation** rates seem to go up during ice ages. Pag 499

Although the latest ice age did not produce a burst of **speciation**, it may have helped to finish off **speciation** between populations that had already diverged, or started the divergence between populations that could lead to **speciation** in the future pag 499

A single **speciation** event often occurs as two species, with different ecological adaptations, evolve from a single ancestral species (Section 14.3, p. 383). Pág 500

A local adaptive radiation occurs when several such **speciation** events occur in a local area. As we shall see in Chapter 23, adaptive radiation can be studied on a global scale, if the adaptive radiation of a taxon persists for a long enough time. But here we shall be looking at smaller scale adaptive radiations a those that are only a slight extension of the **speciation** process we looked at in Chapter 14. pág 500

Inspection of it shows that, although many of the species evolved from ancestors on the same island, a large number of **speciation** events occurred following dispersal between islands. Pág 503

It is called *vicariance biogeography*. The drifting apart of tectonic plates is the sort of event that could cause **speciation** (Section 14.2, p. 382). If the splitting of the land and of the species on it coincide, it results in two or more species occupying complementary parts of a formerly continuous area that was occupied by their common ancestor. Pag 506

Others do not. We saw above how *Anolis* lizards in the Caribbean evolved by **speciation** within each island, but that their distributions within each island do not fit with vicariance. Pág 511-512

We can be sure that **speciation** was not simply by splits in the range of a larger species, because the younger islands did not even exist while the flies were on the older islands. Pag 512

They argued the primary invasions were roughly equal in both directions, and that the takeover of the south by northern mammals was partly a result of two other factors: weight of numbers and different rates of **speciation** after arrival. Pag 514

The conventional dividing line between macro- and microevolution is at **speciation**, so that events below that level are microevolution and those above it are macroevolution. Pág 521

In Chapter 21, we move on to the study of evolutionary rates. We see how they are measured and consider one controversy *a* about the relative rates of evolution during, and between, **speciation** events *ain* detail. Pag 522

The final chapter (Chapter 23) discusses the history of biological diversity *a* the number of forms of life on Earth. Diversity can be measured by the number of species, and this is controlled by the relative rates of **speciation** and of extinction pág 522

A similar conclusion could be drawn about the origin of humans, and of terrestrial plants and vertebrates. In these example, macroevolution proceeds by the same process a natural selection and adaptive improvement a as has been observed within species and at **speciation**; but the process is operating over a much longer period. Pág 551

If the extrapolation is correct, the reason for the **speciation** in the finches was the same process as has been observed in the present a natural selection for changes in beak shape, which were probably in turn due to changes in food types through time and between islands. Pág 596

For example, it has been suggested that species usually change more rapidly during, rather than between, **speciation** events; that structurally more complex forms evolve faster than simpler forms; and that some taxonomic groups evolve more rapidly than others, that mammals, for instance, evolve faster than mollusks (this is an old idea ait was one of Lyell's favorite generalizations). Pág 596

They contrasted phyletic gradualism with their own preferred hypothesis, *punctuated equilibrium* (Figure 21.5a). They used the standard theory of **speciation** a allopatric **speciation**, which we looked at in Chapter 14 ato argue that the fossil record should show a pattern different from phyletic gradualism. Pag 599

If new species arise allopatrically and in small isolated populations then the fossil record at any one site may not reveal the **speciation** event. If the site preserves the record of the ancestral species, the descendant species will be evolving elsewhere pag 599

Between **speciation** events, species may have a low rate of evolutionary change a a condition Eldredge and Gould called *stasis*. Pag 600

The theory ofpunctuated equilibrium holds that stasis is the normal condition within a species. Stasis breaks down only when **speciation** occurs. Evolutionary change is concentrated in **speciation** events. Any observation of change without **speciation** (Figure 21.5c) would contradict the theory of punctuated equilibrium. Pag 600

In the account here, the theory of punctuated equilibrium is relatively “orthodox.”

Eldredge and Gould took the (or a) standard theory of **speciation**, and pointed out that it implies that fossils will usually show sudden, rather than smooth, change. Pág 600

The second source of controversy is that the theory of punctuated equilibrium has also drawn on and been associated with much less widely accepted ideas about **speciation**.

The theory of punctuated equilibrium has been actively developed for about 30 years and exists in many different versions. In particular, “valley crossing” theories of **speciation** (in terms of Section 14.4.4, p. 394) have often been used to predict punctuated equilibrium. **Speciation** requires valley crossing if two species have different adaptations, and the intermediate forms between them have lower fitness pag 600

Darwin did not make his remarks about gradualism particularly in the context of evolutionary rates at and between **speciation** events. Pág 601

When Eldredge and Gould first published their theory in the 1970s, valley crossing theories of **speciation** were more popular than they are now. Pag 601

As we saw (Section 14.4.4, p. 394), the evidence and theoretical trends have moved against valley crossing theories of **speciation**. Thus, punctuated equilibrium has been controversial because it has been associated with a controversial set of theories about **speciation** pag 601

Thus, punctuated equilibrium has been controversial because it has been associated with a controversial set of theories about **speciation**. Punctuated equilibrium has even been associated with the very unorthodox idea that evolution proceeds by macromutations (Section 10.5, p. 266). However, punctuated equilibrium does not depend on any of these valley crossing theories. Punctuated equilibrium can be derived, as we saw, from the well substantiated allopatric theory of **speciation**. Fossils can rarely be used to test between theories about the mechanism of **speciation**. Pag 601

Instead we can concentrate here on the empirical question of what pattern of evolution is observed during **speciation**. Does the fossil record show new species evolving suddenly, or gradually with many intermediate stages? Pág 602

However, the question of what the relative frequencies are of sudden and gradual evolution during **speciation** merits an answer in itself. Eldredge & Gould (1972) posed this question, and they have stimulated a major research program in the past 25 years. Pag 603

Evolution has a range of rates, from sudden to smooth, in real examples of fossil **speciation**. Pag 606

A future research question will be to ask what conditions lead to more gradual evolution, and what conditions to punctuated evolution, but at present paleontologists are still answering the prior question of what the empirical rates of evolution are during, and between, **speciation** events. Pag 606

Dennett (1995, chapter 10) discusses the controversial relation with saltationism. Erwin & Anstey (1995) contains papers on fossil **speciation**. Several chapters in Jackson *et al.* pag 612

The two taxa have exerted evolutionary influences on each other, and evolution leading to **speciation** in one taxa tends to cause **speciation** in the other taxon too. For instance, two subpopulations of one ancestral milkweed species might have become geographically separated

from each other. Each subpopulation of milkweed might well have its own subpopulation of *Tetraopes*. Pág 618-619

Reproductive isolation would probably evolve as a by-product, by the classic process of allopatric **speciation** (Section 14.3, p. 383). After a while, the two forms of plant might meet up but be reproductively isolated because of the genetic differences that had built up between the two. Pág 619

Finally, cophylogenies may arise if two taxa have no evolutionary influence on each other, but some independent factor leads to **speciation** in both. For example, allopatric **speciation** could occur in several non-interacting taxa if they occupy much the same range and something splits all their ranges pag 620

The main mirror-image pattern between the pocket gopher and lice phylogenies is probably due to **cospeciation**. That is, a host species and its parasite species tend to split at the same time. Pág 631

The ancestral gopher, and its ancestral louse, species then split twice. The events down the E→C→A B branch (moving up the figure) look very like **cospeciation**. Pág 631

Why should host and parasite speciate synchronously? Probably because the same circumstances favor **speciation** in both groups pag 631

For instance, the ranges of the two could be fragmented by some biogeographic factor, and the normal process of allopatric **speciation** occur in both parasites and hosts. Pág 631

The same conditions drive **speciation** in both parasite and host and the result is **cospeciation**. Pag 631

Figure 22.8b provides a stronger test of **cospeciation**. Hafner *et al.* used the estimated number of changes in each branch as a molecular clock to estimate the time when the branch originated. Pág 631

If there was real **cospeciation**, the **speciation** events in host and parasite should have occurred simultaneously. Hafner *et al.* used two molecular clocks, one for all the nucleotide substitutions and the other for only the synonymous nucleotide changes. Pág 631

Unless the molecular clock is massively misleading, by three orders of magnitude, the cophylogenies here are not evidence of **cospeciation**. Pág 631

The match between phylogenies would not be due to **cospeciation** but to phylogenetically constrained host switching. The influence of the host's physiology, and particularly its immune system, on host switching, could be analogous to the influence of plant chemistry on insect evolution (Section 22.3.3 above). Pág 632

The main point of the example here is to show that cophylogenies alone are not complete evidence for **cospeciation**. Pag 632

For the gophers and lice, both phylogenetic and molecular clock evidence support **cospeciation**. For the primates and lentiviruses, the phylogenetic evidence is consistent with **cospeciation** but the molecular clock evidence counts strongly against it. Pag 632

For the primates and lentiviruses, the phylogenetic evidence is consistent with **cospeciation** but the molecular clock evidence counts strongly against it. Pág 632

In summary, we have looked at three possible relations between the phylogenies of parasites and hosts. One is that they have cophylogenies caused by **cospeciation**. Pág 632

A second is that they have cophylogenies, but for some reason other than **cospeciation**.
A third is that they do not show cophylogenies. All three patterns can be found in different examples. Pág 632

The diversity of life through time reflects the rates of loss and gain of new life forms.
The loss of species is by extinction, and the gain of species is by **speciation** pág 644

When the **speciation** rate exceeds the extinction rate for a taxon, its diversity increase. When the extinction rate exceeds the **speciation** rate, its diversity decreases. Pág 644

When the extinction rate exceeds the **speciation** rate, its diversity decreases. We can begin by looking at periods when the number of species in a taxon increases during *adaptive radiations*. Pág 644

What factors determine the patterns of **speciation** and radiation? The question has been studied in various ways and in this and the next section we shall concentrate on two ideas: one in which the attributes of the organisms may influence a taxon's probabilities of survival and **speciation**, and the other in which external ecological factors may show such an influence. Pág 658

The relation between larval type and **speciation** and extinction rates can be studied in fossil gastropods. Larval types in fossils are inferred by analogy with modern species.
These kinds of inference were pioneered in the work of Thorson, and several criteria have now been used. Figure 23.7 shows one, which uses the size of regions in the larval shell. Pág 661

Hansen (1978, 1983) looked at the relation between larval type and **speciation** rate. He predicted that snails with direct development will speciate more rapidly than species with planktonic larvae, because the species with non-planktonic development will be more likely to be geographically localized and isolated, which makes allopatric **speciation** easier. Pág 662

Planktonic development increases gene flow and makes allopatric **speciation** less probable. He used this idea to explain an observed trend in snails of the early Tertiary (Figure 23.9). pág 662

The second alternative is that the increase was due to a higher **speciation** rate of the directly developing forms, simply because forms with lower dispersal rates are more likely to speciate. Pág 662

For the trend in Figure 23.9 to be driven by differences in **speciation** rate, it is important that the ancestor–descendant lines of species tend to retain the same mode of development.
(In technical language, heritability is required at the level of species.) pag 664

Currently it is uncertain whether, as Hansen originally argued, the decline in planktonically developing forms in the early Tertiary occurred because they had a low **speciation** rate. Pag 664

In the previous section, we considered the possibility that a character (larval type) might influence **speciation**, and extinction, rates. Pág 664

The influence, if real, is a straight consequence of the character itself: species in which there is direct development are more likely to split, in the process of allopatric **speciation**, than species in which there is planktonic development. A pág 664

A second factor that can influence **speciation** and extinction rates is the nature of the ecological niche occupied by species. Species that occupy niches that last longer will have lower extinction rates than species that occupy shortlived niches. Williams (1992) introduced this idea in terms of a concrete example at the three-spined stickleback (*Gasterosteus aculeatus*). Pág 664

The populations in the coastal niche have a low extinction rate, and probably a higher **speciation** rate pág 665

The populations in the freshwater tributaries have high extinction rates, and probably low **speciation** rates. Pag 664

Species selection means, other things being equal, that those kinds of species that have lower extinction and higher **speciation** rates will tend to increase in frequency over evolutionary time. Pág 665

Within a species natural selection favors one character in one species and another in a different species; but species selection over long periods may cause the species with one of the characters to proliferate, because of the character's consequences for **speciation** or extinction rate pag 666

Speciation and extinction may have been in balance for much of the past 500 million years, with mass extinctions having had little effect on global species diversity. That such a dramatically different picture can be produced now highlights the importance of statistical corrections to the data pág 676

On a related theme, Hubbell (2001) looks at the clade shapes expected on random models of **speciation** and extinction. Pág 680

Polyandrous insect clades have a four times higher rate of **speciation** than sister monandrous clades. Sexual conflict, of the type we met in Section 12.4.7, is the prime suspect, and fits with ideas about **speciation** in Section 14.12. pág 680

Polyandrous insect clades have a four times higher rate of **speciation** than sister monandrous clades. Sexual conflict, of the type we met in Section 12.4.7, is the prime suspect, and fits with ideas about **speciation** in Section 14.12. pág 680

On global species diversity, a further topic is how diversity recovers after mass extinctions. Miller (1998) includes discussion and references. Kirchner (2002) shows that the **speciation** rate can have an upper limit that delays recovery following massive extinctions. Pág 680

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Chapters 6–7 discuss an evolutionary process called random **drift**. Random **drift** is random, but it is completely different process from natural selection. Pag. 12

The effects of random sampling are most powerful when the different genotypes all have the same fitness, and when population sizes are small. The theory of random **drift** has been most important for thinking about molecular evolution. Pag 93

The purpose of Sections 5.11–5.13 has been to illustrate the different mechanisms by which natural selection can maintain polymorphism. In Chapter 6 we look at another mechanism that can maintain polymorphism a genetic **drift**. Then, in Chapter 7, we tackle the question of how important the mechanisms are in nature. Pág 129

The genotypes at a locus may all have the same fitness. Then the gene frequencies evolve by random genetic **drift**. Pag 137

This chapter starts by explaining why **drift** happens and what it means, and looks at examples of random sampling effects. We see how **drift** is more powerful in small than large populations, and how in small populations it can counteract the effects of natural selection pag 137

We then see how **drift** can ultimately fix one allele. The Hardy–Weinberg ratios are not at an equilibrium once we allow for the effects of **drift**. Pag 137

We then add the effects of mutation, which introduces new variation: the variation observed in a population will be a balance between the **drift** to homozygosity and mutation that creates heterozygosity. Pág 137

These random changes in gene frequencies between generations are called genetic **drift**, random **drift**, or (simply) **drift**. The word “**drift**” can be misleading if it is taken to imply an inbuilt bias in one direction or the other. Genetic **drift** is directionless **drift**. Pag 138

Genetic **drift** is not confined to the case of selective neutrality. When selection is acting at a locus, random sampling also influences the change in gene frequencies between generations. The interaction between selection and **drift** is an important topic in evolutionary biology, as we shall see in Chapter 7. However, the theory of **drift** is easiest to understand when selection is not complicating the process and in this chapter we shall mainly look at the effect of **drift** by itself. Pag 138

The rate of change of gene frequency by random **drift** depends on the size of the population. Random sampling effects are more important in smaller populations. Pag 138

If a population is small, it is more likely that a sample will be biased away from the average by any given percentage amount; genetic **drift** is therefore greater in smaller populations. The smaller the population, the more important are the effects of random sampling. Pág 139

Random **drift** would then be unimportant in evolution. In fact reproduction is not like that. The successful gametes are a random sample from the gamete pool. Pag 139

One gene can be substituted for another by random **drift**. The frequency of a gene is as likely to decrease as to increase by random **drift**. On average the frequencies of neutral alleles remain unchanged from one generation to the next. In practice, their frequencies **drift** up and down, and it is therefore possible for a gene to enjoy a run of luck and be carried up to a much higher frequency. In the extreme case, its frequency could after many generations be carried up to 1 (become fixed) by random **drift**. Pag 142

It has a still smaller chance of increasing through three generations, and so on. For any one allele, fixation by random **drift** is very improbable. The pag 143

The probability is finite, however, and if enough neutral alleles, at enough loci, and over enough generations, are randomly **drifting** in frequency, one of them will eventually be fixed. The same process can occur whatever the initial frequency of the allele. Pag 143

A rare allele is less likely to be carried up to fixation by random **drift** than is a common allele, because it would take a longer run of “good” luck. However, fixation is still possible for a rare allele. Even a unique neutral mutation has some chance of eventual fixation. Pag 143

Random **drift**, therefore, can substitute one allele for another. What is the rate at which these substitutions occur? We might expect it would be faster in smaller populations, because most random effects are more powerful in smaller populations pag 143

It will have been fixed by genetic **drift**. Now, because the process is pure luck, each of the $2N$ genes in the original population has an equal chance of being the lucky one pag 144

Any one gene in the population, therefore, has a $1/(2N)$ chance of eventual fixation by random **drift** (and a $(2N - 1)/(2N)$ chance of being lost by it). Pag 144

Figure 6.3 also illustrates another important concept in the modern theory of genetic **drift**, the concept of coalescence (Box 6.2). pag 144

Genetic coalescence is a consequence of the normal operation of genetic **drift** in natural populations. Every gene in the human species, and every gene in every species, traces back to a coalescent pag 144

Let us stay with the case of a single locus, with two selectively neutral alleles A and a . If genetic **drift** is not happening and if the population is large and the gene frequencies will stay constant from generation to generation and the genotype frequencies will also be constant, in Hardy–Weinberg proportions (Section 5.3, p. 98). Pág 145

But in a smaller population the gene frequencies can **drift** around. Pag 145

That is not so, however. The long-term result of genetic **drift** is that one of the alleles will be fixed. The polymorphic Hardy–Weinberg equilibrium is unstable once we allow for genetic **drift**. Pág 145

The same process could have gone off in the other direction, or started by favoring A and then reversed to fix a as a random **drift** is directionless. However, when one of the genes is fixed, the population is homozygous and will stay homozygous (Figures 6.3 and 6.4). pag 145

The Hardy–Weinberg equilibrium is a good approximation, and retains its importance in evolutionary biology. But it is also true that, once we allow for random **drift**, the Hardy–Weinberg ratios are not at an equilibrium. Pag 145

However, random events cause gene frequencies to **drift** about, and one of the genes will eventually be fixed. Only then will the system be stable. The true equilibrium, incorporating genetic **drift**, is at homozygosity. Pág 145

Over the long term, pure random **drift** causes the population to “march” to homozygosity at a locus. The process by which this happens has already been considered (Section 6.4) and illustrated (Figure

6.3). All loci at which there are several selectively neutral alleles will tend to become fixed for only one gene. It is not difficult to derive an expression for the rate at which the population becomes homozygous. Pág 145

That is, heterozygosity decreases at a rate of $1/(2N)$ per generation until it is zero. The population size N is again important in governing the influence of genetic **drift**. If N is small, the march to homozygosity is rapid. Pág 148

With random sampling, two copies of the same gene may make it into an offspring in a future generation. Random sampling has then produced a homozygote. Genetic **drift** tends to increase homozygosity, and the rate of this increase can be exactly expressed by equations 6.2 and 6.3 pag 149-150

So far, it might appear that the theory of neutral **drift** predicts that populations should be completely homozygous. However, new variation will be contributed by mutation and the equilibrium level of polymorphism (or heterozygosity) will actually be a balance between its elimination by **drift** and its creation by mutation pag 150

To find out the equilibrium heterozygosity under **drift** and mutation, we have to modify equation 6.2 to account for mutation. If an individual was born a homozygote, and if neither gene has mutated, it stays a homozygote and all its gametes will have the same gene. Pág 150

The equilibrium is between the increase in homozygosity due to **drift**, and its decrease by mutation. Pág 150

This is an important result. It gives the degree of heterozygosity that should exist for a balance between the **drift** to homozygosity and new neutral mutation. The expected heterozygosity depends on the neutral mutation rate and the population size (Figure 6.6). pag 151

What is “population size”? We have seen that N determines the effect of genetic **drift** on gene frequencies. But what exactly is N ? In an ecological sense, N can be measured by counting, such as the number of adults in a locality. Pag 151

The effect of **drift** is to reduce the amount of variability in the population. Pag 153

The amount of neutral genetic variability in a population will be a balance between its loss by **drift** and its creation by new mutation. Pag 153

In a small population, random sampling of gametes to produce the next generation can change the gene frequency. These random changes are called genetic **drift**. Pág 153

Genetic **drift** has a larger effect on gene frequencies if the population size is small than if it is large. Pag 153

One gene can be substituted for another by random **drift**. The rate of neutral substitution is equal to the rate at which neutral mutations arise. Pag 153

7 Natural Selection and Random **Drift** in Molecular Evolution pag 155

This chapter discusses the relative importance of two processes in driving molecular evolution: random **drift** and natural selection. Pág 155

We begin by looking at what it means for **drift** to be a general explanation for molecular evolution. We then go on to some features of molecular evolution and, in particular, its relatively constant rate (the “molecular clock”). Pág 155

Evolution in the non-coding parts of DNA, and for synonymous changes within genes, is probably mainly by **drift**. The relative contributions of selection and **drift** to non-synonymous (amino acid altering) changes are less clear. Pág 155

Natural selection can leave its signature in the statistical properties of DNA sequences, and the modern genomic era of biology has made it possible to study selection and **drift** in new ways. The chapter finishes by looking at four of these. Pág 155

Random **drift** and natural selection can both hypothetically explain molecular evolution pag 156

Polymorphism within a species, and evolutionary change between species, can be explained by two processes: natural selection and **drift**. This chapter will be looking at the contributions of **drift** and selection in molecular evolution. Pág 156

This chapter will be looking at the contributions of **drift** and selection in molecular evolution. The subject hardly existed before the 1960s. pag 156

The neutral theory does not suggest that random **drift** explains all evolutionary change. Natural selection is still needed to explain adaptation. It is, however, possible that the adaptations we observe in organisms required only a small proportion of all the evolutionary changes that have actually taken place in the DNA. Pág 156

Given a mutation of a certain selection coefficient, the theory of random **drift** or selection (as described in Chapters 5 and 6) applies in a mathematically automatic way. If the selection coefficient is positive, the mutation increases in frequency; if it is negative, it is eliminated; if it is zero, the gene frequencies **drift**.1 pag 156

If neutral **drift** has produced most evolutionary change at the molecular level, the relative frequencies are the other way round. Figure 7.1 illustrates two extreme views, in which most molecular evolution will be driven by selection (Figure 7.1a) or by **drift** (Figure 7.1b) pag 157

Figure 7.1 illustrates two extreme views, in which most molecular evolution will be driven by selection (Figure 7.1a) or by **drift** (Figure 7.1b). pag 157

The neutral theory says that the majority of molecular evolution is driven by neutral **drift** but that does not mean the majority of mutations are neutral. Pag 157

Then, almost all evolution would be by neutral **drift**, just as in the neutral theory. But if most evolution is by neutral **drift**, that does not mean most mutations are neutral pag 157-158

The neutral theory uses selection only to explain why disadvantageous mutations are lost; it uses **drift** to explain how new mutations are fixed pag 158

The other thing that the neutral theory of molecular evolution does not claim is that all molecular evolution is driven by neutral **drift**. It says that most molecular evolution is by neutral **drift**. An important fraction of molecular evolution is almost certainly driven by selection: the fraction of molecular evolution that occurs during the evolution of adaptations. Pág 158

These adaptive functions did not evolve by accident. Random **drift** will not have contributed much, if at all, to adaptive evolution. The evolutionary events that gave rise to the adaptive functions of the modern molecules of life were almost all powered by selection. Pág 158

His modern followers also consider mutations with small positive or negative selection coefficients. Because **drift** is more powerful with small population sizes (Section 6.1, p. 138), these nearly neutral mutations are influenced more by **drift** in small populations and more by selection in large populations. Pág 159

Because **drift** is more powerful with small population sizes (Section 6.1, p. 138), these nearly neutral mutations are influenced more by **drift** in small populations and more by selection in large populations. The mutations become effectively neutral, or nonneutral, depending on population size. Pág 159

The neutral theory suggested that almost all molecular evolution is driven by neutral **drift**. Pág 159

Now the theory has been refined. Some parts of the DNA appear to evolve by neutral **drift**, but the relative contributions of selection and **drift** in other parts of the DNA are less clear. The stark contrast between (a) and (b) in Figure 7.1 has been modified by 30 years of accumulated evidence. Pág 159

In the first half of this chapter we shall look at three lines of less direct evidence that were originally used by Kimura, and King and Jukes, to argue for the importance of neutral **drift** in molecular evolution. Pág 159

In the second half of the chapter we shall look at some additional ways of testing between **drift** and selection that have become possible in the genomic era. Pág 159

Molecular evolution must be driven instead by random **drift**. Random **drift** creates no genetic load, because all the genotypes concerned have equal fitness. Pág 162

The genetic variation must be maintained by random **drift**, which explains polymorphism by a balance of **drift** and mutation (Section 6.6, p. 150). Neutral variation does not create a genetic load. Pág 163

What does a constant rate imply about whether molecular evolution is mainly driven by natural selection or neutral **drift**? Kimura reasoned that constant rates are more easily explained by neutral **drift** than selection. Pág 165

Kimura reasoned that constant rates are more easily explained by neutral **drift** than selection. Neutral **drift** has the property of a random process and its rate will show the variability characteristic of a random process. Pág 165

Neutral **drift** will drive evolution at a fairly constant rate. Natural selection, Kimura argued, does not produce such constant change. Pág 165

Population size only cancels out for purely neutral mutations. For a nearly neutral mutation, the relative power of **drift** and selection depends on population size. Pág 171

Nearly neutral mutations behave as neutral mutations in small populations, and their fate is determined by random **drift**. Pág 171

If it is slightly disadvantageous, its chance of being fixed by random **drift** is slightly less than $1/2N$. In a small population, of 100 or so, the mutation has a fairly high chance (slightly less than one in 200) of ultimately being fixed by **drift**. But in a large population, of a million or so, the chance of being fixed by **drift** is negligible (slightly less than one in 1,000,000). Pág 171

But in a large population, of a million or so, the chance of being fixed by **drift** is negligible (slightly less than one in 1,000,000). This is just to restate the fact that **drift** is more powerful in small populations (Section 6.1, p. 138). Pág 171

Evolution, therefore, is arguably dominated by **drift** in small populations and by selection in large populations. We can be more exact pág 172

The conceptual interest of nearly neutral mutations is that they evolve by random **drift** rather than natural selection. Pag 172

We can now distinguish two random **drift** theories of molecular evolution. According to Kimura's original neutral theory, most molecular evolution occurs as one purely neutral mutation ($s \approx 0$) is substituted for another pág 172

In a species with large populations, natural selection is more powerful than **drift**. The slightly disadvantageous mutations will be eliminated and not contribute to the observed genetic variation in that species. In pág 173

In species with small populations, natural selection is weak relative to random **drift**. Slightly disadvantageous mutations will behave as effectively neutral mutations pág 173

Some of them may **drift** up in frequency, contributing to the observed genetic variation. Genetic variation will be lower than the purely neutral theory predicts when population size is large. This is what is observed in reality (Figure 7.5). pág 173

They may be fixed by **drift**, and the rate of evolution will increase. When population size increases, the slightly disadvantageous mutations will be eliminated by selection and the rate of evolution will slow down. Pág 173

In a species with a long generation length, such as a whale, we now have two factors to consider: (i) DNA is copied slowly per year, which reduces the mutation rate per year; and (ii) population sizes are small, which makes **drift** more powerful than selection. Slightly disadvantageous mutations are less likely to be eliminated by selection, and are more likely to be fixed by **drift**. Pág 174

The relative power of selection and **drift** on these mutations depends on population sizes. The nearly neutral theory, by plausible arguments about population size, can account for several observations that present problems for Kimura's purely neutral theory. Pág 174

For any evolutionary change, in which one version of a gene is substituted for another, we can ask whether the force driving that change was natural selection or random **drift**. Pág 175

In the nearly neutral theory, just as in the original neutral theory, the force driving molecular evolution is neutral **drift**. Pág 175

Drift and selection combine in different ways in the two theories to explain the observed facts of molecular evolution. Pág 175

But a crucial similarity remains: both theories explain evolution by **drift**. Natural selection has only a negative role, acting against disadvantageous mutations. Pág 175

Pseudogenes, once formed, are probably under little or no constraint and mutations will accumulate by neutral **drift** at the rate at which they arise. Pág 176

Other biologists accept the neutralist view for synonymous sites and pseudogenes, but remain undecided whether amino acid changes are driven more by **drift** or positive selection. Pág 178

Most of the biologists who are doing the work probably assume that the molecular changes they are studying occur by random **drift**. Pág 179

This being so, the majority of molecular evolution proceeds by random **drift** rather than selection. Pág 179 Genomic sequences have become available in large amounts recently, and they can be used to look for signs of selection and **drift**. Pág 179

Natural selection is powerfully maintaining the amino acid sequence, while synonymous changes evolve by **drift**. Pág 181

Then the rate of non-synonymous evolution will increase, while the rate of synonymous change will continue as normal, by random **drift**. Thus an elevated dN/dS ratio can result when natural selection has favored a change in the protein coded by a gene. Pág 181

Kreitman's evidence by itself fits with all evolutionary change being by **drift** (there is evidence for selective changes in the Adh gene, but it comes from other research). Wyckoff et al.'s evidence challenges, and possibly refutes, random **drift** as the explanation of evolution in the protamine genes of humans and other apes. Pág 182

If leptin simply evolved by random **drift** in all mammals, then leptin would probably have the same function in humans and mice. Pág 183

A further test between **drift** and selection can be devised using the ratio of nonsynonymous to synonymous evolution. The trick is to compare the ratio within one species and between two related species. Pág 184

In summary, if the dN/dS ratio is similar for polymorphisms within a species and evolutionary change between species, that suggests random **drift**. If the ratio differs within and between species, that suggests natural selection. Pág 184

These sites have probably evolved by random **drift**. But at other sites, the amino acid has changed between related fruitfly species. It looks like selection has acted at those sites. Pág 185

More interestingly, the fraction of sites at which the dN/dS ratio is elevated between species can be used to estimate the fraction of evolutionary substitutions that have been driven by selection, as opposed to **drift**. In this way, Smith & Eyre-Walker (2002) estimated that 45% of non-synonymous substitutions between one pair of fruitfly species (*Drosophila simulans* and *D. yakuba*) were fixed by positive selection. Pág 185

They also show how genomic data may be used to estimate the relative importance of selection and **drift** in molecular evolution. In the future, the sequences of chimp and human genomes will become available. Pág 185

The six codons are synonymous, and we expect them to evolve by random **drift**. Notice two features of the figure: one is that the codon frequencies are unequal within a species. Pág 187

In low use genes, changes are disadvantageous and the codon frequencies evolve by **drift** to be more equal. The difference between high use and low use genes in Table 7.7 is difficult to explain by mutation pressure. Pág 188

Natural selection is a negative force, preventing certain changes. Evolutionary changes, when they do occur, are probably by neutral **drift**. Pág 189

Such evolutionary changes as do take place among synonymous codons are probably mainly driven by **drift**, but selection is acting to prevent some changes. Pág 189

The amino acid changes in the protamine and lysozyme genes have probably been driven by selection rather than **drift**. Pág 189

Secondly, the examples show that neutralism is not the whole story of molecular evolution. Random **drift** probably explains the majority of molecular evolution as provided we count “non-informational” changes. Pág 189

Whole-genome analyses are being used to estimate the exact relative importance of selection and **drift** in amino acid substitutions. Pág 189

It makes sense that selection as well as **drift** should matter in molecular evolution. The molecules in living bodies are well adapted, and natural selection must work at least occasionally to keep those adaptations up to date. Pág 189

In 1968, Kimura proposed the neutral theory of molecular evolution. His original argument was mainly based, in theory, on genetic loads and, in fact, on amino acid evolution. Neither his particular claim that most molecular evolution proceeds by the random **drift** of neutral mutations nor his argument using genetic loads, nor his evidence for proteins, has survived in its original form. Pág 190

Kimura's neutral theory has developed into the nearly neutral theory. The nearly neutral theory shares with its predecessor the claim that most molecular evolution is by random **drift** but the **drift** of nearly neutral ($4N_e \mu \ll 1$ or $N_s \ll 1$) rather than exactly neutral ($s = 0$) mutations. Pág 190

If we use the nearly neutral rather than the original, purely neutral theory, and confine it to substitutions in noncoding DNA and synonymous substitutions in coding DNA, then many (perhaps most) biologists accept a neutralist interpretation of molecular evolution. Most evolution at the DNA level is by random **drift**. Pág 190

We do not know the relative importance of **drift** and selection in driving amino acid change. Indeed, for most of the past 35 years we have lacked a decisive method to find out the relative importance of **drift** and selection. Molecular evolution is now entering the genomics era. Pág 190

Genomic data hold out the promise both of revealing the localities within the DNA where natural selection acts, and also of estimating the fractions of evolutionary substitutions that have been driven by natural selection and by random **drift**. Pág 190

Gillespie (2001) questions whether population size affects the rate of evolution, because the effect via hitch-hiking (Chapter 8) is the opposite of the effect on **drift** at one site. Pág 192

A second factor that can cause linkage disequilibrium is random **drift**. Random processes have the interesting property of being able to cause persistent, not just transitory, linkage disequilibrium. Pág 205

When fitness peaks correspond to optimal adaptations, the question is relevant to the evolution of adaptation; but when they do not, the question still has a technical interest in population genetics. Wright suggested that random **drift** could play a creative role. Pág 217

Drift will tend to make the population gene frequencies “explore” around their present position. The population could, by **drift**, move from a local peak to explore the valleys of the fitness surface. Pág 217

The population could, by **drift**, move from a local peak to explore the valleys of the fitness surface. Once it had explored to the foot of another hill, natural selection could start it climbing uphill on the other side. If this process of **drift** and selection were repeated over and over again with different valleys and hills on the adaptive topography, a population would be more likely to reach the global peak than if it was under the exclusive control of the locally maximizing process of natural selection. Pág 217

Wright's full shifting balance theory includes more than just selection and **drift** within a local population. He also suggested that populations would be subdivided into many small local populations, and **drift** and selection would go on in each. Pág 217

Everything is included: multiple loci, fitness interactions, selection within and between populations, **drift**, and migration. (The theory of adaptive peaks is also relevant to speciation: Section 14.4.4, p. 394.) Pág 217

How can one morph evolve into another? On the shifting balance view, a morph can originate by **drift** within a local population, and then spread if it is advantageous. Pág 218

Can genetic **drift** drive populations across real adaptive valleys? Genetic **drift** is powerful when it is not opposed by selection: that is, when **drift** is between different neutral forms. Pág 218

However, in Wright's theory, **drift** has to work in opposition to selection. This is a much more difficult process, and critics doubt whether it occurs. The selective disadvantages in the valleys between different morphs of *Heliconius*, for example, correspond to 50% fitness reductions. Random **drift** could not establish forms that have such large disadvantages. Pág 218

In the extreme case, when there are an infinity of dimensions, it is certain that natural selection will be able to hill climb all the way to the global peak without any need for **drift**. Pág 218

It refutes Wright's theoretical claim that natural selection will get stuck at local peaks, but leaves open the empirical question of how important selection and **drift** have been in exploring the fitness surfaces of nature. Pág 218

Fisher maintained that natural populations are generally too large for **drift** to be important, that epistatic fitness interactions do not interfere with the operation of selection, that adaptations evolve by selection within a population, and that adaptive evolution can proceed smoothly up to the highest fitness peak. Pág 218-219

Wright thought that populations are small, **drift** and epistatic fitnesses are important, and that adaptive evolution is liable to become stuck at a local optimum. Pág 219

For evolution as a whole, this is a sensible idea. In Chapter 7, for instance, we saw that many evolutionary changes in molecules may take place by random **drift**. Pág 259

The molecular sequences among which **drift** takes place are not different adaptations. They are different variants of one adaptation, and natural selection does not explain why one organism has one sequence variant, and another organism has another. We need **drift** as well as selection in a full theory of evolution. Pág 259

Wright did not invoke macromutations. He argued that adaptive evolution was facilitated by random **drift** in small, subdivided populations. As we saw, Fisher doubted whether real adaptive surfaces have multiple peaks and judged Wright's shifting balance process unnecessary. Pag 268

As we saw, selection itself (when considered in a fully multidimensional context), or neutral **drift**, may lead the population away from local peaks; but it also may not. Some natural populations now may be imperfectly adapted because the accidents of history pointed their ancestors in what would later become the wrong direction (Figure 10.11). pag 281

Others think that the main forms may be historic accidents and the fine details due to random **drift**. Not surprisingly, the evolutionary biologists who study adaptation tend to be among the former and those who criticize it among the latter. Pág 286

Chapters 5–9 looked at the factors that control variation within a population: variation may be maintained by natural selection, or a balance of selection and mutation, or a balance of **drift** and mutation. Pag 359

What is the cause of this chromosomal evolution? The answer is uncertain, but it is thought to be random **drift**. Pag 361

But if it **drifts** up to a locally high frequency, as may easily happen in a local, small, and perhaps inbreeding, mouse population, natural selection will favor it. Pag 261

The variation is more likely to be explained by **drift**, with different individual chromosomal fusions **drifting** up in frequency in different localities. Natural selection may also be at work, depending on the frequency of the chromosomes. But whatever the cause of the pattern in Plate 8, it is a further example of geographic variation. Pág 361

Geographic variation is probably rarely caused only by **drift** or only by selection. Also, more than one selective factor is likely to operate. Pag 361

In the case of the mouse chromosomes, natural selection probably interacts with **drift**, depending on the chromosomes' frequency. Pág 361

But other kinds of natural selection can act, such as meiotic drive (Section 11.2.1, p. 294) and a full account of mouse chromosomal evolution is complex (Nachman & Searle 1995). Moreover, very thorough research is needed to test between selection and **drift**. Pág 361

Wright (1978) considered it to be the best example of how **drift** causes differences between local populations (the first stage in Wright's shifting balance theory of evolution see Section 8.13, p. 216). Pág 362

A small study, over 1 or 2 years, might have supported Wright's interpretation but Schemske and Bierzychudek counted more than 710,000 seeds from more than 42,000 flowers over an 11-year period and they have effectively refuted **drift** as the explanation of variation in this particular species. Pág 362

Hard work is needed to measure the contributions of **drift** and selection in particular species. But in general, patterns of geographic variation can be explained by some mix of selection, as seems to explain body size variation in sparrows, and of **drift**, as seems to explain chromosomal variation in house mice. Pág 362

Or they may result from genetic **drift**. When biologists see a stepped cline, they are interested to know whether it corresponds with an ecotone or has some other explanation. Pág 363

The same can be said about the chromosomal forms of mice, if they are indeed caused by genetic **drift** pag 364

It might form a complicated gradient related to the rainfall or another factor. Different characters form different spatial patterns, related to different adaptive factors or random **drift**. Pág 376

When two geographically separate populations are evolving independently, different genes will be fixed in each, whether by **drift** or adaptation to different environments. The theory of allopatric speciation suggests that two such populations will also, at least sometimes, evolve some degree of reproductive isolation in consequence. Pág 384

Two other results of the experiments are worth noticing. One is that they suggest, though they do not prove, that speciation normally requires natural selection; genetic **drift** alone is not enough. Look at the controls in Dodd's results, for instance (Figure 14.2). pag 386

These populations would have evolved apart by **drift**, but not by selection. Reproductive isolation only evolved between lines kept on different foods, and selection would have been acting differently between them. Templeton (1996), however, has argued that this experimental design is inappropriate for testing the influence of **drift** in speciation. Pág 386

Natural selection and random **drift** are the two main forces of evolution. Natural selection almost always acts to drive species toward a peak on an adaptive landscape pag 394

Random **drift** is only a powerful force when the alternative genotypes are selectively neutral. For **drift** to drive a population across a valley, it has to work contrary to selection, and that is unlikely. Therefore, if speciation requires valley crossing, speciation is a difficult evolutionary process and will not normally happen; it will require some special conditions. Pag 394

Speciation requires the normal action of selection and **drift** to be suspended. The inspiration of these ideas is that speciation is a difficult process, because of the need for valley crossing. This is one view of speciation. Pág 395

In the Dobzhansky–Muller view, speciation happens as an almost automatic consequence of ordinary selection and **drift** within a population, as each population evolves in its own environmental condition pag 395

Associated with this was a second claim, that speciating populations tend to be small and that genetic drift is particularly important in speciation. Pag 417

The second claim, that speciation is often powered by genetic drift now has few supporters. It is the least important of the five claims listed above, and may not have been strongly believed in even during the period from the 1930s to the 1950s. pág 418

The experimental evidence and theory of speciation suggest the genetic drift is not all that important in speciation. Speciation is probably more often a by-product of normal adaptive divergence between populations. Pág 418

Each change requires a gene (or set of genes) to arise by mutation and then to be substituted, either by drift if the change is neutral or by selection; both these processes are improbable. It is much more likely that the same character would have been continuously passed on, in much the same form, from ancestor to descendant by simple inheritance. Pág 445

The small populations in the different refuges would have evolved genetic differences, either by selection or drift. The populations in Spain, Italy, and the Balkans diverged. Then when the ice cap retreated north, all three populations expanded north too. This has had two detectable consequences. Pág 499

A second factor influencing geographic distributions is plate tectonics (informally known as continental drift). The continents have moved over the surface of the globe through geological time. Pág 505

Let us look at one of the main modern research programs that studies the relation between biogeography and plate tectonics. It is called vicariance biogeography. The drifting apart of tectonic plates is the sort of event that could cause speciation (Section 14.2, p. 382). Pág 505

Then, likely in the late Paleocene, the two halves of the American continent drifted apart. At pag 512

It refers to changes in gene frequencies within populations, under the influence of natural selection and random drift. Macroevolution refers to the topics we are looking at in Part 5 of the book. Pág 550

A duplication or deletion will initially be rare in the population; it may arise as a unique mutation. Its frequency may then increase by natural selection or random drift. Pag 559

A gene loss originates as a deletion mutation, which may then spread by drift or selection. Many of the deletions in intracellular bacteria could have spread by drift. Pag 562

Population genetics identifies two main mechanisms of evolution, natural selection and random drift, though drift is arguably unimportant in morphological evolution (Section 7.3, p. 165). Pag 594

Strictly speaking, this does not confirm that the fossil changes were driven by selection and (perhaps) drift. Pág 595

MACROEVOLUÇÃO

The great (or at any rate, one of the great) events in evolutionary biology as I have been writing the third edition is the way genetics is becoming a **macro evolution** ary, as well as microevolutionary, subject. Prefacio xxiii

Historically, there has been a good working distinction between evolutionary research on short and long timescales a between micro- and **macroevolutionary** research. . Prefacio xxiii

I see the distinction between micro- and **macroevolutionary** research as breaking down, in perhaps three ways. The first is through the use of molecular phylogenetics . Prefacio xxiii

The other two ways in which molecular genetics is being used in **macroevolutionary** research are more recent. I have added chapters on evolutionary genomics (Chapter 19) and “evo-devo” (Chapter 20) . Prefacio xxiii

The introduction of new techniques into the study of **macroevolution** creates an excitement of its own. It has also resulted in a number of controversies, where the two methods (molecular genetic and paleontological) seem to point to conflicting conclusions. We shall look at several of those controversies, including the nature of the Cambrian explosion and the significance of the Cretaceous–Tertiary mass extinction. Prefacio xxiii

Part 5 is about **macroevolution**. **Macroevolutionary** changes are large: the kinds of events that can be studied in the fossil record, such as the origin of new organs, or body plans, or of new higher taxa (that is, taxa above the species level) pág 521

The conventional dividing line between macro- and microevolution is at speciation, so that events below that level are microevolution and those above it are **macroevolution**. Pág 521

As said in the Preface to this book, the distinction between micro- and **macroevolution** has traditionally been not only between the timescales of the events but also between the methods used. Pág 521

has been studied with fossil evidence, comparative morphology, and phylogenetic inference. However, modern biology has seen a breaking down of the methodological distinction as genetic techniques are being used to study large-scale, **macroevolutionary** questions. Pág 521

However, modern biology has seen a breaking down of the methodological distinction as genetic techniques are being used to study large-scale, **macroevolutionary** questions. Pag 521

The history of life will lead us into an abstract question: is **macroevolution** really microevolution extrapolated over a long timescale or does **macroevolution** take place by different, though not incompatible, mechanisms from microevolution? This general question will recur at several points in the chapters of Part 5. Chapters 19 and 20 are about two emerging subdisciplines of evolutionary biology: evolutionary genomics and “evo-devo. Pág 521

These historic events are all examples of evolution on the large scale, or **macroevolution**. The chapter ends with a conceptual section on the possible relations between micro- and **macroevolution**, using the historic case studies as examples. Pág 523

The distinction between microevolution and **macroevolution** is the distinction between evolution on the small scale and evolution on the large scale. Microevolution refers to the topics we looked at in Part 2 of this book. Pag 550

Macroevolution refers to the topics we are looking at in Part 5 of the book. It refers to the origin of higher taxa, such as the evolution of mammal-like reptiles into mammals, fish into tetrapods, and green algae into vascular plants. It also refers to long-term evolutionary trends, which we look at in Chapters 21 and 22, and to diversification, extinction, and replacements of higher taxa, which we look at in Chapter 23. pág 550

Microevolution and **macroevolution** can be thought of as vague terms, like “small” and “large,” and as the ends of a continuum from evolution on the smallest scale to the largest scale. However, some biologists have argued that micro- and **macroevolution** proceed by distinct processes. Pág 550-551

We can ask, for any **macroevolutionary** phenomenon, whether it can be explained by microevolutionary processes that persist for a long time. That is, we can ask whether **macroevolution** is due to “extrapolated” microevolution. Pág 551

Some might question whether the past 4 million years of human evolution really amount to a **macroevolutionary** event. The origin of mammals, however, is unambiguously an example of **macroevolution**. Pág 551

The origin of mammals, however, is unambiguously an example of **macroevolution**. Pag 551

A similar conclusion could be drawn about the origin of humans, and of terrestrial plants and vertebrates. In these example, **macroevolution** proceeds by the same process a natural selection and adaptive improvement a as has been observed within species and at speciation; but the process is operating over a much longer period. Pág 551

Then the **macroevolutionary** event would not be extrapolatable from the normal processes of microevolution. No evidence exists for the process of Figure 18.14b, and it is unlikely in theory (Section 10.5.1, p. 266). Pag 551

The two views in Figure 18.14 are only two of the possible relations between microevolution and **macroevolution**. **Macroevolution** might also be unextrapolatable from microevolution, not because their driving processes differ, but because the species that evolve into higher taxa are a non-random subset in some way. Pág 551

If Kemp, Jablonski, and Bottjer, are right, **macroevolution** is not simply extrapolated microevolution. At any one time, natural selection will be favoring a variety of adaptations in different lineages a tropical adaptations in tropical species, polar adaptations in polar species. Pág 552

The theory of **macroevolution** in Figure 18.14b is controversial. If correct, it would challenge some deep tenets of neo-Darwinism. But the general idea that **macroevolution** is not simply predictable from microevolution need not be controversial pág 552

Kemp, Jablonski, and Bottjer’s arguments are orthodox enough. In the other chapters of Part 5 we shall look at several **macroevolutionary** phenomena, and reflect on their conceptual relation with microevolution. In some cases, **macroevolution** will likely be extrapolatable from microevolution; in other cases **macroevolution** will likely not be extrapolatable from microevolution. In this chapter, we have seen that the origin of higher taxa can at least be mainly understood as the evolution of adaptation by natural selection over the long term. Pág 552

Evolutionary genomics and evo-devo are two ways in which genetics is now being used to answer **macroevolutionary** questions. Pág 587

The advance of these two subjects should give us some insights into the grandest questions of **macroevolution**. Pág 587

Escalation is a widely influential idea about **macroevolution**. It features again in the next section of this chapter. It also underlies many hypotheses about the Cambrian explosion (Section 18.4, p. 535). Pág 636

We shall look at Van Valen's (1973) work. Van Valen inferred, from the shape of taxonomic survivorship curves, that **macroevolution** is shaped not only by coevolution, but by a particular mode of coevolution, called the "Red Queen" mode. The kind of escalatory coevolution we looked at in the previous section is (or can be) an example of Red Queen coevolution. But before we come to the coevolutionary interpretation, we must first look at the evidence from taxonomic survivorship curves. Pág 637

Coevolution is one of several general processes that can account for evolution on a large scale a that is, **macroevolution** a as well as on a small scale. No one doubts its importance in microevolution, for instance in the evolution of mutualists or of parasites and their hosts. Pág 640

The contribution of coevolution to **macroevolution** is more controversial. Coevolution is not the only **macroevolutionary** force. Many **macroevolutionary** events are likely caused by changes in the physical environment a climatic change, or tectonic change, or asteroid impacts such as we look at in Chapter 23. pág 640

Evolutionary biologists are interested in the relative contribution of physical and biological factors, and their interaction, in driving **macroevolution**. Pág 640

The question in its general form is too difficult for us to answer yet, but it puts under a spotlight many of the ideas that we need to examine to understand **macroevolution**. Pág 640

When Alvarez's explanation for the Cretaceous– Tertiary mass extinction became widely accepted in the early and mid-1980s, some paleobiologists suggested that there are two **macroevolutionary** regimes. Pág 656

The generally good fit to the Poisson distribution supports the view that variations in extinction rate are mainly random, and that the history of life does not have two distinct **macroevolutionary** regimes pag 656

Species selection is another example of a reason why **macroevolution** cannot simply be extrapolated from microevolution (Section 18.8, p. 550). Pág 666

A similar conclusion can be drawn from the argument about niches. Again, **macroevolution** cannot simply be predicted from microevolution. A microevolutionary study would reveal how natural selection was favoring various characters in the stickleback populations, according to the aquatic environments they were occupying. The key to **macroevolution** is the persistency of the niches over time, and that is irrelevant to the short-term process of natural selection and to investigations of it. (Natural selection does not favor one adaptation over another because it allows the organisms to occupy a longer lasting niche.) Thus pág 666

Thus, there could be distinct “macroevolutionary regimes” during, and between, mass extinctions. In this set of ideas, mass extinctions are the key to understanding much of evolutionary history. Pág 676

RESTRICÃO

The fact that the relation between amino acid and codon can be changed in this way shows that the same genetic code has not been forced on all species by some unalterable chemical **constraint**. Pág 57

Pseudogenes, once formed, are probably under little or no **constraint** and mutations will accumulate by neutral drift at the rate at which they arise. They will show pure neutral evolution in the “pan-neutral” (see Figure 7.1) pág 176

The inference assumes: (i) that the mutation rate in pseudogenes is representative of the genome as a whole; and (ii) all mutations in pseudogenes are neutral (that is, no selective **constraints** exist on them at all). The second assumption may not be valid (see Section 7.8.5 on codon bias). Pág 177

The neutral explanation for the relation between evolutionary rate and functional **constraint** is as follows. In the active site of an enzyme, an amino acid change will probably change the enzyme’s activity. Pág 177-178

What is the explanation for codon biases? Two hypotheses have been suggested: selective **constraint** or mutation pressure pag 187

At least in unicellular organisms, codon biases are thought to be caused more by selective **constraints** than mutation pressure. Evolution in synonymous sites still fits the neutral theory pag 187-189

Natural selection is a negative force, preventing certain changes. Evolutionary changes, when they do occur, are probably by neutral drift. However, the evidence for selective **constraints** means that evolution at synonymous sites is probably not “pan-neutral.” Not all synonymous mutations are neutral. Pag 189

As Maynard Smith (1978) remarked, “if there were no **constraints** on what is possible, the best phenotype would live for ever, would be impregnable to predators, would lay eggs at an infinite rate, and so on.” What are the **constraints** that prevent this kind of perfection from evolving? Pag 272

Genetic **constraints** may cause imperfect adaptation pág 274

This is an example of a genetic **constraint**. It arises because the heterozygotes cannot, under Mendelian inheritance, produce purely heterozygous offspring: they cannot “breed true.” Pag 274

The importance of heterozygous advantage is controversial, but there are undoubted examples such as sickle cell hemoglobin, which is indeed a practical manifestation of imperfect adaptation due to genetic **constraint** pag 274

Developmental **constraints** may cause adaptive imperfection pág 275

A nine-penned discussion (Maynard Smith et al. 1985) of developmental **constraints**

gave the following definition: “a developmental **constraint** is a bias on the production of variant phenotypes or a limitation on phenotypic variability caused by the structure, character, composition, or dynamics of the developmental system.” Pág 275

Developmental **constraints** can arise for a number of reasons. Pleiotropy is an example. A gene may influence the phenotype of more than one part of the body pag 275

The growth of legs probably takes place through a growth mechanism controlling both legs. This mechanism does not have to be inevitable for a **constraint** to exist pag 275

A developmental **constraint** exists whenever there is a tendency for mutants (in this example) to affect both legs, and the tendency is due to the action of some developmental mechanism. Pág 275

Genes influence developmental processes, and a change in development will often change more than one part of the phenotype. Much the same reasoning lies behind a second sort of developmental **constraint**. Pág 276

How can we test between selection and **constraint**? Maynard Smith and his eight coauthors listed four general possibilities: adaptive prediction, direct measures of selection, heritability of characters, and cross-species evidence. Pag 279

If a theory of shell adaptation predicted accurately and successfully the relation between shell form and environment a which forms should be present, and which absent, in various conditions a then, in the absence of an equally exact embryological theory, that would count in favor of adaptation and against developmental **constraint**. Conversely, a successful, exact embryological theory would be preferred to an empty adaptive theory. Pág 279

Thirdly, we can measure the character’s heritability. If a **constraint** is preventing mutation in a character, it should not be genetically variable. Pag 279

Genetic variability can be measured, and the **constraint** hypothesis will be refuted for any character that shows significant heritability. As it happens, this kind of evidence suggests that the gaps in the shell morphospace are not caused by developmental **constraint**. Pág 279

Finally, cross-species evidence may be useful. It has particularly been used for pleiotropic developmental **constraints**. When more than one character is measured, and the values for the two characters in different organisms are plotted against each other, a relation is nearly always found. Pág 279

The observed distribution of points might, once again, be due either to adaptation or to **constraint**. Pág 279

Huxley was an influential early student of allometry, and he liked to explain allometric relations by the hypothesis of **constraint**: “whenever we find [allometric relationships], we are justified in concluding that the relative size of the horn, mandible, or other organ is automatically determined as a secondary result of a single common growth-mechanism, and therefore is not of adaptive significance. This provides us with a large new list of non-adaptive specific and generic characters” (Huxley 1932). Pag 279-280

Some kinds of evidence are more persuasive than others. Allometric relations, in particular, are not strong evidence of developmental **constraint** pag 280

The attempts so far, as in the example of allometry, have not been finally convincing. In particular cases, we can test between the alternatives of selection and **constraint**. Pág 281

For particular characters, adaptation and **constraint** can be alternative explanations. Likewise, differences in the form of a character between species may be due to adaptation to different conditions or to **constraint**. Pág 287

Forms that are not found in nature may be absent because they are selected against or because a **constraint** renders them impossible. Pág 287

Adaptation and **constraint** can be tested between by several methods: by the use of predictions from a hypothesis of adaptation or **constraint**, by direct measures of selection, by seeing whether the character is variable and whether the variation is heritable and can be altered by artificial selection, and by examining comparative trends. Pág 288-289

Byers (1997) is an example discussing the social behavior of the American pronghorn and Macgregor (1991) reviews the remarkable genetic **constraint** in the crested newt and refers to earlier work. Pág 290

On developmental **constraint**, Maynard Smith et al. (1985) and Gould (2002b) are major reviews. McKenzie & Batterham (1994) and McKenzie (1996) discuss the insecticide resistance example (see also the further reading in Chapter 5, p. 135). Pág 290

Chapter 20 looks at evolutionary development, which probably provides the concepts for future studies of developmental **constraint**. Galis et al. (2001) discuss the special case of **constraints** on digit numbers. Pág 290

Biologists do not understand why sexual, as opposed to asexual, reproduction exists and we look at four hypotheses a genetic **constraint**, group selection, deleterious mutation, and parasite–host coevolution. Pág 313

On butterfly spots, see also the general review by McMillan et al. (2002) and the particular contributions of Beldade et al. (2002a, 2002b), the second paper particularly connects with another classic theme, that of developmental **constraints** on evolution a discussed in this text in Chapter 10. pág 589

Between speciation events, species may have a low rate of evolutionary change a a condition Eldredge and Gould called stasis. In theory, the absence of evolutionary change in a species can be explained by stabilizing selection (Section 4.4, p. 76) or **constraint** (Section 10.7, p. 272). **Constraint** means that the species does not change because it lacks genetic variation, or lacks expressed genetic variation. Pág 600

One version of punctuated equilibrium suggests that canalization creates a developmental **constraint**. Evolution is only possible in revolutionary circumstances, such as in a stressed subpopulation at the edge of a species' main range. Pág 600

EFEITO FUNDADOR

A particular example of the influence of random sampling is given by what is called the **founder effect**. The **founder effect** was defined by Mayr (1963) as: the establishment of a new population by

a few original founders (in an extreme case, by a single fertilized female) which carry only a small fraction of the total genetic variation of the parental population. pág 140

We can divide the definition into two parts. The first part is the establishment of a new population by a small number of founders; we can call that a “founder event.” The second part is that the founders have a limited sample of genetic variation. The full **founder effect** requires not only a founder event, but also that the founders are genetically unrepresentative of the original population. pág140

An analogous calculation could be done for a population with three alleles, in which we asked the chance that one of the three would be lost by the **founder effect**. The resulting population would not then be monomorphic, but would have two instead of three alleles. pág141

Founder effect the loss of genetic variation when a new colony is formed by a very small number of individuals from a larger population. pág684

STEANERS

Seleção

Natural **selection** is the correlation of traits with reproductive success; the response to **selection** is the change in the genetic composition of the population caused by variation in reproductive success. Natural **selection** thus works on heritable variation to produce adaptive change. It is described in Chapters 2 and 4 (pp. 27-53, 70-98).

This kind of evolution is called neutral because the variation is neutral with respect to **selection**; no variant has any systematic advantage over any other. It is also called genetic drift to communicate the lack of direction of neutral genes drifting through the population over many generations.

Other biologists emphasize explanations couched in evolutionary terms; they study the impact of **selection**, drift, and history and ask different questions and investigate different kinds of causes in search of answers.

Whereas in proximate analysis the causes can be described as chemical and physical processes, in evolutionary analysis one describes the causes as how natural **selection**, chance events, and descent from shared ancestors shaped the outcome.

A biologist should be able to see the world both ways from the bottom up, from molecules to species, and from the top down, from **selection** and history to molecules.

Selection was strong on the traits directly involved with reproduction: age and size at maturity and size and number of offspring.

The first two examples—sexual cannibalism in spiders and rapid evolution in guppies—illustrate the power of natural **selection**. The second two examples—the puzzle of pemastomid relationships and irreversibility in the evolution of salamanders—illustrate the importance of history. Natural **selection** and history are the two great themes of evolution that combine to explain the evolution of biological patterns. Every organism is a mosaic, some of whose parts reflect the role of recent **selection**, others of which recall its phylogenetic history. One of our goals is to understand the roles of **selection** and history in determining any biological process that interests us.

In that journal, in 1838, he first described natural **selection**. He soon saw that it could explain the origin of adaptations, and when he combined it with geographic separation he could explain the origin of species.

In a malaria-induced period of bed rest, Wallace had also had the idea of natural **selection**.

The response to **selection** is efficient because each step leads to a molecule that is better than the previous one. Because the improvements are inherited, they accumulate (Maynard Smith 1998).

Remember this example if you encounter the false argument that natural **selection** cannot make precise, complicated organs like the vertebrate eye because it starts with random variation. Natural **selection** can rapidly convert initially random variation into highly adapted states. They only appear to be improbable because we have not watched the process at work. The efficiency of natural **selection** makes even extremely precise and complicated structures probable given enough time.

Between 1918 and 1932 Fisher, Haldane, and Wright showed that Mendelian genetics is consistent with natural **selection**. Only then, more than 60 years after the publication of *The Origin of Species*, was the genetic objection to natural **selection** finally removed. We do not understand the origin of life nearly as well as we understand speciation, or **selection**, or many other aspects of evolution. But our failure is not one of principle or logic; it is a failure of imagination and technique.

This claim is often encountered not only among Creationists but also among people, some of them scientists, who have not understood the extraordinary power of natural **selection** to rapidly create complex order out of chaotic variation. Natural **selection** is in fact the only natural process known that can create and maintain order against the tendency of all physico-chemical systems .

The power of natural **selection** efficiently to create structures that at first glance seem highly improbable is discussed in more detail in Chapter 2 (p. 32).

The history and diversity of life, the power of natural **selection** to shape precise adaptations, and the implications of our evolved condition are absolutely astonishing.

Microevolution operates within populations. It includes adaptive evolution, which consists of natural **selection** and the genetic response to it, and neutral evolution, which consists of the random drift of traits and genes that have no effect on reproductive success. It also includes the short-term effects within populations of ancient developmental programs.

Chapter 2 describes adaptive evolution: how natural **selection** works, what forms it takes, and how strong it is in nature. Chapter 3 discusses neutral evolution: how genetic drift comes about, why it is significant for molecular evolution, and how analogous processes generate patterns in biodiversity and history. Chapters 4 and 5 discuss how genetic variation responds to **selection** and how it originates and is maintained in populations.

Thus the central ideas of microevolution are **selection**, drift, genetics, and development. Each of those big ideas has many parts; much of the action in microevolution takes place at their intersection.

This chapter discusses adaptive evolution, introduced in Chapter 1, in greater detail. Adaptive evolution is driven by natural **selection**, and natural **selection** is one consequence of variation in lifetime reproductive success (Variation in reproductive success is also one cause of neutral evolution, take up in Chapter 3, p. 54.)

Variation in lifetime reproductive success arises among material organisms. The response to **selection**, however, is recorded not in the organisms, all of which eventually die, but in the genes transmitted to the next generation—the genes that were in the organisms that had reproductive success.

That is why we distinguish clearly between organisms in the definition of natural **selection** and genes in the definition of the response to **selection**. Natural **selection** occurs in material organisms; the response to **selection** is recorded in information stored in the genes. Both are necessary for adaptive evolution to occur.

Natural **selection** causes adaptive evolution in traits and genes; neutral evolution causes non-adaptive change in traits and genes; and two conditions are necessary for both adaptive and neutral evolution to occur. These two conditions are:

Only if at least some of the variation in the trait is heritable will the genes that are responsible for the trait change in frequency and record the action of **selection** or drift.

When that correlation is positive or negative, natural **selection** is operating on the trait, and evolutionary change will move the trait from generation to generation in the direction of increasing adaptation. When the correlation is zero, natural **selection** disappears, and then the things that are inherited and that vary, whether genes or traits, fluctuate randomly in the population

Such large individual variation in reproductive success translates into strong **selection** on any traits correlated with it.

Given such heritable variation **selection** could elicit a rapid response.

That the potential for a response to **selection** is thus the rule, not the exception, is an important point based on decades of work by many biologists. Dobzhansky, for insects, Mayr, for birds, Stebbins, for flowering plants, and Lewontin and Ayala, for gene products detectable by electrophoresis, along with many others, have shown that a great deal of genetic variation is present in natural populations for many types of trait and organism

The action of **selection** is located in reproductive success and in the many ways that variation in genes and traits connects to reproductive success, creating the key correlation at the heart of **selection**.

The subtlety and power of natural **selection** are hidden in its ordinary causes and revealed in its extraordinary consequences.

Because natural **selection** is the correlation of a trait with reproductive success, survival is only important if it contributes to reproductive success.

That is why male red-backed spiders commit suicide during copulation, that is why senescence evolves, that is why **selection** for mating success (sexual **selection**) can reduce survival, and that is why worker bees will commit suicide to defend their nest. Survival is only a means to achieve reproductive success.

Selection creates order out of disorder. Under strong **selection** populations rapidly produce combinations of genes that are at first glance extremely unlikely. We demonstrate this with two examples. The first, an analogy using the letters of the alphabet, exaggerates the power of **selection** because it describes a process that aims to produce a very specific, concrete goal. This is not how natural **selection** works, but the example makes an important principle clear. We use the first example to prepare the more realistic, and more complicated, second example.

However, natural **selection** causes successful gene combinations to increase in frequency, and accurate replication preserves those increases—it remembers what worked before. In this artificial example let us suppose that strong **selection** retains the correct letter whenever it occurs.

This example is somewhat misleading because natural **selection** does not aim at any particular final state. It doesn't aim at anything. It just produces something that works better from among the variants currently available.

Natural **selection** has great power to shape precise adaptations.

When a trait has evolved to a state of adaptation, the version found in nature has greater reproductive success than the alternatives against which **selection** has tested it. This observation suggests a way of testing for adaptation. To see whether a trait is adapted, we can manipulate it and note the consequences. If it is adapted, the manipulated forms should have lower reproductive success than the natural state. Such a test would be most risky for the **selection** hypothesis if the manipulated trait were directly connected to reproductive success, for then **selection** should certainly have brought it into an adapted state. That is the case for clutch size in birds, a classic life-history trait discussed in greater detail in Chapter 10 (p. 214).

Because strong **selection**, transposition, and integration of resistance genes into the main chromosome of *S. aureus*, some strains have become resistant to many antibiotics, including erythromycin, fusidic acid, tetracycline, minocycline, streptomycin, spectinomycin, and sulfonamides, and even to disinfectants and heavy metals, such as cadmium and mercury.

Strong **selection** applied by antibiotics to large populations with short generation times produces rapid evolution. Since the invention of antibiotics, about 5 million tons of these drugs have been used in humans and domestic animals, exerting massive **selection** on the world's bacteria.

Endler (1986) discusses methods of detecting natural **selection**. In at least 99 species of animals and at least 42 species of plants, adaptive evolution has been demonstrated in morphological, physiological, or biochemical traits.

However, few of those studies measured lifetime reproductive success, few dealt with more than one or two traits, and in most one could not pinpoint the mechanism of **selection**.

Darwin and the early population geneticists thought that **selection** was weak and that evolution was slow and gradual. This view lasted into the 1970s, when studies began to accumulate demonstrating strong **selection** and rapid evolution. Endler's (1986) summary of studies of **selection** in natural populations made clear that **selection** was quite strong on some species, traits, and genes and weak or absent on others.

From studies on 57 species, Endler calculated 592 estimates of the strength of **selection**: 180 of them were significantly greater than zero, and many were impressively large. Because the strength of selection varies from strong to zero, we cannot assume it a priori: if we need to know it, we have to measure it. Endler's survey may have been biased towards strong **selection**, as he acknowledged, for such results are more likely to be published, but that criticism does not affect the main conclusions: selection can be strong, and microevolution can be fast.

Microevolution can be very fast, much faster than one would infer from fossils, and it is fastest in large populations for traits with a great deal of genetic variability experiencing strong **selection**, as happens when predatory fish eat small guppies.

The type of **selection** experienced by a gene in a genome, or a trait in an organism, or an organism in a group, results from an interaction between the environment, the focal gene, trait or organism, and the other genes, traits, and organisms contributing to survival and reproduction. **Selection** thus has both external and internal causes. It always involves interactions between the thing selected and its environment

The external environment is not an absolute but a relative agent of **selection**, for even the selective impact of a physical factor like temperature can depend on such interactions—the impact of cold or heat on animals may depend on competition for places protected from extreme temperatures.

The chromosomal neighborhood is also an important part of the context of **selection** on genes. When a gene comes under **selection** and starts to change in frequency, it will cause changes in the frequencies of all genes close to it on the chromosome.

The action of indirect **selection** is described as a selective sweep, by analogy to a broom that sweeps up whatever it encounters, including much besides the object of attention. In asexual organisms, all genes are subject to selective sweeps caused by **selection** acting anywhere in the genome. In sexual organisms, genes usually only encounter selective sweeps caused by **selection** acting on genes that sit nearby on the same chromosome.

Organisms can sometimes choose the environmental context in which they will live and thus the kinds of **selection** pressures that they will encounter. For example, phoronids are marine worms that live in sand.

To generalize this example, we return to the definition of natural **selection**. The ability of any **selection** process to produce evolutionary change is determined by three things (see p. 2): the variation in the reproductive success of the units being selected, the strength of the correlation between the trait under **selection** and the variation in the reproductive success of the unit (individual or group), and the genetic variation of the trait among the units. When we compare **selection** operating on groups such as populations or species with **selection** operating on genes or the individuals that carry them, we notice striking differences, as follows.

Variation in reproductive success among individuals is often greater than variation in reproductive success among groups. The potential strength of individual **selection** is therefore normally much greater than the potential strength of group **selection**.

The potential response to individual **selection** is therefore normally much larger than the potential response to group **selection**.

Therefore the number of incidents of **selection** on individuals in a unit of time is very much larger than the number of incidents of **selection** on groups.

Natural **selection** operates whenever there is variation in reproductive success and the variation in reproductive success is correlated with heritable variation in the trait.

Because there is always some variation in reproductive success, some trait is usually correlated with the reproductive success, and many traits display heritable variation, natural **selection** is usually acting in all populations, including our own. Because natural **selection** acts on all variable traits that contribute to survival and reproduction, if such a trait is not in the state best for survival and reproduction, then something must be limiting its evolution.

When natural **selection** favors different things in different places, the movement of organisms between habitats transports genes that have been successful in one place to places where they may not be so successful.

Dominant alleles increase in frequency under **selection** more rapidly than do recessive alleles (Chapter 4, p. 78), and knowing that the gene is not on a sex chromosome simplifies the prediction of how its frequency will change under **selection** (see the Genetic appendix for details).

Note that **selection** in nature can be much stronger and evolution much more rapid than it appears to have been in the lactose example (see above), and **selection** on domesticated plants and animals has often yielded dramatic changes quite quickly, in just a few generations.

If there were no tradeoffs, then natural **selection** would drive all traits correlated with reproductive success to limits imposed by constraints.

Other important tradeoffs occur between the ability to eat one thing and the ability to eat many things, especially important in the ecology of plant-eating insects, and between mating success and survival, a key feature of the secondary sexual characteristics produced by sexual **selection** through mate choice

Natural **selection** can only select variants currently present in the population, variation that is often strongly constrained by history, development, physiology, physics, and chemistry.

Natural **selection** cannot anticipate future problems, nor can it redesign existing mechanisms and structures from the ground up. Evolution proceeds by tinkering with what is currently available, not by proactively designing ideal solutions, and the variation currently available is often limited by constraints.

Because mammalian sperm develop better at temperatures lower than those found in the body core, there was **selection**, during the evolutionary transition from cold- to warm-bloodedness, to move the testicles out of the high-temperature body core into the lower-temperature periphery and eventually into the scrotum.

Natural **selection** is not limited to organisms. When things vary, reproduce, have some form of inheritance, and some non-zero correlation between heritable variation and reproductive success, adaptive evolution occurs. Such things do not have to be organisms.

Much of the genome has been shaped not by adaptive evolution driven by **selection** but by neutral evolution driven by genetic drift. That is the topic of the next chapter.

In many species usage of synonymous codons is non-random, indicating **selection** favoring particular codons, possibly caused by differences in abundance of the corresponding transfer RNAs. Because the **selection** involved is believed to be very weak, the assumption of neutrality is approximately true.

Moreover, when a cost of resistance initially exists, natural **selection** tends to reduce the cost by favoring secondary mutations that remove the negative side effects, and the resistance mutation gradually becomes neutral, or nearly so (Anderson and Levin 1999).

Can neutral genetic variation be responsible for evolutionary change? Because neutral variation by definition does not lead to differences in fitness, natural **selection** will not favor one variant over another.

They affect both neutral genetic variations and genetic variation that is responding to **selection** adaptive genetic variation is not immune to random change.

Neutral alleles drift aimlessly unless they are located close to a gene undergoing **selection**, in which case they 'hitchhike' with the selected gene.

Genetic variation correlated with fitness is subject to change directed both by natural **selection** and by genetic drift. Which of the two forces determines the outcome depends on their relative strengths. Thus the two types of gene, neutral and selected, actually lie along a continuum. Change in neutral genes is dominated by drift but influenced by **selection**. Change in selected genes is dominated by **selection** but influenced by drift.

Change in neutral genes is dominated by drift but influenced by **selection**. Change in selected genes is dominated by **selection** but influenced by drift

The strength of **selection** on a trait decreases with the correlation of the trait with reproductive success and with the amount of variation in reproductive success, and genetic drift is stronger in small than in large populations.

In contrast, some non-synonymous substitutions, which change the coded amino acid, experience strong **selection**, while some are neutral. It is thus the rate of change of non-synonymous substitutions that varies greatly among proteins.

At the time, many evolutionary biologists could not accept the idea that evolutionary change could be a random process; they maintained that changes in allelic frequencies in populations are adaptive and largely determined by natural **selection**.

Despite recent progress, how much of the genetic variability measured by molecular methods is produced by random genetic drift and how much by adaptive evolution is still not clear. On the one hand, it is clear that the **selection** forces driving the evolution of DNA sequences that are not expressed and have no direct function must be weak. On the other hand, it also has become clear that several suspected neutral genes have been subjected to weak **selection**. The controversy over genetic drift versus natural **selection** in molecular evolution is further discussed in Chapter 5.

Chapters 1 and 2 discussed several examples of evolutionary change produced by natural **selection** acting on traits. Under natural **selection** trait values change from generation to generation when they are correlated with reproductive success, but only if the trait values are inherited. Thus when traits change as a result of **selection**, genes must also have changed. Knowing how genetic change occurs is essential for understanding and predicting an evolutionary process, for the direction and rate at which traits change under **selection** depends on the relation between genotype and phenotype and on the genetic composition of the population. This chapter discusses the genetic response to **selection**.

Instead it focuses on the variances of traits, estimates how much of the phenotypic variation is due to genetic differences between individuals, and uses that estimate to predict how fast a trait will change under **selection**.

The impact of **selection** on a population depends strongly on the genetic system of the organisms. The two key features of a genetic system are whether reproduction is sexual or asexual and whether the adult organisms are haploid or diploid (Figure 4.1).

We next describe these four genetic systems, then analyze the population genetics of a few cases to see how **selection** produces genetic change and what difference the genetic system makes.

Thus each of the four major systems has numerous and important representatives, and some organisms do not fit into this binary classification. In the next section we consider simple models of population genetic change under **selection**, in particular paying attention to the effects of ploidy and of sex. These models allow us to predict how fast an allele will spread through (or disappear from) the population depending on the strength of **selection** and the genetic system.

With that as background, we now introduce models of genetic change under **selection**.

Next we develop a similar model for **selection** at a single locus in a diploid population.

A newly recessive mutation will initially be present in a heterozygous individual, and if the new allele is completely recessive, **selection** cannot change its frequency, for it is not expressed in the phenotype of heterozygotes. In sexual diploids, a recessive mutation is not completely shielded from **selection**, for although it initially occurs only in heterozygotes, matings between heterozygotes will produce some homozygous recessive offspring that are exposed to **selection**.

Thus there is little scope for **selection** of AR because the recessive allele is not expressed and is 'invisible' to natural **selection** in heterozygotes. This explains the very slow spread of a rare favorable recessive mutation (Figure 4.6c).

These arguments apply both to the spread of favorable mutations and to the removal from diploid populations of deleterious recessive alleles by **selection**.

Particularly at low allele frequencies, most of these alleles are expected to reside in heterozygotes in which they are shielded from **selection** because they are not expressed in the phenotype.

For dominant genes the situation is different. They are expressed in heterozygotes and **selection** can 'see' the allele in both homozygous and heterozygous genotypes. This explains why a dominant favorable mutation will spread much faster (Figure 4.6b). Because most microorganisms are haploid, while most animals and seed plants are sexual diploids, populations of microorganisms are expected to respond to the same **selection** pressure more rapidly than populations of higher eukaryotes.

To what extent do the conclusions we have drawn remain valid for models that consider **selection** involving several loci? We have seen that in haploid populations allele frequency change at one locus is identical under asexual and sexual reproduction.

The term fitness is shorthand for reproductive success. This is not a very precise definition, but sufficient for our purposes. A heritable trait is favored by natural **selection** if individuals carrying this trait have on average higher fitness (greater reproductive success) than individuals without this trait.

Selection operating on differences in inclusive fitness is called kin **selection**, because such interactions are usually between relatives. As early as 1930 Fisher had suggested a similar mechanism for the evolution of distastefulness in some butterfly larvae.

The role of kin **selection** in transforming potential conflict into cooperation is further discussed in Chapter 15 (p. 373).

That genetic variation is at least partially responsible for phenotypic differences follows from plant and animal breeding, where artificial **selection** almost always results in heritable change (Figure 4.11a).

We cannot use population genetics to analyze genetic change caused by **selection** on quantitative traits, for we have no idea what genotypes are present and cannot describe genetic change in terms of allele frequencies. How can we find out how much phenotypic variation is caused by genetic differences? This is an important question, for **selection** on parents will only result in phenotypic change in offspring if some of the phenotypic variation is heritable.

You might think that once the genetic and environmental variances as fractions of the total phenotypic variance have been estimated, we are in a position to judge how effective **selection** can

be in causing genetic change in the population. If most phenotypic variability is due to environmental variation, **selection** is not expected to result in genetic change, while a high genetic variance should give much opportunity for **selection** to bring about genetic changes in consecutive generations. This reasoning is roughly correct, but a complication arises from the fact that not all genetic variance allows a response to **selection** because several interactions among different genetic factors may influence the trait in ways that inhibit a response to **selection**.

The following example illustrates such an interaction, in this case between the alleles at a single locus. Suppose that **selection** favors cold-resistant plants and that a population shows genetic variation for this trait. In particular, suppose that at a locus that contributes to cold resistance the Aa heterozygotes are more cold resistant than either homozygote. The plants favored by **selection** and producing most of the offspring will be the Aa genotypes. But only half of the offspring from these heterozygotes will be heterozygous themselves, while the other half will consist of less well-adapted homozygotes. Even if only heterozygotes breed to form the next generation, 50% of the offspring will be homozygous, preventing a further response to **selection**. Interactions between alleles at different loci may similarly prevent a **selection** response, despite the genetic variability they represent.

Therefore, we need to estimate the part of the genetic variance that is actually available for a response to **selection**.

When this is the case, a response to **selection** for cold resistance is expected for as long as there is genetic variation at the locus. For this reason, quantitative geneticists focus on the portion of total phenotypic variance in a trait that can be attributed to additive genetic effects.

The calculation of genetic change requires specification of the diploid genotype frequencies, because **selection** acts in the diploid phase of the life cycle.

The heritability is a useful measure of the expected response to **selection**.

In general, traits directly connected to reproductive success have low heritabilities and traits less strongly correlated with fitness have higher heritabilities. Part of the reason is that continued **selection** on a trait tends to exhaust additive genetic variation by fixing advantageous alleles, causing the heritability to decrease, so long as beneficial mutations do not occur frequently enough to replace the variation fixed by **selection**. Because fitness is under continuous **selection** in natural populations, we expect low heritabilities for traits that are strongly correlated with fitness—and we find them.

The model developed above predicts that under directional **selection** the rate of phenotypic change depends on the narrow-sense heritability.

Little additive genetic variance implies a poor response to **selection**. Artificial **selection** experiments support the validity of the model!

For example, Yoo (1980) got an impressive response to **selection** on abdominal bristle number in *Drosophila*, a trait with a high heritability (Figure 4.14). After 90 generations of intense **selection** the increase in bristle number was 16 times the standard deviation in the original population (recall that less than 1% of a normally distributed population is more than three standard deviations from the mean). On the other hand, **selection** on rate of egg production in chickens, a trait with low heritability, has been largely unsuccessful (Nordstrog 1977).

Many examples from plant and animal breeding testify that strong directional **selection** can produce large phenotypic changes. Just think of the different breeds of dogs and the many cereal crops that are so different from their wild ancestors.

Such cases of fast change under strong directional artificial **selection** contrast sharply with what we know of long-term evolutionary change under natural **selection**, where rates of change estimated from the fossil record over very long periods of time are many orders of magnitudes slower (Gingerich 1983).

How can we explain these different rates of evolutionary change? One possibility is that continued strong directional **selection**, as applied in artificial **selection**, is rare in nature.

Thus strong natural **selection** produced rapid phenotypic change, but the direction reversed within 7 years. Occasional strong **selection** of variable direction may look like very slow change when averaged over long time periods.

Another reason for the slower rate of evolution in natural systems may be that the extreme trait values produced by directional **selection** reduce fitness because of negative side effects of the alleles selected. A common experience in artificial **selection** is that after relaxation of **selection** the selected trait tends to return towards its original value. This indicates that natural **selection** is opposing artificial **selection**.

Chapter 4 discussed the genetic response to **selection**, and it assumed that genetic variation was present. If all individuals in a population were genetically identical and produced offspring identical to themselves, evolutionary change would be impossible.

Natural **selection** would remove deleterious variants, and occasionally a favorable variant would spread through the population.

In an extreme case, with great genetic variability associated with great variability in fitness, **selection** could be so strong, removing such a large fraction of the population each generation due to low survival or fertility that it might go extinct.

Thus mutation rates can be changed by natural **selection**.

Sexual and asexual species differ in the ease with which mutation rates can be adjusted by **selection**.

It is often stated that natural **selection** produces adaptations by acting on variation resulting from random mutations. What does the word random mean in this context? Because some parts of a genome experience much higher rates of mutations than other parts, mutation is not random with respect to where it occurs.

The critical question, however, is this: do mutations with a specific phenotypic effect occur more often when they are advantageous than when they are not? If so, adaptations could be produced by mutation alone, and natural **selection** would be less important.

The examples mentioned in Chapter 4 (p. 93) of large and rapid phenotypic change under directional **selection** in *Drosophila* and in dogs illustrate this point. **Selection** can be so effective because the traits are affected by many genes whose recombination generates many combinations of alleles across multiple loci.

Then we consider some models that aim to understand how mutation, genetic drift, and natural **selection** affect the level of genetic variation in a population.

No one believes that all genetic variation is selectively neutral. The abundant evidence of adaptation through natural **selection** (Chapter 2, pp. 35 ff.) must be reflected in DNA sequences

Nei (1989), however, found that in the antigen-recognition region more nonsynonymous than synonymous substitutions had occurred, indicating natural **selection** for fast change in the antigen-recognition properties of histocompatibility genes.

Statistical tests have been developed that discriminate between natural **selection** and neutrality as the most likely cause for observed differences in homologous DNA sequences within and between species.

Several studies based on these methods now agree that a large fraction (perhaps 30-45%) of protein divergence is adaptive and driven by **selection** (Fay et al. 2001, 2002, Smith and Eyre-Walker 2002). It thus appears that both natural **selection** and genetic drift play a significant role in evolutionary change at the molecular level.

We will now discuss some of the theoretical models that try to predict the quantitative effects of genetic drift and **selection** on the genetic variability of a population.

They therefore concentrate on the equilibrium states caused by mutation, **selection**, migration, and drift. There are two reasons for this approach

We now calculate the expected frequency of a recurrent deleterious mutation at mutation-**selection** balance. The calculation is simple for the case of a haploid population and is shown in Box 5.1.

If the selective disadvantage of the mutation is very small (that is, for very low values of s) the frequency will be higher, which makes sense because then **selection** is less effective in removing such mutations from the population.

Each generation the sequence of events is: **selection**, mutation, reproduction (by random mating). The relative allele frequencies after **selection** are calculated in the usual way, by dividing the surviving fractions by their sum.

The equilibrium assumption implies that at mutation-**selection** balance the allele frequency remains constant in consecutive generations.

The assumption of equilibrium between mutation and **selection** may also be questionable for many populations. Migration and genetic bottlenecks can move a population well away from equilibrium, and the return to equilibrium can take a long time.

This suggests that many populations are not in mutation-**selection** equilibrium for these loci, probably due to historic population events. For example, phenylketonuria (also called PKU; see also Chapter 4, p. 95) has a higher incidence in eastern than in western Europe.

Whether or not it leads to equilibrium, mutation-**selection** balance is a powerful mechanism for maintaining genetic variation. It guarantees a certain amount of genetic variability at all loci.

Intuitively, this seems to make sense, because if the heterozygotes have superior fitness, the genotype favored by **selection** contains both alleles, so that both are 'protected.'

As with mutation-**selection** balance, the equilibrium assumption is not fulfilled. A particular behavior or interaction depends on what others are doing. **Selection** favoring rare types may then be common. Consider, for example, two genotypes that differ in the type of prey they eat.

A study by Rozen and Lenski (2000) demonstrated coexistence due to frequency-dependent **selection** of two clones of the bacterium *E. coli* during 14 000 generations of serial propagation in a common glucose-limited medium.

Many quantitative characters are under stabilizing **selection**: some intermediate trait value is the best, smaller and larger values reduce function.

Artificial **selection** has often demonstrated that genetic variability exists to change body size in both directions: consider the sizes of the different breeds of dogs.

Thus natural **selection** often favors some intermediate trait value at which the net benefit of the different functional aspects of the trait is highest. This means that often **selection** is stabilizing: deviations from the optimum phenotype are selected against.

For example, horses have evolved from ancestors that were about the size of a very small pony 50 million years ago, but the mean rate of change was so slow that it can be explained by very weak directional **selection** or even by genetic drift.

Throughout that long history the body size of horses could have often been under stabilizing **selection**.

One of many well-documented examples of stabilizing **selection** is the birth weight of human babies (Figure 5.10).

One of many well-documented examples of stabilizing **selection** is the birth weight of human babies (Figure 5.10).

How is genetic variation maintained under stabilizing **selection**? In theory, over dominance or negative frequency-dependent **selection** could be responsible. It is hard to tell as long as the genes involved are not known. On a priori grounds it does not seem likely that overdominance predominates at the many loci involved in quantitative traits under stabilizing **selection**.

The a priori case for frequency-dependent **selection** is perhaps stronger.

But **selection** pressures on individual alleles are then likely to be very weak (see below), and empirical evidence of the involvement of widespread frequency-dependent **selection** is lacking.

Thus the average effect of a mutation on fitness will be very small, and such mutations may reach relatively high equilibrium values at the mutation-**selection** balance.

The mutation-**selection** balance explanation does not exclude other explanations for the maintenance of genetic variability. There may be over dominance at some loci and some frequency-dependent **selection**. Changes in the direction of **selection** may also play a role. The optimal phenotypic value may also shift with environmental conditions (remember **selection** on beak size in Darwin's finches; chapter 4, pp. 93 f.), contributing to the maintenance of alleles by increasing the frequency at which they shift between being advantageous and disadvantageous. But when we

consider all factors together, it seems most likely that much of the genetic variation for quantitative traits under stabilizing **selection** is maintained by mutation.

Parallelisms are the patterns produced when lineages descended from a common ancestor evolve in similar ways because they share developmental mechanisms rather than because they encounter similar **selection** pressures

We could not understand either innovations or parallelisms if our evolutionary explanations consisted only of natural **selection** acting on genetic variation without paying attention to how traits are produced by development. Natural **selection** acts on organisms produced by developmental mechanisms that have a long history and that differ among lineages. Those differences in developmental mechanisms make important differences in how organisms from different lineages will respond to the same **selection** pressures

Particularly important are effects that cause phenotypic variation to differ from genetic variation, for natural **selection** operates with phenotypic variation (Chapter 2, p. 27), whereas the response to **selection** depends on genetic variation (Chapters 4 and 5, pp. 70-123).

Ancient developmental mechanisms shared by an entire lineage may only permit the expression of certain phenotypes, as we saw in Chapter 6 with the different ways that frogs and salamanders respond to **selection** for fewer digits.

Discontinuous growth, found in most arthropods, generates phenotypic variation that interacts with size-specific **selection** in surprising ways

However, if the range of birth sizes were large enough to generate two or more instar groups, as is usually the case, then **selection** against large adults could produce stabilizing **selection** on birth sizes for one range of birth sizes (approx. 0.9-1.2 mm), and disruptive **selection** on birth sizes for another range (approx. 0.7-1.1 mm). Thus the kind of **selection** operating on size at birth in *Daphnia* depends in a complex way on the range of offspring sizes at birth and on growth rates.

Because offspring of various sizes are always entering *Daphnia* populations, there can never be a single, stable type of **selection** on offspring size driven by **selection** on adult size.

The butterfly wing plan and discontinuous growth in arthropods exemplify lineage-specific developmental mechanisms that determine the kinds of variation presented to natural **selection**.

The trait is insensitive to environmental variation, expresses no genetic variation, and cannot respond to **selection**.

A trait like fecundity in Figure 7.7(b) can respond to **selection** at low and high population densities, where it expresses genetic variation, but not at medium density.

Selection to increase the sensitivity of fecundity to density would increase the frequency of G1. **Selection** to decrease the sensitivity of fecundity to density would increase the frequency of G3.

When survival of offspring born at high density is extremely poor, and survival of offspring born at low density is quite good, then **selection** will increase the sensitivity of fecundity to density. When there is little difference in offspring survival at low and high densities, **selection** may decrease the sensitivity of fecundity to density. Thus natural **selection** can shape phenotypic plasticity to react appropriately to ecological problems, but only if there is genetic variation for the slopes of reaction norms.

The response to **selection** of a single quantitative trait depends on its heritability, the amount of phenotypic variation that can be ascribed to additive genetic effects (Chapter 4, p. 90).

When one trait is selected, but is genetically correlated to another trait because some genes influence both traits, the second trait will respond to **selection** on the first trait whether it is directly under **selection** or not. Thus the response of a trait to **selection** depends both on its heritability and on its genetic correlations to other traits also under **selection**.

But if the reaction norms for the two traits behave like those in Figure 7.8, then **selection** to increase eyespot size in the warm, wet season would cause the color of the ring around the eyespot to become lighter, not darker, in the next dry season.

for more rapid development strictly within ponds of long duration would select for smaller body size at metamorphosis. Genetic correlations of pairs of traits can change with the environment in which they are expressed, the potential response to **selection** of a set of correlated traits depends on the environment.

We do not know whether this is because there is strong stabilizing **selection** for a particular structure, or whether developmental mechanisms only permit certain structures to be produced.

Third, the size of the eyespots responds to artificial **selection**; when one eyespot is selected, other respond as well; and **selection** of eyespots on the ventral surface (the more striking surface) does not produce very strong correlated responses on the dorsal surface (Holloway et al. 1993).

Thus the genetic changes involved in a response to **selection** for larger or smaller eyespots influence both the characteristics of the eyespot focus and the characteristics of the surrounding cells (Monteiro et al. 1994).

Artificial **selection** can uncouple the size of the anterior and posterior eyespots, essentially removing one while retaining the other (Beldade et al. 2002b). Thus it is easy to eliminate one eyespot module while retaining another.

One of the genes responding to **selection** for eyespot size is *distalless* itself (Beldade et al. 2002a). Thus the gene thought to represent a deeply conserved phylogenetic constraint itself responds rapidly to microevolutionary **selection** pressures with allelic change.

And as we have seen, some things that appear to be constraints in this system can be modified by **selection** and mutation.

Part 1 of this book dealt with the basic mechanisms of microevolution: **selection**, drift, inheritance, and development. **Selection** acts on material organisms. The strength of **selection** on a trait is determined by the correlation between variation in the trait and variation in reproductive success. If the trait is heritable, the response to **selection** is recorded in genetic information.

We now consider how natural **selection** has designed organisms for reproductive success. Consider an organism that is about to start life and imagine its options.

Thus most-if not all-traits have proven their usefulness for reproductive success and have been shaped by natural **selection** to contribute directly or indirectly to reproduction.

In general, asexuals have a wider distribution than the sexuals, and sexuals are found in habitats where **selection** appears to be driven more by interactions with other organisms than by interactions with the physical environment

Once mating types exist, there will often be **selection** to increase their number, for the greater the number of mating types present in the population, the more likely it is than an individual encountered will be of different mating type and hence a potential mate.

This difference in investment drives sexual **selection**, which involves competition for and choice of mates. Because a female gamete is expensive and a male gamete is cheap, one expects females to be choosy, selecting sperm of high quality for fertilization, and males to compete with each other for access to females.

Because all isogamous gametes require the same investment, no further differences have evolved between isogamous individuals of different mating types, for in these species sexual **selection** is non-existent or very weak.

Another indirect consequence of sex follows from the male/female difference. It is caused by natural **selection** acting on the distribution of the male and female functions among individuals, on the allocation of reproductive effort to male versus female offspring, and on the relative frequency of males and females.

To summarize, a plausible scenario for the evolution of male/female differences starts with **selection** for better-provisioned zygotes, leading to anisogamy in which two types of gamete are produced: big, expensive female gametes and small, cheap male gametes. The difference in the cost of the two types of gamete led to sexual **selection**, and sexual **selection** (Chapter 11, p. 251) then shaped the often striking differences between male and female organisms.

Thus natural **selection** may favor recombination or not, depending on the distribution of two-locus genotypes in the population.

At best it could stay constant if the population size is so large that **selection** maintains genomes in which no new mutations have occurred, but even in large populations mutations with very small deleterious effects will accumulate.

In fact, most interactions between species where the partners affect each other's fitness are likely to result in frequency dependent **selection** on the traits that mediate the interaction.

Natural **selection** in the pathogen population will favor virulence mutants that have the most reproductive success in interaction with the commonest resistance type in the host population.

This is simply because a pathogen most often encounters a common host genotype, and a host most often encounters a common pathogen genotype. Rare resistance types are favored because **selection** on pathogens for specific virulence against them is weak, and rare virulence variants are favored because **selection** on hosts for specific resistance against

Thus negative frequency-dependent **selection** favors rare genotypes in both sexual and asexual species of hosts and pathogens. Such biotic interactions lead to frequent changes of direction of **selection**. Because a rare genotype is selectively favored, it increases in frequency. As it becomes common, it is selected against. This again causes it to become rarer and thus again selectively favored, and so on. In such a system it is important that a genotype that is temporarily selected against does not completely disappear before it is favored again-**selection** should not change

genotype frequencies too quickly at low frequencies. When **selection** regularly changes direction, sexual populations, which recreate genotypes by recombination, retain temporarily bad genotypes longer than asexual populations under most conditions (Jaenike 1978, Hamilton 1980). A simple model of an extreme situation illustrates this for one locus with two alleles. Suppose that **selection** often changes direction

that genotype-specific host-parasite interactions must occur, whereby the resistance and infectivity depend on the genotype of both opponents, thus enabling the operation of negative frequency-dependent **selection**

Perhaps natural **selection** would favor asexual reproduction in humans if it could occur. We are forced to conclude that sex occurs among mammals for historic reasons that fixed genomic imprinting in the lineage, making the asexual alternative impossible, not because natural **selection** favors sex for some reason.

Those consequences are sometimes very important, for properties of the genetic system can make the response to natural **selection** surprisingly subtle and complex. We emphasize the two features of genetic organization that produce the conditions under which conflict among different parts of the genome can become serious: multilevel **selection** and asymmetric transmission

Individual organisms vary, part of Individual organisms vary, part of

Thus cells are also subject to natural **selection**. So are mitochondrial genomes and repeated DNA sequences on nuclear chromosomes.

One important consequence of multilevel evolution, genomic conflict, occurs when a trait is favored at one level but selected against at another, or when different genes affecting the same trait experience contradictory **selection** pressures because they follow different transmission modes.

Because mitochondria are transmitted only in the female line, mitochondrial mutations that enhance female fitness are favored by natural **selection**, irrespective of their impact on male fitness.

Thus there is genomic conflict: natural **selection** favors hermaphroditic flowers coded by genes in the nucleus and male-sterile flowers coded by genes in the mitochondria.

The concept of multilevel **selection** can be extended to higher levels. Individuals occur in groups and groups make up a species.

Just as conflicts can occur between genetic levels within an individual organism, so do conflicts arise between the effects of natural **selection** operating at higher levels

When there is genetic variation among viruses within a rabbit, **selection** within rabbits increases virulence. However, **selection** on the virus for transmission between rabbits favors viruses that have the greatest probability of being transmitted to new hosts, i.e. those living in rabbits that survive for a long time.

Thus there is a conflict between two levels: **selection** among viruses within hosts increases virulence, and **selection** among hosts reduces virulence.

Hurst et al. (1996) suggest that genomic conflicts had a role in the origin of chromosomes, mating types, sex, meiosis, sexual **selection**, diploidy, genome size, and speciation.

We first analyze the simplest type of multilevel **selection**, two-level **selection**, to see how it gives rise to genomic conflicts.

If both mitochondrial types replicate at the same rate and are fairly distributed to the daughter cells (Figure 9.3a), there is no natural **selection** at the lower, mitochondrial level.

If A replicates faster than a (Figure 9.3b), the proportions of A and a mitochondria change in the next cellular generation, and natural **selection** does operate on mitochondria. Whether it is in conflict with **selection** at the cellular level depends on the effects of A and a on the cell's phenotype. If A contributes more to the cell's fitness than a, there is no conflict, for **selection** works in the same direction at both levels. But if a benefits the cell more than A, there is genomic conflict because **selection** favors a at the level of the cell but A at the level of the mitochondria.

If A and a mitochondria replicate at the same rate but are distributed unequally—with biased segregation—to the daughter cells (Figure 9.3c), **selection** also operates on mitochondria. As in case 2, genomic conflict arises if the mitochondrial type favored at segregation is selected against at the cell level.

Mitochondrial mutations in yeast and the yeast cells that contain them both experience two-level **selection** that produces genomic conflict.

What is the fate of petite mutants in a yeast population? **Selection** at the two levels—mitochondria and cells—occurs on different time scales. The process of mutation, increase in frequency, and fixation at the mitochondrial level takes place in only a few cell generations because there are many mitochondrial divisions between two successive cell divisions.

Because the mutation lowers the fitness of the yeast cells, petites are selected against in competition with normally growing yeast, and in time they must disappear if natural **selection** among the yeast cells is sufficiently effective. Taylor et al. (2002) tested this prediction (Figure 9.4) by varying population size to vary the strength of **selection** at the level of the yeast cell.

They varied population size because they expected **selection** among the yeast cells (against the petite mutations) to be very effective in large populations but not in small populations.

As population size decreases, sampling error increasingly obscures the fitness differences among the cell genotypes (Chapter 3, pp. 62 ff.), and cell genotype frequencies are increasingly determined by genetic drift instead of **selection**. The experimental results confirm the expectation: petites are victorious only in small cell populations; in large populations **selection** among the yeast cells is strong enough to eliminate petites.

The yeast example shows that genomic conflicts arise less easily in asexual systems for two reasons. First, a genomic conflict presupposes **selection** acting at two or more levels.

It cannot 'escape' by moving into another replicator, and because genomic conflict lowers fitness at the higher level, such a gene will be removed by **selection**.

Neither reason why asexual systems are protected against genomic conflicts applies to sexual systems, for sex combines genomes from different lineages, and it can generate genetic diversity upon which natural **selection** can act at several replication levels (the input aspect of sex, see Figure 9.5).

If they lowered the cell's fitness, natural **selection** would remove them from bacterial populations by favoring cells that did not have such plasmids.

The genomic conflict that is caused by opposing **selection** pressures at the level of the gametes (favoring t) and the individual (favoring +) results in both types of chromosome being maintained.

Here again are the ingredients of genomic conflict: natural **selection** favors a gene at one level (the cytoplasmic genome) but selects against it at another level (the individual organism).

The interesting suggestion has been made that it may have been the other way round: that male/female or mating-type differentiation evolved to regulate uniparental cytoplasmic inheritance. In other words, **selection** to improve an imperfect mechanism of uniparental cytoplasmic inheritance triggered the evolution of two sexes or mating types.

Therefore-so the proponents of this hypothesis argue-there is no need for the regulation of uniparental cytoplasmic inheritance and consequently no **selection** for sexual differentiation. In their view, this exception suggests the rule (Hurst and Hamilton 1992).

In addition to the asymmetry in cytoplasmic transmission, sexual **selection** (see Chapter 11, pp. 251 ff.) has shaped additional asymmetries between males and females.

Selection should eliminate the genotypes that cause male sterility.

In response (see Chapter 10, pp. 236 ff.), **selection** on nuclear sex-ratio genes will act to establish equal investment in offspring of both sexes.

When the frequency of male steriles in a population increases because **selection** favors a mitochondrial gene causing male sterility, that increase in turn selects any nuclear mutation that suppresses cytoplasmic male sterility and restores a more equal sex ratio.

Such nuclear 'restorer genes' are found in gynodioecious species, where **selection** for mitochondrial male sterility conflicts with **selection** for nuclear restorers of male fertility (e.g. Benrolila et al. 2002)

Life-history traits are directly related to natural **selection**, for survival, maturation, and reproduction determine reproductive success, and variation in reproductive success causes natural **selection**. It is variation in life-history traits that leads to natural **selection**.

To do that, we have to combine information from five sources: (1) the demography of the population, (2) the risk of reproductive failure, (3) the heritability and plasticity of the traits, (4) tradeoffs among traits, and (5) the phylogenetic context of the species in question and how that affects the potential response to **selection**.

Demography connects age and size-specific variation in survival and fecundity to variation in fitness and thereby tells us the strength of natural **selection** on life-history traits. For example, natural **selection** on reproductive performance is stronger in younger than in older adults (what is young and what is old depends on the species).

Two principles from probability theory tell us how the outcome of natural **selection** is shaped by risks like these: Risk does not need to be variable in time or heterogeneous in space for **selection** to favor organisms that spread their risk.

Recall that only a certain part of the genetic variation of a trait determines its reaction to **selection**; this part is the additive genetic variation. pag219

Thus most life-history traits that have been investigated could respond to **selection** (Chapter 4, p. 92). pag219

When the reaction norms of traits cross across environments, they alter the expression of genetic variation, changing both the strength of **selection** on traits and the capacity for a genetic response to **selection** across environments (Chapter 7, pp. 159 ff.).

Thus to explain the evolution of life-history traits, we need to understand how demographic **selection** operates on them; the role that risk minimization plays; the quantitative genetics that determines their response to **selection**; the tradeoffs, both genetic and physiological, that connect traits; and the phylogenetic context in which they sit. pag221

The explanation has an intrinsic part-genetics, tradeoffs, phylogenetic effects-and an extrinsic part-**selection** expressed as effects on age- and sizespecific mortality and fecundity rates. With that in mind, we discuss next the major life-history traits: age and size at maturity, dutch size and reproductiveinvestment, and lifespan and aging. pag221

Age at maturity is a dividing line, for up to maturation natural **selection** for survival is strong, and after maturation aging begins. pag221

Because age and size at maturity vary among closely related species, among populations within species, and among individuals within populations, we know they can respond rapidly to natural **selection**. Age at maturity responds to artificial **selection** in flour beetles and fruit flies, and genetic variation for age and size at maturity has been documented in many species. Thus age and size at maturir}' can be adjusted by natural **selection** to local conditions within populations.

Analysis of the development time-body size-fecundity relationship suggested that they should choose the first option, and they did. Within 2 years of **selection** they had evolved precisely the differences predicted by a reproductiveeffort mode!, and, like the guppies, traits expressed early in life, development time and early fecundity, were the first to change (Figure 10.6).

The guppy and fruit fly examples confirm a basic tenet of the evolutionary theory of aging, our next topic: **selection** on reproductive performance earlier in life is stronger than **selection** on reproductive performance later in life.

For this reason, **selection** on survival rates and fecundities must always decline with age after reproduction begins. They decline at different rates in organisms with different life histories. In humans in industrialized countries, the **selection** to improve survival has dropped almost to zero by the time one is 50 years old, a fact that does not lighten the hearts of the middle-aged (Figure 10.9).

Thus life-history theory views the evolution of the reproductive lifespan as a balance between **selection** to increase the number of reproductive events per lifetime and tradeoffs that increase the intrinsic sources of mortality with age. The first lengthen life, the second shorten it

The factors causing **selection** to lengthen life decrease the reproductive value of juveniles and increase the reproductive value af adults. These include lower adult mortality rates, higher juvenile mortality rates, increased variation in juvenile mortality rates, and decreased variation in adult

mortality rates. Thus age-specific **selection** will adjust the length of life to an intermediate optimum determined by the interaction of **selection** with tradeoffs intrinsic to the organism and viewed as physiological effects between age classes.

Selection against a deleterious mutation in such a gene is stronger if it is expressed in younger organisms that contribute more reproductive success. In a population at evolutionary equilibrium, the number of mutations present for a given trait depends on the per-trait mutation rate and the strength of **selection** operating on the trait.

The strength of **selection** is stronger on traits only expressed in younger organisms (see Figure 10.9), where it reduces genetic variation. Thus we expect to find more mutations with age-specific expression present for traits only expressed in older organisms, where **selection** (Chapter 5 pp. 111 ff.) is relaxed.

Thus the evolutionary answer to the question, why age?, has two parts. The force of **selection** declines with age; after a certain age organisms are irrelevant to evolution.

Lifespan responds rapidly to **selection** in the laboratory in a manner consistent with evolutionary theory, and longer life must be paid for by reductions in performance early in life, either in lower fecundity, smaller body size, or lower juvenile survival and competitive ability.

What should be the sex ratio favored by **selection** under the simplest assumptions?

Fisher (1930) answered this question as follows: consider a large population with two sexes, well mixed, with random mating (no social structure), external

In this manner deviations from equal frequencies of the two sexes produce frequency-dependent **selection** that leads to a stable 50:50 sex ratio.

for a 50:50 sex ratio probably led to the evolution of sex chromosomes, which in the simplest XXJXY system constrain the offspring sex ratios of individual females to average 50:50

These examples show that **selection** acting on phenotypes may favor a 50:50 sex ratio in many species, and that the genetic mechanisms that produce that sex ratio can be quite diverse

In these examples the connections between sex allocation, mating systems, sexual **selection**, and life-history evolution are strong. There is no distinction here between ecology, evolution, and behavior. All three fields are associated in how the examples described are explained.

Traits like the displays of male sage grouse puzzled Darwin, for they obviously increase mortality rates. Darwin's solution was sexual **selection**, the component of natural **selection** represented by success in mating.

Note that the word choice in the context of sexual **selection** does not necessarily refer to a conscious mental event. It refers to anything intrinsic to an individual that makes that individual more likely to mate with some partners than others.

Note that the word choice in the context of sexual **selection** does not necessarily refer to a conscious mental event. It refers to anything intrinsic to an individual that makes that individual more likely to mate with some partners than others.

When males and females have different ecologies, their different morphologies may be caused by natural **selection**.

Sexual dimorphism may also reflect primary sex differences, the differences in morphology that are directly associated with reproduction rather than mating success. However, even primary sex differences may be subject to sexual **selection**.

If sexual **selection** has been responsible for producing sexual dimorphism, then two types of interaction were probably involved.

The reason that sexual **selection** by mate choice can lead to surprising results is that the genes that determine mate preference and the genes that determine the traits preferred come together in the offspring.

Sexual **selection** is thus **selection** for traits associated with mating success and partner choice. Mating success and partner choice trade off with other components of fitness, primarily adult survival, as do other reproductive traits, such as fecundity.

If a change in a trait increases lifetime reproductive success sufficiently by improving the ability of an individual to attract mates and fertilize them, it will be favored by **selection** even though it lowers survival probability. Sexual **selection** will change traits influencing mating success until the improvement in mating success is balanced by costs in other fitness components; then the response will stop.

Thus sexual **selection** involves a tradeoff, as does **selection** on life-history traits. However, because the tradeoff is influenced by interactions between two or more individuals, it produces special features not found in standard life-history tradeoffs

This suggests that sexual **selection** is one of the fastest and strongest types of **selection**.

Sexual **selection** operates via mating success.

How can sexual **selection** be one of the strongest evolutionary forces when it affects primarily one sex, produces a trait in that sex whose expression is detrimental in the other sex, affects only one fitness component, and is exposed to **selection** for only part of the lifetime in the favored sex? The answers are to be found in the way that the sexes differ in variation in lifetime reproductive success (Chapter 2, pp. 28 ff.). pag251

When this difference is large enough, **selection** for mating success in males will be stronger than the opposing viability **selection** in females and in males at earlier life stages. pag251

The road from the origin of sexual **selection** to the sage grouse lek has been a long one. When life originated about 3.8 billion years ago, reproduction was asexual, and it remained so for about 2 billion years.

Selection for mating types is driven in part by inbreeding avoidance. It is also driven by frequency-dependent **selection**, for rare types can easily find many partners, but common types have a hard time finding an appropriate partner because they frequently encounter their own type

The reduction to two mating types was necessary for the evolution of anisogamy, the critical step on the path to sexual **selection**.

Once some isogamous population evolved two mating types, **selection** could change those mating types into organisms that differed in the size of their gametes.

Now, a key principle of sexual **selection** came into play. The lifetime reproductive success of females is limited by the number of eggs they can produce, that of males by the number of eggs they can fertilize.

Secondary sexual characters have been shaped by sexual **selection** for success in mating, for example the antlers of male deer, used in male-male competition for mates, and the extravagant display of the peacock's tail, which peahens use in choosing mates.) Males and females with striking secondary sexual characters are the product of a long history of sexual **selection** in anisogamous organisms.

Choice based on immediate phenotypic reward can explain size dimorphism and some exaggeration of traits that produce particular benefits, but it cannot explain the extravagant morphologies and displays of peacocks, sage grouse, and birds of paradise (Figure 11.2) that led Darwin to suggest sexual **selection** in the first place.

Guppies illustrate the balance of natural and sexual **selection** on the same trait

Thus natural **selection** and sexual **selection** through female preference exert opposing pressures on male coloration and courtship behavior in guppies.
pag258

The process is self-reinforcing. Now every time a mutation arises that increases female preference for orange spots, it will spread, and the stronger the preference in the females for orange spots, the stronger the **selection** for big orange spots in males. The ever-stronger preference in the females causes the ornament in the males to evolve with ever-increasing speed. For this reason the process is called Fisherian runaway **selection**
pag260

The spectacular plumage of birds of paradise is largely the product of sexual **selection** by female choice, and some of it is so exaggerated (Figure 11.2) that a Fisherian runaway process must have been involved. pag261

Such a genetic correlation of male trait and female preference, a necessary condition for the Fisherian process, could also result from **selection** for indicators of parasite resistance.
pag261

Andersson (1994) summed up as follows: 'No critical test has been performed that supports Fisherian sexual **selection** and excludes the alternatives, or estimates their relative importance.'
pag261

The third hypothesis for the evolution of female preferences focuses on their origin. Which male trait is exaggerated by sexual **selection** may depend on its fit to pre-existing features of the female sensory system (Ryan 1985). pag261

However, fitness is certainly under directional **selection** to increase, and under continued strong directional **selection**, the genetic variation for fitness should be reduced to near zero (recall the discussion of **selection**-mutation balance in Chapter 5, pp. 111 ff.). It would appear that female preferences for indicators of male genetic quality could not evolve because there would not be enough genetic variation among males to give females any benefit from their choice.

pag262

In fact, three factors could maintain enough genetic variation for fitness to allow sexual **selection** to work: spatial variation, temporal variation, and mutations affecting fitness. pag263

Also, if there is a steady flow of favorable mutations into a population, which will happen if the population is large enough, then natural **selection** will be continually pulling some favorable mutations through to fixation. pag263

Thus there is an objection to the theory of sexual **selection**: genetic variation for fitness in males is expected to vanish. However, this objection is not fatal, for it is based on a simplified view of how **selection** works in natural populations. How much genetic variation for male fitness can be maintained in natural populations by these mechanisms is a question not yet answered; it needs to be enough to allow female choice to work as a mechanism of sexual **selection**. pag263

Andersson (1994) cites studies of 186 species, mostly insects, fish, anurans, and birds, in which sexual **selection** has been demonstrated 232 times. pag263

Natural **selection** may be preventing further increases in male tail length, for females preferred much longer tails than are found in natural populations. pag264

Darwin saw a relationship between patterns of parental care, the mating system, and the strength of sexual **selection**. pag265

the sex with the higher potential reproductive rate competes more strongly for mates and is the sex subject to stronger sexual **selection**. pag265

How these factors interact to influence the strength of sexual **selection** can be seen in the determinants of the operational sex ratio, the ratio, at any given place and time, of receptive females to sexually active pag265

The operational sex ratio is an important determinant of the opportunity for sexual **selection**. pag265

However, the strength of sexual **selection** does not depend just on the local operational sex ratio. That is only the sole determinant of the difference between the sexes in **selection** when each male has the same number of mates. When the variation in number of mates per male is large, then that variation contributes strongly to the sex difference in the opportunity for **selection**. pag265

Temporal aggregation. Mating opportunities vary in time just as much as they do in space. When females are synchronously receptive, the ability of a few males to mate with many females decreases, the variation among males in reproductive success declines, and sexual **selection** becomes less strong. pag266

Female life histories. Female life history also influences the strength of sexual **selection** and the criteria that females use in choosing males. pag266

The key impact of space, time, and female life history on sexual **selection** and on the difference in the opportunity for **selection** in the two sexes is realized through the number of mates per lifetime of males and females. Therefore the classification of mating systems is based on those numbers (Shuster and Wade 2003). The opportunity for sexual **selection** is weakest under monogamy and strongest under polygyny and polyandry. pag266

When the full variation of receptive partners in space and time is taken into account, we find that there are many categories of mating system, among which the strength of sexual **selection** and the difference in the opportunity for **selection** in the two sexes vary enormously. pag269

Sexual **selection** has apparently been strongest in species with harems or leks where the operational sex ratio is strongly female-biased and where receptive females are concentrated in both space and time pag270

The strength of sexual **selection** can vary among the species within a matingsystem category. Rather than dealing with qualitative categories and expecting them to match the diversity of nature, it is better to measure the strength of sexual **selection** and the difference in the opportunity for **selection** in the two sexes. The pag270

They provide a test case for sexual-**selection** theory: males are the limiting resource, so females should compete for males and males should choose mates. pag270

Sexual **selection** in plants occurs through competition among pollen grains to reach the ovary and through competition among flowers for pollinators. Sexual **selection** differs in plants because many plants are hermaphrodites, with male and female functions combined in a single individual, and because many plants use insects as pollinators. pag271

Sometimes the exaggeration of female traits is driven by the avoidance of nectar-stealers that do not pollinate rather than by sexual **selection**, for example, the Madagascar star orchid with its 30 cm floral tube and pollinator with a 30-cm-long tongue (Figure 2.8). pag271

Up to now we have discussed sexual **selection** as a process operating on the large, diploid stage of the life cycle. pag271

Speciation also connects micro- and macroevolution. A by product of **selection** and drift pag276

Second, if two groups do not interbreed, there is no gene flow between the gene pools, allowing further genetic divergence between the groups by natural **selection** and genetic drift. pag281

Before they separate completely, while they are still existing as populations or races among which interbreeding occurs and gene flow is substantial, a few genes differentiate because of differences in **selection** among the populations, but the majority of genes for which there are no selective differences among populations mix freely (Figure 12.7; stage I). pag286

It is easy to imagine that speciation starts when populations become geographically isolated, are exposed to divergent **selection**, and evolve independently. pag289

Often ecological conditions cause partial isolation of subpopulations, reducing gene flow between subpopulations but not stopping it completely. Does incomplete isolation between subpopulations under divergent **selection** allow speciation? pag290

The key new feature of the theoretical models is the combination of disruptive **selection** with assortative mating (Dieckmann and Doebeli 1999, Kondrashov and Kondrashov 1999). pag290

Selection will start to adapt each part of the population to its resource, but because interbreeding is frequent, adaptation will be quite imperfect. pag291

If one part of the population not only specializes on one of the resources but also has a tendency to mate with others specializing on that resource, then the two processes-adaptation to efficient exploitation of the resource and mate **selection** to avoid producing offspring that are inefficient at exploiting the resource-will reinforce each other. pag291

The explosive speciation of cichlid fishes belonging to the genus *Haplochromis* in Lake Victoria in Africa is another example of sexual **selection** driving speciation. pag297

As in the Hawaiian drosophilids, sexual **selection** for particular types of males (here males with striking colors) may be the first stage in speciation pag297

The second stage in the speciation of haplochromines in Lake Victoria is thought to be diversifying **selection** on feeding habits and other specializations. pag298

Thus recent progress, both theoretical and empirical, supports the idea that sexual **selection** has an important role in speciation and suggests that a significant element of mate choice occurs at the gamete stage. pag299

Many experiments (mostly with *Drosophila*) confirm that divergent **selection** applied to allopatric populations can produce pre- and postzygotic reproductive isolation as a byproduct. pag299

There is also experimental support for the evolution of reproductive isolation between sympatric populations connected by gene flow, provided that divergent **selection** is strong relative to the gene flow. Evolution of reproductive isolation in sympatry was particularly successful when divergent **selection** was applied to several characters simultaneously and when hybrid viability was zero. pag299

The similarity of their molar teeth, adapted to bamboo-feeding in both species, misled us about their relationships, for their teeth resembled each other because natural **selection** had shaped them to similar tasks, not because that morphology had been inherited from a common ancestor (Figure 13.6). pag309

In addition to the terminology that describes natural-monophyletic-andunnatural-paraphyletic and polyphyletic-groups, we also need terms to describe the two major reasons that traits and DNA sequences can look the same: either because they are descended from common ancestors, or because natural **selection** or drift shaped them in similar ways so that they now look the same although they are descended from ancestors who were unrelated and looked different. pag312

There are algorithms that align sequences automatically, introducing some objectivity, but the **selection** of an algorithm can be subjective, and the algorithms are not always reliable. In practice many alignments are performed manually. pag325

There are several problems with this idea. First, the genomes of all organisms within a group share a similar structure that determines both the mutation rate and which parts of the genome are exposed to **selection**. pag325

To avoid such loss, the polymorphisms must have been maintained by **selection** pressure. pag336

With **selection** for heterozygotes with an advantage of 0.3 in a population of 1000 individuals, most alleles are lost within 1000 generations (Klein et al. 1990). 336

One explanation is that stasis results from stabilizing **selection** on adults as a byproduct of precise habitat **selection** by larvae. pag433

Thus some evidence supports the idea that long-term changes in body size seen in the fossil record are a byproduct of **selection** forces acting on life histories. pag435

We now take a deeper look at two of the many issues in which micro- and macroevolution are thoroughly intertwined: coevolution and evolutionary medicine. The same could be done for the evolution of life histories, sex, sexual **selection**, and other major themes pag442

Once that has started to happen, there will be **selection** for assortative mating with individuals who interact well with the partner species and **selection** against mating with individuals, either locally born or recently arrived from other populations, who interact poorly with the partner species. Even with a fair amount of gene flow there is likely to be some steady improvement in **selection** of mates who perform well in the interaction. pag446

Males and females coevolve in many ways, the most striking of which centers around the sexual **selection** of male traits and female preferences in Fisher's runaway process (Chapter 11, pp. 260 ff.), but there are many others pag452

The acquisition of a trait through cultural inheritance creates new **selection** pressures on genes whose products influence the ability of the organism to learn and to carry out the culturally inherited trait. pag456

Selection on traits occurs when there is variation in reproductive success and when variation in the trait is correlated with reproductive success. A response to **selection** occurs when some of the variation in the trait is genetic. pag457

The direction in which an interaction will evolve depends both upon the co-occurrence of several conditions and upon the opportunities for **selection** that they create. We now discuss those conditions. pag458

Frequency-dependent **selection** makes life difficult for common virulence and resistance types and should maintain offset cycles of frequencies of virulence and resistance alleles in host and pathogen (Figure 18.5). pag460

Another consequence of spatial heterogeneity is that it provides the contrasting **selection** pressures in different places that maintain both niche width and genetic variation within the focal species. pag462

Volumes have been written on the outcomes of coevolution, and it is not easy to make an illustrative **selection** from the abundance of striking examples pag463

And in both of these cases the plant has some control over the degree to which such destruction of its seeds can evolve, for if too many of the seeds in any given fruit are destroyed, the plant will abort the fruit, thereby destroying the larvae of the pollinator and imposing negative **selection** on the further evolution of the tendency to destroy seeds. pag468

Similar **selection** forces were operating on the plague bacterium, *Yersinia pestis*, as it made its way northward through Europe in the 14th century: the initial virulence was high, with mortality over 70% in some towns in southern Europe, and then declined towards 30% in northern France and Scandinavia as the pathogen evolved to increase transmission opportunities. pag474

The **selection** criterion. This is the most stringent: we observe the evolution of the interaction itself and document changes in the reproductive success of both partners as the interaction evolves. pag475

Both-of the main branches of evolutionary thought-the reconstruction of history and the analysis of the consequences of natural **selection**-shed light on these topics. The chief players are Homo sapiens, its pathogens, and how they interact with each other. pag481

This chapter has two main sections. In the first, we consider what the historical aspect of evolution has to say about some medical issues. In the second, we do the same for **selection**. pag481

Having looked at a few of the ways in which history sheds light on medical issues, we now turn to ways in which thinking about **selection** does the same pag488

We also discuss some of the subtle ways in which **selection** has shaped human physiology, focusing on selective atresia of oocytes and selective abortion of zygotes. pag488

If symptoms associated with virulence alter the probability that the pathogen will be transmitted, then **selection** will shape the pathogen to increase the intensity of those symptoms if it can thereby increase its lifetime transmission probability. Similarly, **selection** will shape the pathogen to decrease that intensity if it can thereby increase its lifetime transmission probability. pag488

These cases are the extremes of a continuum: vertical transmission largely excludes within-host competition, and serial-passage experiments exclude between-host **selection**. pag489

The parallel evolution suggests that **selection** has favored an ordered acquisition of genes that progressively built up the molecular mechanisms that increase virulence (Reid et al. 2000). E. coli virulence genes have levels of nonsynonymous change five to ten times greater than housekeeping genes. pag489

Thus both **selection** and history shed light on the evolution of virulence. pag490

A **selection** arena is a **selection** process occurring inside an entity that is a unit of **selection** in its own right at a higher level (see Ch. 9, p. 200, multilevel **selection**). Here natural **selection** has produced an adaptation that uses natural **selection** to achieve its effect. **Selection** arenas have been invoked to explain the vertebrate immune system, the overproduction of zygotes (Stearns 1987), the elimination of defective mitochondria from the germ line by oocytic atresia (Krakauer and Mira 1999), and **selection** among pollen tubes growing down flower style pag490

where divorce is possible and children can be born more quickly with a new partner, the strength of **selection** to improve the mechanism would be greater. pag493

Natural **selection** is always at work; gene frequencies do drift; both have often been observed in the laboratory and in the field. pag496

That organisms might be related by descent was recognized by Aristotle, and evolutionary ideas were widespread before Darwin, but Darwin changed everything by proposing a mechanism to produce adaptation: natural **selection** of heritable traits. pag498

Because all genes are exposed to mutation, and because environments change considerably over long periods of time, it is unlikely that extrinsic stabilizing **selection** has maintained so many traits in so many lineages in a fixed state for hundreds of millions of years. pag499

Do the fixed traits affect the further evolution of the traits that remain genetically variable, thus producing elade-specific patterns of response to **selection**? pag500

On the other hand, field studies and laboratory experiments have shown that evolutionary change can happen with surprising speed when **selection** is strong and genetic variation is available. pag500

RNA molecules, linear chains of four nucleotides, are among the simplest entities that can evolve by natural **selection**, as is apparent from the test-tube evolution experiments described in Chapter 2 (pp. 32 ff.). pag502

Hox gene

Examples in mammals include genes coding for heat-shock proteins (involved in protection of cells against environmental stress), globin proteins (involved in oxygen transport), apolipoproteins (involved in lipid metabolism), oncogenes (implicated in cancer), **HOX genes** (very important in development; discussed in Chapter 6, pp. 137 ff.), and genes involved in the immune system. Figure 5.1 depicts the evolutionary history of the human globin genes.

We will see that both groups have independently evolved a similar solution to that problem by using the general principle of combinatorial control implemented in plants through MADS genes and in animals through **HOX genes**

The **HOX genes** were discovered as mutants in silk moths and fruit flies. Mutations in these transcription factor genes result in homeotic mutations, mutations that cause the development of appendages in inappropriate places, such as a leg where an antenna would normally develop.

After the **HOX genes** were sequenced, it was discovered that they all coded for transcription factors and contained a DNA motif, a so-called box, that coded for a binding site that was given the name homeobox. Later other genes were found to contain the same conserved DNA sequence; they are also called homeobox genes.

The **HOX genes** are thus a subset of the homeobox genes, the ones that were found first. They also form a cluster, sitting next to each other on one chromosome. The other homeobox genes occur outside this cluster. In early development the **HOX genes** of most animals determine the fate of the segments along the body axis; later in development they play many different roles

The **HOX genes** have both a remarkable evolutionary history and a remarkable genetic configuration (Figure 6.7)

The same **HOX genes** that determine where the head, thorax, and abdomen of a fly develop do the same job in the embryo of a mouse. We can recognize that the same genes are doing the same job because the DNA sequence in the homeobox has been so well conserved

The **HOX genes** also occur on the chromosome in a linear sequence that corresponds to the part of the body axis whose development they control (Figure 6.8). This property of linear position on chromosome corresponding to position of effect along body axis is called colinearity.

The phylogeny, function, and chromosomal organization of the **HOX genes** suggest a certain evolutionary history. First single genes were duplicated in tandem to form a cluster of analogous genes with related functions sitting next to each other on the same chromosome.

Supporting this interpretation are the following observations (see Figure 6.7): some **HOX genes** are found in Cnidarians, but by no means all of them. In the Lophotrochozoa (annelids, mollusks, and their relatives), there are from six to eight **HOX genes**; in the Ecdysozoa (arthropods, nematodes, and their relatives), from six to 10; in the Deuterostoma (chordates, echinoderms, and their relatives), from 10 to 14. The branch leading to the vertebrates the entire HOX cluster was duplicated twice vertebrates have four copies of most of the cluster.

Both the deep conservation and the co-linearity of the **HOX genes** can be seen in Figure 6.8. In both fly and mouse, the **HOX genes** located to the left control anterior development, those located to the right control posterior development, and the genes in the middle of the HOX cluster control the development of the middle of the body.

One of those structures is the vertebrate limb, and most of the **HOX genes** used to control its formation are the last five members of the first (the A) and the fourth (the D) copy. Two striking facts about how these five transcription factors control limb development emerge from knockout experiments in mice (Figure 6.9).

The correspondence between the evolution of the **HOX genes** and the evolution of the body plans of bilateral animals clearly suggests that Geoffroy St. Hilaire was right: all bilateral animals do share a body plan, and the reason that they share that body plan is that they all use the same set of developmental control processes, inherited from a common ancestor, to construct their bodies (Slack et al. 1993)

No group better displays new uses for **Hox genes** than the echinoderms, which change symmetry patterns during development. The echinoderms **Hox genes** are used to control the patterning of structures with a geometry unlike anything found in other phyla, including S-fold radial symmetry in adults (Figure 6.10).

Unlike the **HOX genes**, the MADS genes are scattered throughout the genome. In Arabidopsis, they occur on all five chromosomes, and there is nothing resembling the co-linearity of position and function of **HOX genes**.

The same combinatorial principle has evolved both in MADS and **HOX genes** through completely independent evolutionary paths—a beautiful example of convergence, and strong evidence for the claim that this method of control must be an extremely good one.

The Ecdysozoa (the animals that grow by molting) we have pieces of that history, and it suggests that changes in body plans were brought about through changes in the parts of the body controlled by particular **HOX genes**.

The conversion of velvet worm to fly may have involved the following steps (this is just one of several possible scenarios). (1) The leg-bearing segments were progressively restricted to the thorax of flies by shifting the expression domains of the **HOX genes** Ultrabithorax (Ubx = Hox 7) and Abdominal-A (abd-A = Hox 8) forward from the tail towards the head and controlling other genes determining segment identity so that the expression of legs was eventually turned off behind the thorax in all insects, leaving them with three pairs of legs.

The wing-bearing segments were progressively restricted to the central thorax. While this was happening in insects, the expression domains of the **HOX genes** along the body axis did not change; they continued to provide the basic patterning of the thorax and abdomen.

Changes in the expression domains of wing-forming genes were involved, probably dependent on combinatorial control involving **HOX genes** as well as other as-yet-unknown control genes. (3) The fly head was sculpted by restricting the expression domains of other **HOX genes**, including Antennipedia (= Hox 6), Ultrabithorax, and Labial (= Hox 1), from several segments in spider-like ancestors to one or two segments in insects.

The transcription factor gene that controls the initiation of eye development, pax-6 or eyeless, is one of many developmental control genes in animals that is not a **HOX gene**.

Others have acquired new functions, such as HOX D9-D13, the control genes used in the evolution of the tetrapod limb from the fish fin, and the **HOX genes** in echinoderms

The echinoderms-the starfish, sea urchins, and sea cucumbers-have evolved radial symmetry from bilaterally symmetrical ancestors and deploy **HOX genes** in entirely different contexts than their bilaterally symmetrical relatives.

When duplicated in the vertebrate line, one set of **HOX genes** continued to control the body axis; a duplicate set was co-opted to control limb development. pag501

Desenvolvimento

Thus all biologists are in some sense evolutionary biologists, for evolutionary biology is not a specialty, like genetics or **development-it** is an explanation of what is investigated by all biological specialties.

How does photosynthesis work?, what determines the sex of an organism?, and what causes disease? are questions about immediate causes whose answers can be sought in fields like physiology, genetics, cell biology, biochemistry, and **development**.

The bones and muscles previously associated with lung breathing have moved forward in the thorax where they help to construct a protractible tongue used in capturing food. In species that switched from larval to direct **development**, the structures previously used in larval gills have also found new application in adult structures.

Thus key innovations, such as lunglessness and direct **development**, imply irreversibility because they allow morphological elements to be used in other structures with different functions, functions so important that a return to the original state would involve costs too high to pay.

How to recognize homologies remains an important issue on which the most sophisticated methods of molecular and **developmental** biology are now brought to bear.

These are normally sequestered early in animal **development**; cells from the rest of the body, the soma, do not later move into the gonads. Now we also know, as the central dogma of molecular biology puts it, that DNA makes RNA makes proteins.

Modern molecular and **developmental** genetics have confirmed in exquisite chemical detail the key aspects of genetics necessary for Darwin's ideas to work: that the genetic material is DNA, that DNA has a sequence that can be replicated precisely, that DNA mutates, and that DNA contains

information in its genetic code that determines the precise structure of the proteins whose structures and activities form the materials and control the processes out of which organisms are built.

Developmental biology studies how information stored in genes is used to build organisms.

Development is central in evolution because all changes in organisms require changes in **development**. Chapter 6 focuses on ancient **developmental** programs that control the construction of organisms. Chapter 7 discusses how variation is expressed in the phenotype. One key idea is the reaction norm, which describes how one genotype can interact with the environment to produce different phenotypes.

Thus the central ideas of microevolution are selection, drift, genetic, and **development**.

Each of those big ideas has many parts; much of the action in microevolution takes place at their intersection.

Its consequences include the mechanisms of **development** and physiology, the structure and performance of flowers, brains, eyes, hearts, and other organs, much of behavior, much of population dynamics, and much of the ecological interactions of species: in short, much of biology

The timing of reproduction, **development**, and hatching are coordinated precisely with the rhythm of the tides.

Early **development** in mammals requires one egg-derived and one sperm-derived haploid nucleus.

Early **development** requires the expression of some genes derived from the father and some genes derived from the mother, which is determined by the sex-specific imprinting that occurs in the germ line of the parent.

The parental patterns are erased later in **development**, allowing the offspring to imprint the genes that are appropriate to their own sex and making it possible to clone some mammals from adult cells. If all the genes came from the mother, then some normally paternal genes would not be turned on at the right time, and early **development** would fail.

As we will see in Chapter 9 (p97), this pattern may have resulted from genomic conflict between the paternal and maternal genes over the issue of asexuality—the pattern is consistent with the interpretation that the paternal genes have been selected for a pattern of **development** that prevents the spread of asexuality and the elimination of males.

Once such a **developmental** mechanism evolved, it could not be changed without destroying sight in the intermediate forms that would have to be passed through on the way to a more 'rationally designed' eye.

This evolutionary progression in adults is replayed in the **developmental** progression of the testes from the embryo to adult (Figure 2.15). As they descend from the body cavity into the scrotum, the testes wrap the vas deferens around the ureters like a person watering the lawn who gets the hose caught on a tree.

If it were not for the constraints of history and **development**, a much shorter vas deferens would have evolved that cost less to produce and might have done a better job.

These are called canalized characters because the final phenotypic outcome is kept constant, as though **development** were confined within a canal that does not allow deviations from its course.

Because of **developmental** buffering, the phenotypic effect of mutations in genes affecting a canalized trait is usually suppressed; such mutations are neutral so long as they are not expressed

The first data on molecular evolution were on amino acid sequences, but since further technological **developments** enabled us to look directly at nucleotide sequences in DNA, molecular evolution has usually been described as nucleotide substitutions in DNA sequences

Continuously distributed traits result both from the sensitivity of traits to environmental change and from **development** influenced by many genes, such that no single allele has a large-enough effect to create an easily recognizable phenotype.

The traits are grouped into four categories: life-history traits like fecundity, viability, survival, and **development** rate; physiological traits like oxygen consumption and resistance to heat stress; behavioral traits like alarm reaction and activity level; and morphological traits like body size and wing length.

The construction of complicated organisms from single cells is astonishing, one of the most precise and complicated processes in biology. Imagine what is involved when **development** turns a single-celled egg into a multicellular organism (Figure 6.1).

In recent years, we have learned a great deal about how genes control **development**. Some **developmental** control genes are broadly shared among distantly related groups, and some of the processes they control are surprisingly similar in organisms as superficially different as flies and mice.

This chapter is here because ancient, conserved **developmental** control genes, to which you are about to be introduced, construed the framework within which microevolution occurs-which traits exist in any particular organism, how they interact, and how they vary. Thus organisms do not simply transmit genetic information passively. Through **development** they actively shape the variation in traits that is presented to selection. This complicates the connection between genotype and phenotype in important and interesting ways.

We begin this chapter by explaining why evolutionary biologists are interested in **development**. After a brief description of **development** in which we introduce the process and concepts relevant to evolution, we then summarize the major messages of recent work on the role of **development** in macroevolution, a role that creates the context within which microevolution occurs. In the next chapter we describe how organisms are fine-tuned by **development** to the particular set of environmental circumstances that they encounter while they

Between those ancestors and these descendants quite different body plans evolved. Thus one reason to study **development** is to understand the evolution of major differences in body plans.

In organisms as different as flies and mice the genetic control of the **development** of body plans is strikingly similar, genes of similar sequence and organization acting in similar parts of the body at similar stages of **development** to elicit similar structures. Some of the genes involved in the **development** of flies and mice are even present and play important roles in the **development** of jellyfish. How evolution has maintained some basic similarities while creating other major differences is a fundamental macroevolutionary question

A second reason to study **development** follows from viewing a life cycle as a repeated sequence of three processes; one ecological, one genetic, and one developmental: Thus each life cycle contains

an element-ecology-in which material interactions predominate, an element-genetics- which transmission of information predominates, and an element-development-that converts information into matter. We cannot understand evolution without understanding what difference each of the three processes makes to the outcome.

We also study **development** because of interest in the evolution of traits. True enough, neutral changes in DNA and protein sequences can occur without much consequence for traits. But other than that, all evolutionary change in the appearance, function, organization, and performance of the organism involves **development**. None of those things are present in the egg, and all of them are present in the adult.

A fourth reason to study **development** is that only by incorporating **development** in our thinking can we understand two major features of evolution: innovations and parallelisms.

One pattern suggests that innovations originate when a **developmental** control gene is duplicated, allowing the new copy to be used to control a process in a new context while the old copy continues to function in the old context. For example (see details below), the **developmental** control genes that determine the major divisions of the vertebrate body-head, thorax, abdomen, tail-were duplicated twice in the lineage leading to tetrapods, and one copy now functions to control the **development** of the tetrapod limb.

Another pattern suggests that a **developmental** control gene with one function early in **development** can be used to initiate different structures in different lineages later in **development**. Thus a gene involved in early segmentation in all insects is used later in **development** in butterflies to initiate eyespot **development** in the middle of wings and in flies to determine what types of structure form on the ends of legs (see Chapter 7, pp. 165-70, for details).

Parallelisms are the patterns produced when lineages descended from a common ancestor evolve in similar ways because they share **developmental** mechanisms rather than because they encounter similar selection pressures.

The pattern can also be elicited by experimental manipulations during **development**, and within a lineage the same pattern is elicited in experiments as is found in evolution.

Frogs lose the first digit; salamanders lose the fifth. In both cases, the digit lost is the last one to form in **development** (Alberch and Gale 1985). Thus frogs have one **developmental** program for digit **development**; salamanders have another. Digit loss, when selected, occurs at the same stage in the **development** process in both groups, but because the order of digit **development** is different in the two groups, different digits are lost.

We could not understand either innovations or parallelisms if our evolutionary explanations consisted only of natural selection acting on genetic variation without paying attention to how traits are produced by **development**.

Natural selection acts on organisms produced by **developmental** mechanisms that have a long history and that differ among lineages. Those differences in **developmental** mechanisms make important differences in how organisms from different lineages will respond to the same selection pressures. Some will do it one way, some another, and we can only understand why if we include the evolution of **development** in our thinking.

The study of the **development** of eggs into adults, called **developmental** biology, provides a perspective on **development** that concentrates on detailed mechanisms. But as seen by evolutionary

biology, **development** does not stop with the construction of the adult phenotype; it continues after maturation through reproduction to death, including the entire life cycle from start to finish. That provides a perspective on **development** that concentrates on broad consequences.

Development occurs in stages that characterize groups of organisms. The **developmental** stages of many frogs include eggs, tadpoles, several I stages during which the tail disappears and limbs develop, and adults.

The **developmental** stages of mammals include zygotes, many intrauterine embryonic stages (Figure 6.1), infants, juveniles, and adults. Genes control the progression through stages of **development** in all organisms.

The major features of life cycles, the striking patterns of **development**, vary among the major groups of organisms

is among the most complex and precise processes that have evolved. Complex as it is, we can understand it in simpler terms.

Development consists of cell fusion, cell division, cell growth, and cell differentiation.

Transcription factors are produced by **developmental** control genes. Those genes are themselves turned on or off by responding to other transcription factors. Thus networks of **developmental** control genes are built up that control gene expression over much of the genome.

Cells interact during development through cell-cell signaling, maintaining a picture of what stage of **development** the whole organism and their immediate neighboring cells are in.

In animals, **development** proceeds as a process of sequential subdivision: first the larger parts are formed, then they are subdivided into smaller parts, and then those are further subdivided until all the body parts and tissue types are formed.

In both plants and animals gene regulation precisely determines which genes are switched on and which are switched off in every cell at every step in **development**.

Developmental control genes can have other functions. A gene that controls the **development** of a large part of the organism early in development may affect a much smaller and different part of the organism late in **development**. Thus **developmental** control genes associated with basic body plans and broad phylogenetic patterns can have microevolutionary functions as well.

If a gene has several such binding sites, then the same transcription factors can act in various combinations to elicit different gene expressions in different tissues and at different stages of **development**.

It solves one central problem of **development**, which is how to take cells that were originally identical and turn them into cells that are appropriately different: brain cells in brains, liver cells in livers, skin cells in skin, leaf cells in leaves, root cells in roots, and so forth.

Because they are highly conserved for these reasons, boxes are a signal in the DNA sequence indicating that the sequence functions as a **developmental** switch.

The function of that **developmental** switch is quite sensitive to changes in the DNA sequence inside the box.

If there were a mutation within the box that changed an amino acid in the binding site of the protein transcription factor, then the binding site would be the wrong shape, it would not bind to the DNA, and it would not be able to control the gene expression necessary for proper **development**.

Thus a part of **developmental** control genes has been conserved, and it has been conserved for several reasons. The remainder of the sequence of these genes, the part that is not in the box, has not been conserved; it can be quite variable.

For example the genes in the MADS family perform many different functions at many stages of **development**. They were free to do so because the old copies continued to control the part of **development** that had existed up to that point.

The initial stages of **development** often involve a concentration-dependent response by control genes. For example, in fruit flies the genes that divide the embryo into a front and a rear half are sensitive to the concentration of maternal proteins diffusing from the front and rear ends of the embryo.

Combinatorial control is a general feature of **developmental** logic that makes possible the production of many cell types under specific conditions

This hierarchy allows the same **developmental** switches used early in **development** to specify patterns in the embryo to be used later in **development** in a different place to specify the formation of a different tissue, for example, in the brain.

With that brief sketch of the mechanics of **development** in hand, we now discuss how **developmental** patterns are associated with phylogeny, then how to explain those patterns in terms of the evolution of **developmental** control genes.

They also share **developmental** patterns, some of the most basic of which are controlled by ancient genes that have retained their function across groups that are now only distantly related.

In addition to three cell layers the Bilateria all have, at some stage of their **development**, a front and a back end as well as a left and a right, and a top and a bottom.

Each group has its own body plan formed during **development**, and the groups that originated more recently have body plans that are more complex.

Both their phylogenetic position and their **developmental** genetics suggest that roots are derived from shoots. Roots evolved again, apparently independently, in the euphyllophytes (ferns and their relatives plus the seed plants-Figure 6.6).

Thus if we want to understand how **development** maps genetic information into phenotypic matter in land plants, we must at least understand the evolutionary and **developmental** origins of apical meristem, shoots and roots, leaves, and flowers.

The other homeobox genes occur outside this cluster. In early development the HOX genes of most animals determine the fate of the segments along the body axis; later in **development** they play many different roles.

The HOX genes also occur on the chromosome in a linear sequence that corresponds to the part of the body axis whose **development** they control (Figure 6.8). This property of linear position on chromosome corresponding to position of effect along body axis is called colinearity.

Both the deep conservation and the colinearity of the HOX genes can be seen in Figure 6.8. In both fly and mouse, the HOX genes located to the left control anterior **development**, those located to the right control posterior **development**, and the genes in the middle of the HOX cluster control the **development** of the middle of the body. The double-headed arrows indicate strong sequence similarity, establishing orthology. Flies and mice most recently shared ancestors 550-650 Ma. This pattern of **developmental** control has persisted since then, over a period so long that it is hard to imagine, in a form that can still be recognize

When the HOX cluster was duplicated twice in the ancestors of the vertebrates, not all of the copies were needed to control the ancestral **developmental** processes.

Some became available to control the **development** of novel structures. One of those structures is the vertebrate limb, and most of the HOX genes used to control its formation are the last five members of the first (the A) and the fourth (the D) copy. Two striking facts about how these five transcription factors control limb **development** emerge from knockout experiments in mice (Figure 6.9).

Thus the property of colinearity observed in the **developmental** control of the body axis is preserved in the **developmental** control of the limb axis.

One of the most charming features of our expanding understanding of the role of **development** is its ability to answer basic questions posed by biologists in the 19th century.

The correspondence between the evolution of the HOX genes and the evolution of the body plans of bilateral animals clearly suggests that Geoffroy St. Hilaire was right: all bilateral animals do share a body plan, and the reason that they share that body plan is that they all use the same set of **developmental** control processes, inherited from a common ancestor, to construct their bodies (Slack et al. 1993).

The fact that a sequence in a **developmental** control gene has been conserved for a long period of time does not mean that the structure whose **development** that gene controls has likewise been conserved

The fact that a sequence in a **developmental** control gene has been conserved for a long period of time does not mean that the structure whose **development** that gene controls has likewise been conserved.

This makes it difficult to infer the morphological phenotype of the last common ancestor from the fact that certain organisms currently living share **developmental** control genes with impressive DNA sequence homologies. For example, the gene for the transcription factor that initiates the **development** of eyes in mice is orthologous to the gene that initiates the **development** of eyes in flies (Halder et al. 1995), but the mouse eye differs so dramatically from the fly eye that all we can infer about the eye of the ancestor is that it was an epidermal light-sensitive organ connected to the central nervous system in a multicellular organism

genes cause us to forget the number of genes involved in building a complex organ. Hundreds to thousands of genes are involved in the **development** of an eye, a limb, or a brain. Many more genes

are involved in building a structure than in controlling when and where it will appear in **development**, and if the degree to which they are conserved did not vary considerably, the diversity of life would not be possible.

No group better displays new uses for Hox genes than the echinoderms, which change symmetry patterns during **development**. The way these genes are used, which differs from class to class among the echinoderms, suggests that the role of some transcription factors was changed in evolution to organize new **developmental** functions.

This required transcription of the genes at new times and places to change the determination of basic symmetry patterns and the **developmental** control over very different larval and adult morphologies (Lowe and Wray 1997).

Molecular genetics thus sheds light on the origin of the **developmental** control genes used to build the diverse morphology found in much of the animal kingdom.

We get further insight into the great age and functional nature of **developmental** control genes from their role in eye **development**.

The transcription factor gene that controls the initiation of eye **development**, pax-6 or eyeless, is one of many **developmental** control genes in animals that is not a HOX gene.

The **developmental** constraints on eye **development** (see Chapter 2, p. 50) arose later.

Whatever changes are made, they must result in the **development** of a functional organism that can survive and reproduce. All other changes will disappear.

The genes that control **development**, genes coding for transcription factors, are very old, hundreds of millions of years old. During that time, some of them, such as pax-6, have retained an ancient function.

Do **developmental** mechanisms constrain evolution in the sense that they make possible only certain phenotypes and not others? The answer is often yes in the short term and often no in the long term. **Development** is complex, highly integrated, and involves some mechanisms that have not changed for a very long time. It can only be changed while retaining organismal function. This all suggests that the range of functioning phenotypes that can be produced by evolutionary changes in **development** must be restricted, and there are examples that suggest that it is

Their example shows us that **developmental** systems, such as the HOX determination of the body axis that appears so deeply conserved in the comparison of mice and flies, can evolve to be applied to shape fundamentally different outcomes.

Do genes cause **development**? That is a metaphor, not an explanation. True enough, there is variation in the number and the function of transcription factor genes, and that variation is associated with differences in **development**.

But those observations do not imply that the genetic element of control is a sufficient cause of **development**, that when we have understood the role of the genes, we have understood all that is necessary to explain **development**.

Development integrates genetic and environmental information. During **development** genetic information is expressed in signals transmitted within and between cells. The environment

influences the course of **development** by intervening in the internal signaling pathways used by the genes. In this way all aspects of the phenotype become the products of gene-environment interactions to a greater or lesser extent.

Genes are linked to organisms by **development**, and **development** gives to organisms a role in evolution missed by a strictly gene-centered approach. Not only the genes' method of making more genes, organisms determine through **development** and through interactions with the environment how genes are expressed and which genes will survive.

A gene not embedded in a functioning life cycle has no future, and a functioning life cycle is one in which **development** succeeds in producing an organism that can deal successfully with ecological challenges to grow, differentiate, survive, and reproduce.

We often discuss evolutionary genetics (Chapters 3-5, pp. 54-123) as though genetic variation were directly expressed as phenotypic variation. This is only occasionally true, for the links that **development**

This chapter explores some complexities in how **development** links genotype to phenotype.

Such **developmental** effects can have at least two causes: ancient mechanisms shared by many species within a lineage, and the current interactions of developing organisms with their environments.

Ancient **developmental** mechanisms shared by an entire lineage may only permit the expression of certain phenotypes, as we saw in Chapter 6 with the different ways that frogs and salamanders respond to selection for fewer digits.

To illustrate such effects we begin this chapter with two examples that show how lineage-specific **developmental** mechanisms interact with variation in the environment to structure phenotypic variation.

They are also the product of a well-understood, phylogenetically conserved, **developmental** mechanism (Nijhout 1991). Butterfly wings develop during pupation from wing discs that are easily accessible for manipulation through the walls of the cocoon.

This **developmental** pattern has been conserved in the radiation of thousands of species of butterflies, functioning as a filter that determines what phenotypes are possible.

Thus the **developmental** mechanisms that control this pattern shape the expression of genetic variation in the phenotype.

Developmental mechanisms not only produce patterns in morphology. They also, very importantly, determine how organisms grow. Differences in growth patterns among major lineages have strongly affected how the species in those lineages have evolved.

The butterfly wing plan and discontinuous growth in arthropods exemplify lineage-specific **developmental** mechanisms that determine the kinds of variation presented to natural selection. Other mechanisms have evolved primarily to produce phenotypes appropriate to the environment where **development**

Induced responses are adaptations that illustrate the capacity of one genotype to produce quite different phenotypes depending on the environment encountered either by its mother or during its own **development**.

We need conceptual tools that enable us to think clearly about the roles of genetic variation, **developmental** mechanisms, and environmental variation in producing patterns of phenotypic variation. This section discusses some concepts that help.

Given the correlations between the two traits described in Figure 7.9, selection for more rapid **development** strictly within ponds of short duration would select for larger body size at metamorphosis. Selection for more rapid development strictly within ponds of long duration would select for smaller body size at metamorphosis.

To that we can add metamorphosis: from tadpoles to frogs in amphibians, from caterpillars to pupae to butterflies in insects, from underwater to aerial leaves in aquatic buttercups, and other **developmental** transformations in the life of a single individual. In all such cases the genome contains the information needed to produce several strikingly different phenotypes.

If the same sets of developmental pathways exist in all individuals of a species, and all that is needed to produce different phenotypes is to flip switches at a few branch points, then a single gene on a sex chromosome could switch on male rather than female development, a signal from a predator could switch on one gene that controlled **development**

When regulatory genes turn **developmental** pathways on or off as a function of the environment, many relations between genotype and phenotype become possible. This has happened in many multicellular organisms whose **developmental** mechanisms are becoming better known. Why it has not happened in single-celled ciliates is not clear.

The study of the **developmental** mechanisms that control gene expression is becoming much easier because of the continuing **development** of new tools in molecular genetics

Because regulatory genes are highly conserved, we can take a gene out of *Drosophila*, where its function is well known, clone it, use it to find orthologous genes in some other organism, study their expression, and have a good chance of uncovering a role for that orthologous gene that sheds as much light on the **development** of that organism as it did in *Drosophila*.

Next we consider an example where the **developmental** control of gene expression can be followed from genetic and **developmental** studies in the laboratory to the fitness consequences of changes in expression in organisms released in the field.

There it served as an example of a conserved **developmental** pattern that influenced how genetic variation could be expressed in a large group with many species.

Second, the wet- and dry-season forms are not discrete phenotypes; they represent the end points of continuous reaction norms that react to the temperature of the environment during **development**

This suggests that the **developmental** regulation of eyespot production extends to all the eyespots on a wing surface, resulting in an eyespot pattern that behaves as an integrated unit; that there is partially independent control over the **development** of the ventral and dorsal wing surfaces; and that there are many genes that modify the intensity of the basic pattern.

Fourth, the **developmental** foci that produce eyespots can be grafted into new positions on the wings of the same or different individuals. Such grafts have been done both from lines selected for large eyespots into lines selected for small eyespots, and in the other direction.

This system appears to give a straightforward answer to the question: how does plasticity interact with conserved **developmental** patterns? The shared ancestors of butterflies and flies had **developmental** control genes that shaped appendage structure. In the lineage leading to flies they evolved to control the **development**

in the lineage leading to butterflies they evolved to control the **development** of wing spots. In both lineages the places in which the **developmental** control genes are now expressed are constrained. In butterflies they can only induce the production of spots in certain parts of the wing and not in others.

Once, however, it is determined that an eyespot will develop in a certain place, its size and color can be altered during the **development** of a single individual by temperature

This yields a picture of a phylogenetically conserved **developmental** pattern expressed early in **development** that lays down structures that are then subject to fine-tuning by plasticity later in **development** (Figure 7.12).

One could imagine that there were **developmental** control genes that produced the conserved structure and plasticity genes that adjusted the interactions with the environment. The **developmental** control genes created a vase, the eyespot, that held a bundle of reaction norms for size and color like a spray of flowers, representing the phenotypic plasticity of the butterfly population in seasonal Africa. Just as a vase holds a bouquet of flowers on a table, so might the phylogenetically conserved **developmental** control over the eyespot hold the reaction norms in position on the wing.

The example of the butterfly wing shows that a phylogenetically fixed **developmental** mechanism widespread in butterflies is controlled by identified genes of known effect.

We may think we see plasticity fine-tuning the phenotype within a long-established framework of phylogenetic and **developmental** constraint, when in fact one network of interactions may be causing the entire pattern, interactions of effects that cannot be cleanly assigned on the one hand to phylogeny and constraint and on the other hand to plasticity, interactions that produce the appearance of constraint in one part and the appearance of plasticity in another part of the same system, both as byproducts.

They can be used to monitor the intensity, quality, direction, and duration of light and to modify **development** appropriately.

Part 1 of this book dealt with the basic mechanisms of microevolution: selection, drift, inheritance, and **development**.

Development transforms genetic information into material organisms in interaction with the environment. It has two key features: conserved mechanisms that lay down the major features of body plans, and plasticity determined by interactions of genes with environment.

At critical stages of **development** only the allele that came from the mother is expressed and the paternal allele is inactivated, while at other stages the paternal allele is active and the maternal allele is silent. Imprinting is usually removed after early **development** in the offspring.

diploid egg that could start **development** on its own, would not survive, for **development** would cease as soon as an essential paternal gene was required to carry out an essential function.

At loci where imprinting occurs, individuals are effectively haploid because only one allele is active. Imprinting is usually removed after the early **developmental** stages of the offspring. Note that imprinting prevents parthenogenesis in mammals: a parthenogenetic mutant would possess only maternal alleles, and **development** would be disrupted by the lack of expression of necessary genes coming from the male germ line (see Chapter 2, p. 49).

Both causes of variation in traits-genetic and physiological-are constrained by features of **development** that are fixed within a lineage, for example how the nymphalid ground plan constrains genetic variation for wing-spot patterns in butterflies (Chapter 7, pp. 165 ff.).

Analysis of the **development** time-body size-fecundity relationship suggested that they should choose the first option, and they did. Within 2 years of selection they had evolved precisely the differences predicted by a reproductive effort model, and, like the guppies, traits expressed early in life, **development** time and early fecundity, were the first to change (Figure 10.6).

Such tradeoffs are in part fixed effects-effects present in all individuals in the population-caused by the common **development** and physiology that characterize the species and represent part of its phylogenetic heritage.

The male and female forms that one individual displays in the course of its **development** are so strikingly different that taxonomists have often classified them as separate species (Figure 10.13).

Macroevolution influences microevolution by providing a context of older traits that constrain microevolution's course. These include modes of growth and **development**; body plans; ability to live in water or on land; the ability to produce wood, to branch, to fix carbon dioxide with alternative biochemical pathways, and so forth.

Development and drift link micro- to macroevolution. The macroevolutionary aspect of **development** resides in the deep conservation of **developmental** control genes; its microevolutionary role arises most clearly in phenotypic plasticity and reaction norms.

Today those characters that 'have been long inherited' include DNA sequences, which systematic biologists supplement with data of many other sorts, mainly morphological and **developmental**.

Two morphological structures are called homologous by morphologists if they are built by the same **developmental** pathway and share the same relative position to other structures, such as nerves and blood vessels (see Figure 13.13). pag315

The hypothesis for their similarity is derivation from a common ancestor from which similar **developmental** mechanisms were inherited. pag315

When DNA sequence similarity and morphological homology have different phylogenetic patterns, the difference tells us to look for something interesting in the evolution of **development** (Wagner 1989).

pag315

This simple procedure is ignored by anyone who compares just a nematode, a fly, and a mouse—three popular model systems for molecular genetics and **developmental** biology sampled from widely separated twigs on the Tree of Life—and dares to talk about ancestral and derived states. pag349

This may explain why **development** in multicellular organisms usually starts from a single cell, guaranteeing maximal relatedness between the cells of an individual. pag369

In most animals the separation between reproductive and non-reproductive cells is nearly absolute and almost always occurs early in **development**. In plants and fungi differentiation into reproductive and somatic cells also occurs, but it happens later during **development** and is less absolute, for somatic cells may dedifferentiate into stem cells that can form reproductive cells; the reverse is also possible.

Microevolutionary genetic drift within populations allows molecular systematists to reconstruct the macroevolutionary Tree of Life from DNA sequence data. Deeply conserved **developmental** control genes help to build the framework within which microevolution and phenotypic plasticity fine-tune the phenotypes of individual organisms. Microevolutionary processes produce speciation as a byproduct, generating macroevolutionary biodiversity

The types of variant that can be produced are constrained within lineages by **developmental** mechanisms specific to those lineages. pag457

Organisms often have to eat different things at different stages of their **development** if only because they start smaller and end larger. pag461

The second half of the 20th century has seen the emergence of molecular biology, the assimilation into evolutionary biology of molecular genetics, the reinvigoration of the interaction between evolutionary and **developmental** biology, and the emergence of evolutionary and behavioral ecology. pag499

The influx of these alternative approaches to explanation—molecular, **developmental**, and ecological—and the recognition of the complexity of the determination of phenotypes—through the interaction of **developmental** mechanisms with the environment—have brought evolutionary biology closer to the goal of logical sufficiency. But it is not there yet. pag499

It seems reasonable to look for additional reasons for long-term maintenance of traits in fixed states in the genotype-phenotype relation, in **development**, and in the constraints inherent in multi-trait evolution (Stearns 1994). pag499

The first is, how did the fixed traits—which are not just fixed genes—become invariant? How did trait fixation evolve? It must have had something to do with the **developmental** control of gene expression, for all DNA sequences mutate, all genes become variable. pag500

The importance of broadly shared **developmental** control systems was highlighted in Chapter 6 (pp. 124 ff.). What is not clear is the extent to which deeply conserved **developmental** control systems constrain evolutionary change, or the extent to which they enable such change, for they appear to do both. pag501

When duplicated in the vertebrate line, one set of HOX genes continued to control the body axis; a duplicate set was co-opted to control limb **development**. pag501

It is thus not at all clear that one can point to deeply conserved **developmental** control genes and assert that they are a source of phylogenetic constraint on the set of phenotypes that evolution can attain.

pag501

One consequence of **developmental** constraints should be some of what we call parallelism-the tendency for the same traits to evolve repeatedly in the same clade. pag 501

It would be interesting to know to what extent conclusions from this study apply to the evolution of traits in organisms, but for no trait in a real organism do we have such complete information on mutations and **development** as in the case of the RNA molecules. pag502

Especiação

One key process in macroevolution is **speciation**, the splitting of one species into two; it is described in Chapter 12 (p. 277). And one key method in macroevolution is phylogenetics, the part of evolutionary biology that infers relationships among species (phylogenies); it is described in Chapter 13 (p. 303).

Macroevolution resembles microevolution in several ways. **Speciation** is like reproduction; extinction is like death; and species can disappear in mass extinctions for reasons that have nothing to do with their performance under normal conditions, just as genes can disappear randomly when their effects are not correlated with reproductive success, this being one way that chance is introduced into history

That this objection is true does not detract from the status of evolution as a major scientific insight. We do not understand the origin of life nearly as well as we understand **speciation**, or selection, or many other aspects of evolution.

The key process in macroevolution is **speciation**. One project within experimental evolution is to produce **speciation** in the laboratory. Some important elements of **speciation**-the evolution of mate choice leading to reproductive isolation coupled with subsequent divergence of the two populations-have already been achieved (see Chapter 12, pp. 299 f.).

Moreover, for more than 50 years biologists have recreated in the laboratory the **speciation** of many plants, among them those in the cabbage family, through hybridization. It would be unwise to claim that **speciation** will not someday be based on a substantial and convincing program of laboratory experiments. It already is in part

If two or more species are very similar to each other, they may be virtually neutral-virtually substitutable-with respect to the ecological forces that affect their abundance, such as competition, predation, pathogens, and abiotic factors. Just as mutation is a source of new alleles, **speciation** is a source of new species. If the **speciation** rate is reasonably high, enough new, essentially similar species may be injected into a continental or oceanic species pool to maintain local biodiversity at a fairly high level as they drift slowly through to extinction. A group of nearly equivalent species is called a guild.

Hurst et al. (1996) suggest that genomic conflicts had a role in the origin of chromosomes, mating types, sex, meiosis, sexual selection, diploidy, genome size, and **speciation**.

This polymorphism may have been present in mouse populations for about 3 million years, predating the **speciation** events leading to the present species in the *Mus* subgenus (other trans-species polymorphisms are discussed in Chapter 14, pp. 334 ff.).

Macroevolution occurs among species and clades, involves **speciation**, extinction, and biogeographic patterns, and occurs slowly. Whereas microevolution concentrates on process, macroevolution focuses on pattern. We can watch microevolution occurring, but we must usually infer macroevolution indirectly from fossils and the comparative method.

Microevolution influences macroevolution by designing traits that affect the probability of extinction and rates of **speciation**.

Speciation also connects micro- and macroevolution. A byproduct of selection and drift, it produces the species whose differences generate macroevolutionary patterns. We therefore begin our discussion of macroevolution with **speciation** (Chapter 12),

Given relationships, we can use comparative methods to investigate history (Chapter 14).

With macroevolutionary principles in hand—**speciation**, phylogenetics, and comparative methods—we go on to consider, in Part 4, The history of life.

Speciation connects micro- to macroevolution

The bridge between micro- and macroevolution is **speciation**, which is responsible for the diversity of life.

Hybrid zones are much studied because they may provide insights into processes that contribute to **speciation**, as we will see later in this chapter.

Sequential, cumulative genetic changes are associated with **speciation**

When we estimate the rate of **speciation** in generations rather than years, African elephants appear to speciate faster than fruit flies. The rapid **speciation** of elephants in Africa is matched by their performance in the fossil record, where one of the fastest rates of morphological change is that of the dwarfing of elephants on Mediterranean islands in the Pleistocene era.

Speciation is a central process in evolution. A theory of evolution that could not explain **speciation** would be seriously flawed.

Do species originate as an inherent consequence of microevolution, or must different, additional processes be involved? Is **speciation** caused by natural selection acting on variations produced by mutation and recombination and by neutral genetic drift, the same processes that drive microevolutionary change within populations?

At present there are no reasons to think that **speciation** requires mechanisms beyond those that generate change within species: **speciation** appears to be a byproduct of intra-specific evolution.

Is complete geographic isolation of populations, with no gene flow, necessary to start **speciation**? Some think that most **speciation** events occurred in allopatry,

Others hold that **speciation** in sympatry, where the subpopulations diverge while continuing to live in the same place, has also played a significant role

It is easy to imagine that **speciation** starts when populations become geographically isolated, are exposed to divergent selection, and evolve independently.

If isolation is complete, **speciation** has occurred. This is the allopatric model of **speciation** (Mayr 1963), represented in its simplest form by Figure 12.8.

According to this model, the first step in **speciation** is for one population to split into two or more completely isolated subpopulations. Such splitting may be caused by migration, by local extinctions of intervening populations, or by geological events.

Darwin's finches exemplify allopatric **speciation**

If birds from two populations did not interbreed, or if their offspring were inviable or sterile, **speciation** had been completed in allopatry.

This aspect—secondary reinforcement—is further considered below (p. 296), where we discuss the origin of reproductive isolation during **speciation**.

Sympatric **speciation** occurs despite continued gene flow between the diverging groups

Does incomplete isolation between subpopulations under divergent selection allow **speciation**?

This model is called sympatric **speciation** (**speciation** occurring within a single population; see Figure 12.9) in contrast to allopatric **speciation**, which assumes complete geographic isolation at the start of the **speciation** process

While allopatric **speciation** is undisputed, whether sympatric **speciation** is likely and common, or can only occur under restrictive conditions, was long controversial (Bush 1994).

The main problem was whether subpopulations can become reproductively isolated and differentiate despite the presence of some gene flow. Recently both theory and data have accumulated that make sympatric **speciation** appear to be both plausible and, in some cases, the **speciation** scenario most likely to explain the facts (Via 2001).

Sympatric **speciation** works when disruptive selection coevolves with assortative mating

It is now well accepted that in theory at least this process will cause sympatric **speciation**. It is a process in which intraspecific competition drives the separation of one population into two coexisting populations that then through improved assortative mating become reproductively isolated. Schluter (2000) therefore calls it competitive **speciation**.

Competitive **speciation** in lake fish exemplifies sympatric **speciation**

One of the most plausible examples of competitive **speciation** is the differentiation of fish living in lakes into forms specialized either on the shore and pelagic habitats or on the deep and shallow habitats.

Another convincing set of cases of sympatric **speciation** involves host shifts in parasites or phytophagous insects. Some individuals start to lay their eggs in a new species of host, perhaps because it has recently arrived or increased in numbers. Such a situation has been studied by Bush and Smith (1998) in *Rhagoletis pomonella* flies

Therefore, although in nature considerable reproductive isolation has evolved, the potential for full interbreeding remains. **Speciation** is not yet complete, but the genetic differentiation and partial reproductive isolation observed in *Rhagoletis* did occur in sympatry.

The phylogenetic distribution of some plant-eating insect taxa suggests sympatric **speciation** by host shifts. For example, there are hundreds of species of fig wasp, each breeding on its own species of fig

Allopatric **speciation** seems implausible here, for it would require a history of many geographic isolation events, whereas many fig species and their wasps are now sympatric.

Sympatric **speciation** can also occur through divergence in flowering times of plants

Sudden sympatric **speciation** by polyploidization is undisputed

A special and undisputed form of sympatric **speciation** is caused by a change in the genetic system that produces sudden reproductive isolation.

Speciation by polyploidization has been particularly important in flowering plants, where 70-80% of the species are thought to have originated as polyploids.

Speciation by polyploidy is less significant among animals, because animal mating systems often do not allow self-fertilization and vegetative reproduction.

Parapatric **speciation** occurs along a border shared by two populations

There may be some gene flow between them. One scenario for parapatric **speciation** is basically allopatric; it starts with the founding of a daughter population near to the parental population but geographically isolated from it.

Another scenario for **speciation** starts with range expansion. For example, a population of frogs may move steadily northward through the eastern United States following the retreat of the glaciers; a population of seagulls may expand

Reproductive isolation is a criterion of **speciation**

According to the allopatric **speciation** model, the divergence built up during allopatry will have caused intrinsic reproductive isolation as a byproduct that only becomes apparent in secondary sympatry.

Allopatric **speciation** leading to complete prezygotic or postzygotic reproductive isolation is unproblematic. How frequently **speciation** has followed this course remains to be seen.

Thus sequence divergence could be the general barrier to recombination characterizes fully completed **speciation**.

How much gene flow between the different populations or races will stop the **speciation** process? Under what condition reproductive isolation become more complete and when will it break down?

We return to the reinforcement below when we discuss experimental evidence on **speciation**.

Sexual selection may have driven **speciation** in Hawaiian flies and

African fish

Speciation of drosophilids (fruit flies in the genus *Drosophila*) in Hawaiian archipelago has been studied since the 1960s by Carson, Kaneshiro and their coworkers.

About 800 *Drosophila* species are endemic to the Hawaiian islands (compared to about 2000 species in the rest of the world). **Speciation** among the Hawaiian drosophilids has probably followed a course similar to Darwin's finches on the Galápagos islands.

Here prezygotic reproductive isolation appears to originate through allopatric changes in courtship behavior, possibly as a chance event in a small founder population, and has often initiated **speciation** in Hawaiian *Drosophila*, preceding adaptation to different food sources and divergence in other characters.

The explosive **speciation** of cichlid fishes belonging to the genus *Haplochromis* in Lake Victoria in Africa is another example of sexual selection driving **speciation**.

As in the Hawaiian drosophilids, sexual selection for particular types of males (here males with striking colors) may be the first stage in **speciation**. Many incipient species could coexist, separated by mate choice. The second stage in the speciation of haplochromines in Lake Victoria is thought to be diversifying selection on feeding habits and other specializations.

Theory suggests that competition for fertilizations will increase the variation in male gamete-recognition proteins; this initiates sympatric **speciation**.

Thus recent progress, both theoretical and empirical, supports the idea that sexual selection has an important role in **speciation** and suggests that a significant element of mate choice occurs at the gamete stage.

Experiments on **speciation** yield two important results

It is often impossible to reconstruct the **speciation** processes that have led to presently existing species. Even though much circumstantial evidence might point to sympatric **speciation**, how could we be sure that there never was an allopatric stage?

For this reason, experiments designed to duplicate part of the **speciation** process under controlled laboratory conditions help to obtain information about the feasibility and relative importance of the various aspects of **speciation**.

An alternative explanation is 'reproductive character displacement,' which assumes that **speciation** was already complete when the species came into secondary contact, but that prezygotic isolation mechanisms diverged in secondary sympatry simply to reduce the amount of time spent mistakenly courting partners that were already reproductively isolated.

Speciation is the birth, extinction, the death of a lineage

As stated at the start of this chapter, **speciation** connects micro- to macroevolution.

Much of this chapter has been concerned with describing the present state of our understanding of the microevolutionary processes that lead to reproductive isolation and the separation of evolving lineages.

We now consider the consequences of **speciation** in preparation for the next two chapters.

When we look at an entire evolving clade, we can see that some of its lineages are speciating and branching, increasing the number of species in the clade, and others are losing diversity because extinctions are more frequent than **speciations**.

There is thus a kind of demography at the species level, a balance between **speciation** (birth) and extinction (death), which underpins patterns of radiation and determines how much biodiversity the clade generates.

A gene genealogy can differ from a species phylogeny because mutations do not occur simultaneously and are not constrained to occur during **speciation** (Figure 13.23).

One gene may have diverged prior to a **speciation** event, another gene may have diverged after that **speciation** event

Remember, this is a comparison only of alleles within a single locus. At least some of the MHC polymorphism must be older than the **speciation** event that separated humans from chimpanzees.

Three patterns were formed. In the first, there is a single **speciation** event when the dispersers arrive on a new island. In the second, there are multiple

speciation events upon arrival associated with local geographic isolation, sexual selection, sympatric **speciation**, or all three..

Those species then dispersed to other islands, retaining their morphology and habitat preference. In this first scenario, each ecomorph evolves once. In the second, the lizards disperse among the islands, and then the **speciation** and differentiation into ecomorphs happens independently on each island. Pag 343

The solution, suggested by Felsenstein (1985), is depicted in Figure 14.12. The key insight in this figure is that the change that occurs after a **speciation** event in one daughter species is independent of the change that occurs after that event in the other daughter species.

Together Parts 3 and 4 constitute an overview of evolution at and above the level of species where the processes of **speciation** and extinction over long periods of time have produced major patterns in the history of life.

Eldredge and Gould (1972) observed that in many fossil lineages long periods of stasis were broken by brief periods of rapid change, and that these periods of rapid change-punctuations-seemed to be associated with apparent **speciation** events. Pag 343-344

They thought that most morphological change occurred during **speciation** and that during the rest of their existence most species did not change very much.

But not all traits and lineages show this pattern of stasis and punctuation, and only in some lineages does most morphological change occur during or soon after **speciation** events.

Some groups-such as Pleistocene corals in New Guinea and bryozoans in tropical America-display stasis over several million years broken by nearsimultaneous **speciation** events associated with major climatic change.

Some groups-such as mollusks in Lake Victoria-display morphological change during **speciation** events and stasis between **speciation** events. Jackson and Cheetham (1999) found that 29 of 31 species with well-documented fossil histories displayed punctuated morphological change associated with cladogenesis

Other groups, including rodents, change as much between as during **speciation** events. And it is difficult to separate **speciation** in time from ecological replacement in space in a fossil record that is usually quite patchy in space even when it is fairly continuous in time.

Deeply conserved developmental control genes help to build the framework within which microevolution and phenotypic plasticity fine-tune the phenotypes of individual organisms. Microevolutionary processes produce **speciation** as a byproduct, generating macroevolutionary biodiversity.

This process of ecological **speciation**, sketched in Chapter 12 (pp. 290 ff.), could result in the local **speciation** of both partners-cospeciation-that would cut off gene flow from the rest of the geographic mosaic and accelerate the evolution of the specialization of the interaction,

Not all specialized interactions must have involved cospeciation, but in those that have, the mutual isolation of both interacting species from other gene pools will have made specialization easier and carried it further than would have otherwise been possible.

The example of crabs and snails provides a transition to the issue of coevolving clades. Clades interact when the coevolutionary interactions between species persist through the **speciation** event and continue to characterize the interactions between the two radiating clades. This is the case for cospeciation of hosts and parasites, plants and pollinators, and plants and herbivores.

The phylogenetic pattern does not have to be as precise as is implied by cospeciation for the clades to continue to interact. Cospeciation simply represents the precise extreme of interactions that can be diffuse. pag 445

Cospeciation simply represents the precise extreme of interactions that can be diffuse. Pag 455

Speciation may now result from **speciation** of the partner. Pag 457

This microevolutionary co-adaptation has led to a high degree of specialization and to the macroevolutionary consequence of frequent cospeciation of the figs and their wasps. Each fig species has its own unique species of wasp pag 469

The phylogenetic trees of figs and fig wasps are partially congruent, suggesting that cospeciation may have played a role during their evolution (Figure 18.8). pag 469

The case for cospeciation is strengthened when one finds monophyletic groups of pollinators with conserved associations with their hosts (Weiblen 2002), and some are found in several segments of these two phylogenies. Pág 469

The phylogenetic data are as yet incomplete, but the data that are available do not suggest that **cospeciation** has been as frequent in yuccas and yucca moths as it has been in figs and fig wasps.

This example combines macroevolutionary **cospeciation** with a parasite-host arms race in one of the most remarkable biological objects on the planet. Leafcutter ants (*Atta* spp.) pág 471

Ecological **cospeciation** in a geographical mosaic connects the concept of adaptive-ecological-**speciation** to congruent phylogenies. If positive reciprocal influence promotes assortative mating for efficient interactions in both partners, **cospeciation** becomes more likely. Pág 476

In the coevolutionary context, we need to remember that the pattern of **cospeciation** detected in clades does not necessarily imply reciprocal effects on interacting adaptations in partnerspecies.

Anthropologists continue to debate two hypotheses for our origin: a single origin in Africa followed by spread to the other continents, or multiple origins in Africa and Asia (incipient **speciation**) followed by fusion upon secondary contact. Pág 481

Deriva

It is as so called genetic **drift** to communicate the lack of direction of neutral genes **drifting** through the population over many generations. Drift produces random change in both large and small populations, but it works more rapidly and over a broader range of conditions in small populations.

To see one of its important effects, consider an example of **drift** simulated on a computer (see Hartl 1994). We start 12 populations, each with eight individuals. Each individual has two versions of the same gene, one from its father and one from its mother, and at the start those versions-A1 and A2-are different.

The process is exactly like flipping a coin twice; in 25% of the cases you will get two heads, in 50% of the cases you will get one head and one tail, and in 25% of the cases you will get two tails. So is it also with **drifting** genes. In some of the populations,

Other biologists emphasize explanations couched in evolutionary terms; they study the impact of selection, **drift**, and history and ask different questions and investigate different kinds of causes in search of answers.

Microevolution operates within populations. It includes adaptive evolution .which consists of natural selection and the genetic response to it.and neutral evolution. which consists of the random **drift**

Chapter 2 describes adaptive evolution: how natural selection works.what forms it takes. and how strong it is in nature. Chapter 3 discusses neutral evolution: how genetic **drift**

Thus the central ideas of microevolution are selection. **drift**. genetics. and development. Each of those big ideas has many parts; much of the action in microevolution takes place at their intersection.

Only if at least some of the variation in the trait is heritable will the genes that are responsible for the trait change in frequency and record the action of selection or **drift**.

The same variation in reproductive success that causes adaptive evolutionary change in the first trait will cause neutral **drift** in the second.

To detect selection of traits, we can manipulate the trait and note the consequences for lifetime reproductive success. To detect selection of genes, we can measure changes in gene frequencies and rule out other causes, such as **drift**. Such measurements suggest that the strength of selection in nature varies from strong to zero.

If heritable variation is not correlated with reproductive success, then the traits or genes involved will **drift** at random within boundaries set by constraints. Much of the genome has been shaped not by adaptive evolution driven by selection but by neutral evolution driven by genetic **drift**. That is the topic of the next chapter.

Random change in the genetic composition of a population caused by chance events is called genetic **drift**. Neutral alleles **drift** aimlessly unless they are located close to a gene undergoing selection, in which case they 'hitchhike' with the selected gene. Genetic variation correlated with fitness is subject to change directed both by natural selection and by genetic **drift**. Which of the two forces determines the outcome depends on their relative strengths. Thus the two types of gene, neutral and selected, actually lie along a continuum. Change in neutral genes is dominated by **drift** but influenced by selection. Change in selected genes is dominated by selection but influenced by **drift**.

The strength of selection on a trait decreases with the correlation of the trait with reproductive success and with the amount of variation in reproductive success, and genetic **drift** is stronger in small than in large populations. Next we discuss the processes that contribute to genetic **drift**, and then we model the **drift** of gene frequencies as a statistical sampling process.

Therefore we now consider a simple model of genetic **drift** as a statistical sampling process. This model is called the gene-pool model. In it the formation of the next generation is represented by sampling gametes from a large gamete population, very much like drawing red or blue balls from an urn. The red and blue balls correspond to A and a, respectively, two alleles at one genetic locus. This model approximates the genetics of a population in which individuals mate randomly.

The dispersion of gene frequencies due to chance is called genetic **drift**. In statistics it would be called the propagation of sampling error. It is stronger in small populations than in large populations, because a small random sample from a population is likely to deviate more from the population composition than is a large sample. Another consequence of genetic **drift** is that it tends to make populations homozygous,

Thus, genetic **drift** reduces genetic variability within a population but increases genetic differentiation among populations.

Cavalli-Sforza and his colleagues (Cavalli-Sforza 1969) tested the predictions of the genetic-**drift** model in humans. From villages and towns near Parma, Italy, they collected blood samples from which they estimated gene frequencies for the ABO, MN and Rh blood-group loci.

In an influential paper, Kimura (1968) proposed that most of the evolutionary change at the molecular level occurs as a consequence of random genetic **drift** of mutant alleles that are selectively neutral or nearly neutral.

Note, however, that Kimura did not suggest that all evolutionary change is driven by genetic **drift**, only most of the nucleotide changes observed at the molecular level. There was never disagreement on the adaptive significance of much morphological, life-history, and behavioral evolution.

Despite recent progress, how much of the genetic variability measured by molecular methods is produced by random genetic **drift** and how much by adaptive evolution is still not clear. On the one hand, it is clear that the selection forces driving the evolution of DNA sequences that are not expressed and have no direct function must be weak. On the other hand, it also has become clear that several suspected neutral genes have been subjected to weak selection. The controversy over genetic **drift** versus natural selection in molecular evolution is further discussed in Chapter 5.

If the speciation rate is reasonably high, enough new, essentially similar species may be injected into a continental or oceanic species pool to maintain local biodiversity at a fairly high level as they **drift** slowly through to extinction. A group of nearly equivalent species is called a guild.

The change in the genetic composition of the population is only caused by the selective differences between the genotypes specified in the model; other possible influences such as genetic **drift** (treated in Chapter 3, pp. 62 ff.) are neglected.

His theory caused considerable controversy about the relative importance of genetic **drift** and adaptive evolution in molecular evolution. We next discuss some attempts to measure fitness consequences of molecular genetic variation. Then we consider some models that aim to understand how mutation, genetic **drift**, and natural selection affect the level of genetic variation in a population.

Smith and Eyre-Walker 2002). It thus appears that both natural selection and genetic **drift** play a significant role in evolutionary change at the molecular level.

We will now discuss some of the theoretical models that try to predict the quantitative effects of genetic **drift** and selection on the genetic variability of a population. They all share the important assumption that populations are in genetic equilibrium, which implies a balance between the forces that increase and decrease genetic variation.

They therefore concentrate on the equilibrium states caused by mutation, selection, migration, and **drift**. There are two reasons for this approach.

Mutations that do not change the fitness of their carriers are solely subjected to genetic **drift**.

This can be shown as follows. The probability that an allele becomes fixed by genetic **drift** is equal to its current relative frequency.

In this context it is the size of an abstract population consisting exclusively of individuals with equal reproductive success that would experience the same amount of genetic **drift** as a real population of size N . In real populations individuals differ in reproductive success.

Real populations may also be subdivided, vary in size, and have different sex ratios, factors that also influence the rate of genetic **drift**. The effective size is therefore often much smaller than the actual size.

There is a steady input of new mutations, most of which are quickly lost, while a few **drift** slowly to fixation, their number representing a balance between mutation and **drift** (Figure 5.4).

For example, horses have evolved from ancestors that were about the size of a very small pony 50 million years ago, but the mean rate of change was so slow that it can be explained by very weak directional selection or even by genetic **drift**. Throughout that long history the body size of horses could have often been under stabilizing selection.

In Chapters 3, 4, and 5 we looked at evolution in a fairly abstract way, asking how do alleles change in frequency under **drift** and selection, what is the origin of genetic variation, and how is genetic variation maintained? We did so without specifying what genes actually did. In this chapter we provide some details. Many genes control how organisms get built. When they change, organisms change in structure, function, and appearance. The link between genes and organisms is made by development.

Part 1 of this book dealt with the basic mechanisms of microevolution: selection, **drift**, inheritance, and development. Selection acts on material organisms.

This process is called Muller's Ratchet. In a sexual population, in contrast, an optimal genotype lost by **drift** can be reconstituted by recombination.

As population size decreases, sampling error increasingly obscures the fitness differences among the cell genotypes (Chapter 3, pp. 62 ff.), and cell genotype frequencies are increasingly determined by genetic **drift** instead of selection. The experimental results confirm the expectation: petites are victorious only in small cell populations; in large populations selection among the yeast cells is strong enough to eliminate petites.

Parts 1 and 2 discussed microevolution; Parts 3 and 4 discuss macroevolution.

Microevolution occurs within populations and species, involves changes in gene frequencies, genetic **drift**, and phenotypic design for reproductive success, and occurs rapidly.

Macroevolution occurs among species and clades, involves speciation, extinction, and biogeographic patterns, and occurs slowly

Development and **drift** link micro- to macroevolution. The macroevolutionary aspect of development resides in the deep conservation of developmental control genes; its

Microevolutionary role arises most clearly in phenotypic plasticity and reaction norms.

While genetic **drift** is a key process in population genetics, it is also a necessary assumption for the methods of molecular systematic that reconstruct the Tree of Life.

Speciation also connects micro- and macroevolution. A by product of selection and drift, it produces the species whose differences generate macroevolutionary patterns.

Genetic recombination within the common gene pool thus prevents strong divergence of any subgroup of individuals. Second, if two groups do not interbreed, there is no gene flow between the gene pools, allowing further genetic divergence between the groups by natural selection and genetic **drift**.

Is speciation caused by natural selection acting on variations produced by mutation and recombination and by neutral genetic **drift**, the same processes that drive microevolutionary change within populations? Pág 288

In addition to the terminology that describes natural-monophyletic-and unnatural-paraphyletic and polyphyletic-groups, we also need terms to describe the two major reasons that traits and DNA sequences can look the same: either because they are descended from common ancestors, or

because natural selection or **drift** shaped them in similar ways so that they now look the same although they are descended from ancestors who were unrelated and looked different. Pág 312

It is a synonym for morphological convergence, which is one reason for homoplasy, a term broader than analogy that indicates similarity for any reason other than common ancestry, including **drift** pag 317

Third, even if the minimum number of individuals did, at one point in time, actually contain the maximum possible number of alleles, random **drift** would have led to the loss of most of the polymorphisms in a small population. Pág 336

In contrast the mitochondrial results suggest that all human mitochondria descend from one female who lived less than 1 million years ago; the other mitochondria then in the population have since disappeared, as would be expected with random **drift** of mitochondria. Pag 336-337

Since the ancestral populations were moderately large, the **drift** was probably caused by variation in female reproductive success rather than by founder effects and genetic bottlenecks. Pág 337

The upwards **drift** hypothesis notes that at the origin of a new group, all species in it are usually small, perhaps because new groups usually originate after mass extinctions have wiped out most of the large organisms. Subsequent changes in body size could be random. Pág 434

Several connections between micro- and macroevolution have already been made.

Microevolutionary genetic **drift** within populations allows molecular systematists to reconstruct the macroevolutionary Tree of Life from DNA sequence data. Deeply conserved developmental control genes help to build the framework within which microevolution and phenotypic plasticity fine-tune the phenotypes of individual organisms. Microevolutionary processes produce speciation as a byproduct, generating macroevolutionary biodiversity.

Evolution is as well tested as any major idea in science. It did happen, and it is continuing. Natural selection is always at work; gene frequencies do **drift**; both have often been observed in the laboratory and in the field. The fossil record, molecular systematics, and the mechanisms shared by all living cells clearly demonstrate the ancient origin of life and the continuity of descent with modification from shared ancestors. Evolution is a reality that cannot be ignored. Pág 498

Macroevolução

The evolutionary processes that occur slowly, where the history of life is written both in the fossil record and in the relationships of living species, are called **macroevolution**.

Macroevolution deals with broad patterns and deep time, time measured in millions and billions of years and space at scales as large as the planet. One key process in **macroevolution** is speciation, the splitting of one species into two; it is described in Chapter 12 (p. 277).

And one key method in **macroevolution** is phylogenetic, the part of evolutionary biology that infers relationships among species (phylogenies); it is described in Chapter 13 (p. 303). The history of life and the planet are approached from three different angles in Chapters 15 (p. 355), on key events, 16 (p. 375), on the geological theater, and 17 (p. 403), on the fossil Record

Macroevolution resembles microevolution in several ways. Speciation is like reproduction; extinction is like death; and species can disappear in mass extinctions for reasons that have nothing to do with their performance under normal conditions, just as genes can disappear randomly when their effects are not correlated with reproductive success, this being one way that chance is introduced into history.

A good example of **macroevolution** is the distribution of ratites, a group of related birds consisting of ostriches, their living relatives the rheas, emus, cassowaries, kiwis, and tinamous, and the extinct elephant birds of Madagascar and moas of New Zealand.

The key process in **macroevolution** is speciation. One project within experimental evolution is to produce speciation in the laboratory.

That is a **macroevolutionary** message. But this is a chapter in a section on microevolutionary principles, so it is logical to ask, why put this chapter at this point in the book?

After a brief description of development in which we introduce the process and concepts relevant to evolution, we then summarize the major messages of recent work on the role of development in **macroevolution**, a role that creates the context within which microevolution occurs.

Some of the genes involved in the development of flies and mice are even present and play important roles in the development of jellyfish. How evolution has maintained some basic similarities while creating other major differences is a fundamental **macroevolutionary** question.

And questions are raised about how one should think about genetic determination, for the same gene is involved in both **macroevolutionary** patterns and microevolutionary change.

When we contrast the **macroevolutionary** pattern of sexually selected traits with the microevolutionary process that produces them, we notice an apparent paradox (Shuster and Wade 2003). The **macroevolutionary** pattern indicates that closely related species can differ dramatically in sexually selected traits; there is no better example than the strikingly different plumage of closely related male birds of paradise (Figure 11.2). This suggests that sexual selection is one of the fastest and strongest types of selection. Pag 249-250

Parts 1 and 2 discussed microevolution; Parts 3 and 4 discuss **macroevolution**. Microevolution occurs within populations and species, involves changes in gene frequencies, genetic drift, and phenotypic design for reproductive success, and occurs rapidly. Pag 276

Macroevolution occurs among species and clades, involves speciation, extinction, and biogeography patterns, and occurs slowly. Whereas microevolution concentrates on process, **macroevolution** focuses on pattern. We can watch microevolution occurring, but we must usually infer **macroevolution** indirectly from fossils and the comparative method. Pag 276

Microevolution influences **macroevolution** by designing traits that affect the probability of extinction and rates of speciation. **Macroevolution** influences microevolution by providing a context of older traits that constrain microevolution's course. Pag 276

Development and drift link micro- to **macroevolution**. The **macroevolutionary** aspect of development resides in the deep conservation of developmental control genes; its microevolutionary role arises most clearly in phenotypic plasticity and reaction norms. While genetic drift is a key process in population genetics, it is also a necessary assumption for the methods of molecular systematics that reconstruct the Tree of Life. Pag 276

Speciation also connects micro- and **macroevolution**. A by product of selection and drift, it produces the species whose differences generate **macroevolutionary** patterns. We therefore begin our discussion of **macroevolution** with speciation (Chapter 12), then examine how to infer the relationships of species-phylogeny and systematics (Chapter 13). Given relationships, we can use comparative methods to investigate history (Chapter 14). With **macroevolutionary** principles in hand-speciation, phylogenetics, and comparative methods-we go on to consider, in Part 4, The history of life. 276

Chapters 2~ 11 described the microevolutionary processes that occur within populations. In this chapter we start to make the transition to **macroevolution**, the patterns in fossils and phylogenies above the species level. The bridge between micro- and **macroevolution** is speciation, which is responsible for the diversity of life. Pág 277

As stated at the start of this chapter, speciation connects micro- to **macroevolution**. Much of this chapter has been concerned with describing the present state of our understanding of the micro evolutionary processes that lead to reproductive isolation and the separation of evolving lineages. Pág 300

Third we ask, in Chapter 17, what are the major patterns of **macroevolution**, as revealed first in fossils, then in the radiations of the major clades? Here we highlight the messages of **macroevolution** and discuss some of its major controversies-stasis, punctuation, largescale trends, and the issue of progress

When we contrast the perspectives of microevolution (Parts 1 and 2) with those of **macroevolution** (Parts 3 and 4), it is natural to wonder how they fit together. They are not independent. They influence each other, and the arrows of causation point in both directions, from micro to macro and from macro to micro. How they do so is explored in Part 5.

Several connections between micro- and **macroevolution** have already been made. Microevolutionary genetic drift within populations allows molecular systematists to reconstruct the **macroevolutionary** Tree of Life from DNA sequence data.

We now take a deeper look at two of the many issues in which micro- and **macroevolution** are thoroughly intertwined: coevolution and evolutionary medicine. The same could be done for the evolution of life histories, sex, sexual selection, and other major themes.

In evolutionary medicine the **macroevolutionary** context describes the origin and spread of *Homo sapiens* across the planet, the histories of contact of diverging populations with different diseases in different places, and the local evolution of differential susceptibility to drugs and disease. The microevolutionary processes relevant to medicine include the evolution of antibiotic resistance, of pathogen virulence, of selective abortion, and of mate choice for resistance genes.

We conclude the chapter by discussing the criteria we can use to judge a claim of coevolution, and how coevolution illustrates the interaction of micro- and **macroevolution**. Pág 445

This micro evolutionary co-adaptation has led to a high degree of specialization and to the **macroevolutionary** consequence of frequent cospeciation of the figs and their wasps. Pág 469

Thus patterns seen in microevolutionary time, such as the stories of rinderpest in Africa and *Phytophthora* in Australia, are reflected in the history of entire faunas in **macroevolutionary** time

when naive species encounter efficient predators, pathogens, and competitors that evolved elsewhere and whose arrival comes as a shock. Pág 475

Thus microevolutionary process produces **macroevolutionary** pattern, here as elsewhere, but pattern does not imply one processo pag 476

Restrição

There are physical **constraints** on this method of 'seeing.' Sound waves rapidly lose energy with distance.

Four limiting factors are particularly important: gene flow, sufficient time for adaptation to occur, tradeoffs, and **constraints**. We now discuss each in turn

Also interesting are evolved **constraints**. Past adaptations can become future **constraints**, placing the imprint of history on a lineage, as we saw in the plethodontid salamanders discussed in Chapter 1 (p. 11).

If heritable variation is not correlated with reproductive success, then the traits or genes involved will drift at random within boundaries set by **constraints**.

For example, histone proteins evolve very slowly, while fibrinopeptides change about 80 times faster. The differences in rates are caused by chemical and functional **constraints**. Histones interact very closely with the DNA, where almost every amino acid has a precise role and is hard to replace without loss of function. In fibrinopeptides, involved in blood clotting, many amino acid changes have little effect on function.

The fact that eye development has been initiated by pax-6 for 600 million years has not constrained the type of eye that is built, simple or compound. The developmental **constraints** on eye development (see Chapter 2, p. 50) arose later.

Such lineage-specific **constraints** combine with the laws of physics and chemistry to influence the interactions of developing organisms with their environments to change the relationship between genetic and phenotypic variation.

One of the genes responding to selection for eyespot size is distalless itself (Beldade et al. 2002a). Thus the gene thought to represent a deeply conserved phylogenetic **constraint** itself responds rapidly to microevolutionary selection pressures with allelic change.

Plasticity and **constraints** are determined in part by the same genes

That suggests the notion of a phylogenetic **constraint** holding a bundle of reaction norms like an old and durable vase holding an ephemeral bouquet of flowers. In some general sense that may be an appropriate analogy, but it may mislead us as much as it guides us. We may think we see plasticity fine-tuning the phenotype within a long-established framework of phylogenetic and developmental **constraint**, when in fact one network of interactions may be causing the entire pattern, interactions of effects that cannot be cleanly assigned on the one hand to phylogeny and **constraint** and on the other hand to plasticity, interactions that produce the appearance of **constraint** in one part and the appearance of plasticity in another part of the same system, both as byproducts. And as we have seen, some things that appear to be **constraints** in this system can be modified by selection and mutation.

Because this seems to be an absolute **constraint**, it is meaningless to discuss the potential optimality of sexual or asexual reproduction in mammals. Perhaps natural selection would favor asexual reproduction in humans if it could occur.

Thus age and size at maturity can be adjusted by natural selection to local conditions within populations. There are also **constraints** on age and size at maturity imposed by history and design.

Deviations from the optimal clutch may also result from **constraints** within lineages.

For example, all birds in the order Procellariiformes lay one egg, in some species not every year.

These include modes of growth and development; body plans; ability to live in water or on land; the ability to produce wood, to branch, to fix carbon dioxide with alternative biochemical pathways, and so forth. Many of these **constraints** are not absolute but relative—the slowly evolving process constraining the rapidly evolving one.

The historical component of a pattern is a mixture of adaptation and **constraint**.

Fourth, comparative methods cannot, by themselves, tell us how much of a pattern to ascribe to adaptation and how much to **constraint**, for the historical component of a pattern is usually a mixture of the two.

Without that limit on places to

stas replication, there was less of a time **constraint** on the amount of DNA that can be copied, and thus less of a limit on the size of a genome that can be copied within a reasonable fraction of a generation. Pág 365

If age at maturity decreases and fecundity increases, then longevity often decreases. Such coordinated adjustments usually occur among all the life-history traits, not just two or three, keeping lifetime reproductive success as high as possible within the limits of **constraints** imposed by tradeoffs among the traits. Pág 449

The answer is couched in terms of the balance of factors favoring specialization or generalization and the **constraints** on ability to evolve in one direction or the other.

In the process, two major puzzles may be solved: how traits are fixed and how **constraints** evolve.

It seems reasonable to look for additional reasons for long-term maintenance of traits in fixed states in the genotype-phenotype relation, in development, and in the **constraints** inherent in multi-trait evolution (Stearns 1994).

Microevolution does not yet explain how varying traits evolve into fixed traits, nor does it explain how fixed traits become **constraints** on the further

Efeito fundador

The Mendelian lottery, variation in family size, **founder effects**, and genetic bottlenecks all have one thing in common: they all involve statistical sampling. The Mendelian lottery, the gametes (and with them the alleles they contain) that form the actual offspring are a random sample from all the gametes available for fertilization. PP 62

A **founder effect** and a genetic bottleneck can both be viewed as drawing a small sample from a much larger population to obtain the next generation. PP 62

Just as genetic **founder effects** can create gene pools with high frequencies of genes that were rare in the founder population, so, after a mass extinction or colonization of an isolated island, can a few species founders that were rare in the previous geological era or in the continental source pool suddenly achieve high frequency in the new geological era or on an oceanic island. If the reasons for their survival or colonization are fairly arbitrary, such that they represent a nearly random sample of the species that were available, then they introduce noise into the historical and biogeographic process. Isolated islands and new geological eras then fill up with groups of organisms that elsewhere or previously were rare or inconspicuous. PP 67

Several processes cause random changes in allele frequencies. The most important are sexual transmission (the Mendelian lottery), random variation in family size, **founder effects**, and genetic bottlenecks. Pp68

Just as **founder effects** change the frequencies of genes sampled from the source population, so do **founder effects** change the balance of biotas on isolated islands and in eras following mass extinctions. pp68

Since the ancestral populations were moderately large, the drift was probably caused by variation in female reproductive success rather than by **founder effects** and genetic bottlenecks. The surviving mitochondria may have spread in part because they contributed to reproductive success, but we do not have to posit an adaptive advantage to explain the result pp 337

Anexo 12 - Livros De Zoologia

HICKMAN

SELEÇÃO

Darwin's hypothesis of natural **selection**, for example, explains the observations that many different species have properties that adapt them to their environments. pag12

The hypothesis of natural **selection** was invoked to explain variation observed in British moth populations (Figure 1-11). pag12

Another testable prediction of the hypothesis of natural **selection** is that when polluted areas are cleaned, the moth populations should demonstrate an increase in the frequency of lightly pigmented individuals. Observations of such populations confirmed the result predicted by natural **selection**. pag12

Natural **selection** is a good example. Our example of the use of natural **selection** to explain observed pigmentation patterns in moth populations is only one of many phenomena to which natural **selection** applies. pag12

Natural **selection** provides a potential explanation for the occurrence of many different traits distributed among virtually all animal species. pag12

Note, however, that falsification of a specific hypothesis does not necessarily lead to rejection of the theory as a whole. Natural **selection** may fail to explain the origins of human behavior, for example, but it provides an excellent explanation for many structural modifications of the pentadactyl (five-fingered) vertebrate limb for diverse functions. pag13

Darwin articulated the complete theory when he published his famous book *On the Origin of Species by Means of Natural Selection* in England in 1859 (Figure 1- 12). pag14

The theories are (1) perpetual change, (2) common descent, (3) multiplication of species, (4) gradualism, and (5) natural **selection**. The first three theories are generally accepted as having universal application throughout the living world . pag14

The theories of gradualism and natural **selection** are controversial among evolutionists, although both are strongly advocated by a large portion of the evolutionary community and are important components of the Darwinian evolutionary paradigm. Gradualism and natural **selection** are clearly part of the evolutionary process, but their explanatory power might not be as widespread as Darwin intended. Legitimate controversies regarding gradualism and natural **selection** often are misrepresented by creationists as challenges to the first three theories presented above, although the validity of those first three theories is strongly supported by all relevant observations. pag14

Natural **selection** is therefore a creative process that generates novel features from the small individual variations that occur among organisms within a population. pag15

Natural **selection** explains why organisms are constructed to meet the demands of their environments, a phenomenon called adaptation (Figure 1-15). pag15

Darwin's theory of natural **selection** faced a major obstacle when it was first proposed: it lacked a theory of heredity. pag16

Natural **selection** would be completely ineffective in this situation. pag16

Once this stage of organization was reached, natural **selection** (pp. 121–123) would have acted on these primitive self-replicating systems. pag31

When self-replicating systems became responsive to the forces of natural **selection**, they began to evolve. pag31

Mendel's classic observations were based on the garden pea because it had been produced in pure strains by gardeners over a long period of time by careful **selection**. pag78

Darwin's theory of natural **selection** when he first proposed it (p. 16). If traits were blended, variability would be lost in hybridization between individuals. pag82

The creative force of evolution is natural **selection** acting on biological variation. Without variability among individuals, there could be no continued adaptation to a changing environment and no evolution (Chapter 6). pag99

Helpful mutations are of great significance to evolution because they furnish new possibilities on which natural **selection** works to build adaptations. Natural **selection** determines which new alleles merit survival; the environment imposes a screening process that passes the beneficial and eliminates the harmful. pag99

Darwin already had been gathering information on artificial **selection** of animals under domestication by humans. After reading Malthus's article, Darwin realized that a process of **selection** in nature, a "struggle for existence" because of overpopulation, could be a powerful force for evolution of wild species. pag108

Darwin was stunned to find that in a few pages, Wallace summarized the main points of the natural **selection** theory on which Darwin had been working for two decades. pag108

For the next year, Darwin worked urgently to prepare an "abstract" of the planned four-volume work. This book was published in November 1859, with the title *On the Origin of Species by Means of Natural **Selection**, or the Preservation of Favoured Races in the Struggle for Life*. pag108

Darwin devoted an entire book, *The Descent of Man and **Selection** in Relation to Sex*, largely to the idea that humans share common descent with apes and other animals. pag113

As the newly expressed variation is sorted by natural **selection**, large changes in phenotype and reproductive properties occur, hastening the evolution of reproductive barriers between the ancestral and newly founded populations. pag118

Natural **selection** is the centerpiece of Darwin's theory of evolution. It gives us a natural explanation for the origins of adaptation, including all developmental, behavioral, anatomical, and

physiological attributes that enhance the organism's ability to use environmental resources to survive and to reproduce. Darwin developed his theory of natural **selection** as a series of five observations and three inferences drawn from them:

pag121

Natural **selection** acting over millions of years should be even more effective in producing new types than the artificial **selection** imposed during a human lifetime. Natural **selection** acting independently on geographically separated populations would cause them to diverge from each other, thereby generating reproductive barriers that lead to speciation.pag123

Natural **selection** can be viewed as a two-step process with a random component and a nonrandom component. Production of variation among organisms is the random component. pag124

The phenomenon of differential survival and reproduction among varying organisms is now called sorting and should not be equated with natural **selection**. pag123

Selection states that sorting occurs because certain traits give their possessors advantages in survival and reproduction relative to others that lack those traits. **Selection** is therefore a specific cause of sorting. pag123

Darwin's theory of natural **selection** has been challenged repeatedly. On challenge claims that directed (nonrandom) variation governs evolutionary change. pag123

Natural **selection** was considered ineffective at stopping the antlers eventually from becoming so large and cumbersome that they forced the Irish elk into extinction (Figure 6-26). Orthogenesis explained apparently nonadaptive evolutionary trends that forced species into decline. pag123

Another recurring criticism of natural **selection** is that it cannot generate new structures or species but can only modify old ones. pag123

Most structures in their early evolutionary stages could not have performed the biological roles that the fully formed structures perform, and it is therefore unclear how natural **selection** could have favored them. pag123

Natural **selection** then could act to improve the usefulness of feathers for flying.pag123

kind to those that we observe within species, it is reasonable to propose that **selection** can lead beyond the species pag123

Mendelian genetics eventually clarified the particulate inheritance that Darwin's theory of natural **selection** required (p. 81). Ironically, when Mendel's work was rediscovered in 1900, it was viewed as antagonistic to Darwin's theory of natural **selection**. When mutations were discovered in the early 1900s, most geneticists thought that they produced new species in single large steps. These geneticists relegated natural **selection** to the role of executioner, a negative force that merely eliminated the obviously unfit.pag123-124

In large biparental populations, allelic frequencies and genotypic ratios attain an equilibrium in one generation and remain constant thereafter unless disturbed by recurring mutations, natural **selection**, migration, nonrandom mating, or genetic drift (random sorting). Such disturbances are the sources of microevolutionary change. pag124

It is practically impossible. Because only the homozygous recessive individuals reveal the phenotype against which artificial **selection** could act (by sterilization, for example), the allele would persist through heterozygous carriers. pag125

For a recessive allele present in 2 of every 100 persons (but homozygous in only 1 in 10,000 persons), it would require 50 generations of complete **selection** against the homozygotes just to reduce its frequency to one in 100 persons. pag125

Genetic equilibrium is disturbed in natural populations by (1) random genetic drift, (2) nonrandom mating, (3) recurring mutation, (4) migration, (5) natural **selection**, and interactions among these factors. pag125

Migration prevents different populations of a species from diverging. If a large species is divided into many small populations, genetic drift and **selection** acting separately in the different populations can produce evolutionary divergence among them. pag127

Natural **selection** can change both allelic frequencies and genotypic frequencies in a population. Although the effects of **selection** are often reported for particular polymorphic genes, we must stress that natural **selection** acts on the whole animal, not on isolated traits. pag127

Darwin used the term sexual **selection** to denote the **selection** of traits that are advantageous for obtaining mates but may be harmful for survival. Bright colors and elaborate feathers may enhance a male bird's competitive ability in obtaining mates while simultaneously increasing his vulnerability to predators (Figure 6-29). Changes in the environment can alter the selective value of different traits. The action of **selection** on character variation is therefore very complex. pag127

Subdivision of a species into small populations that exchange migrants is an optimal situation for promoting rapid adaptive evolution of the species as a whole. Interaction of genetic drift and **selection** in different populations permits many different genetic combinations of many polymorphic genes to be tested against natural **selection**. pag127

Natural **selection**, genetic drift, mutation, nonrandom mating, and migration interact in natural populations to create an enormous opportunity for evolutionary change; perpetual stability, as predicted by Hardy-Weinberg equilibrium, almost never occurs across any significant amount of evolutionary time. pag128

Selection can act on quantitative traits to produce three different kinds of evolutionary response (see Figure 6-31B, C, and D). One outcome is to favor average values of the trait and to disfavor extreme ones; this outcome is called stabilizing **selection** (Figure 6-31B). pag129

Directional **selection** favors an extreme value of the phenotype and causes the population average to shift toward it over time (Figure 6-31C). When we think about natural **selection** producing evolutionary change, it is usually directional **selection** that we have in mind, although we must remember that this is not the only possibility. A third alternative is disruptive **selection** in which two different extreme phenotypes are simultaneously favored, but the average is disfavored (Figure 6-31D). pag129.

Evolutionary change at the second tier provides a new perspective on Darwin's theory of natural **selection**. pag130

This species-level process that produces differential rates of speciation and extinction among lineages is analogous in many ways to natural **selection**. It represents an expansion of Darwin's theory of natural **selection**. pag129-130

Species **selection** is the differential survival and multiplication of species through geological time based on variation among lineages in emergent, species-level properties
pag131

Certain social systems may increase the likelihood that a species will survive environmental challenges through cooperative action. Such properties would be favored by species **selection** over geological time. pag131

Effect macroevolution is similar to species **selection** except that differential speciation and extinction among lineages is caused by variation in organismal-level properties (such as specialized versus generalized feeding) rather than species-level properties (see p. 6).
pag131

Sometimes, lineages favored by species **selection** or effect macroevolution are unusually susceptible to mass extinction. pag132

Selective discrimination of particular biological traits by events of mass extinction is termed catastrophic species **selection**. pag132

Natural **selection**, species **selection**, effect macroevolution, and catastrophic species **selection** interact to produce the macroevolutionary trends that we see in the fossil record
pag132

becomes more intense, and genetic variability—new genotypes produced by recombination in sexual reproduction—furnishes the diversity that permits a population to resist extinction. pag140

Sexual reproduction is therefore favored by species **selection** (species **selection** is described on p. 131). pag140

The type is at best an average form that will change as organismal variation is sorted through time by natural **selection**. pag205

There are no spicules or scales on the oral pedal shield, an organ apparently associated with food **selection** and intake. pag331

They are capable of observational learning; when one octopus observes another being rewarded by making a correct choice, the observer learns which choice is rewarded and consistently makes the same **selection** when given the opportunity. pag348

Many patterns of insect behavior such as feeding, mating, habitat **selection**, and host-parasite relations are mediated through chemical senses. pag422

Even the saliva of harmless snakes possesses limited toxic qualities, and it is logical that there was a natural **selection** for this toxic tendency as snakes evolved. pag575

The target is often small, and natural **selection** relentlessly prunes off individuals making errors in migration, leaving only the best navigators to propagate the species. pag599

This has led to a **selection** of herbivores capable either of defending themselves or of detecting and escaping carnivores. pag620

Darwin devoted an entire book, *The Descent of Man and Selection in Relation to Sex* (1871), largely to human evolution. pag629

Biologically, *Homo sapiens* is a product of the same processes that have directed the evolution of every organism from the time of life's origin. Mutation, isolation, genetic drift, and natural **selection** have operated for us as they have for other animals. pag633

With food procurement as one of the most potent driving forces in animal evolution, natural **selection** has placed a high priority on adaptations for exploiting new sources of food and the means of food capture and intake. pag707

The tick's impoverished sensory world, devoid of sensory luxuries and fine-tuned by natural **selection** for the world she will encounter, has ensured her single goal, reproduction. pag724

Distance chemoreception, usually called smell or olfaction, guides feeding behavior, location and **selection** of sexual mates, territorial and trail marking, and alarm reactions of numerous animals. pag738

Charles Darwin, with the uncanny insight of genius, prepared for the reception of animal behavior by showing how natural **selection** would favor specialized behavioral patterns for survival. pag783

Natural **selection** favors evolution of a brain that imprints in this way, in which following the mother and obeying her commands are important for survival. pag798

Thus although the song must be learned, the brain is constrained to recognize and to learn vocalizations produced by males of its species alone. Learning the wrong song would result in behavioral chaos, and natural **selection** favors a system that eliminates such errors. pag790

Leks characterize some birds, including prairie chickens and sage grouse. In these systems, sexual **selection** (p. 127) is often intense, resulting in evolution of bizarre courtship rituals and exaggerated morphological traits. pag795

Most instances of altruistic behaviors were explained using a group **selection** argument. pag795

Group **selectionists** suggested that animals that helped others or that failed to mate did so for the benefit of the other members of the group. pag795

According to proponents of this argument, **selection** occurs at the level of the group, not at the level of the individual as Darwin suggested. However, the group-**selection** argument as originally proposed by V. C. Wynne-Edwards in 1962 has been rejected by the vast majority of behavioral ecologists for a number of reasons. pag795

Hamilton's hypothesis based on this genetic explanation for altruism and cooperation is called kin **selection**. Essentially, kin **selection** is the **selection** of genes by individuals assisting the survival and reproduction of individuals who possess the same genes by common descent. pag795-796

Thus, kin **selection** and inclusive fitness may be able to explain many altruistic behaviors that have perplexed biologists for many years. pag796

A good example of altruism and kin **selection** in nature is the remarkable cooperation and coordination among eusocial insects such as ants, bees, and wasps. pag796

Thus, alarm-calling behavior, even if it is risky, may be favored by **selection** if it increases inclusive fitness of the caller. pag796

Its effectiveness is ensured because natural **selection** favors the evolution of males with antennal receptors sensitive enough to detect the attractant at great distances (several miles)
pag797

Selection would favor a benign relationship, because a parasite's fitness is diminished if its host dies. pag834

DESENVOLVIMENTO

The order of chapters in Part Two is altered to offer a better study sequence for students, providing a grounding in genetics and evolutionary theory before undertaking the chapters on reproduction and **development**. There are numerous places in the **development** chapter in which an understanding of genetics is crucial. (prefácio)

Chapter 8, Principles of **Development**, was extensively revised in both text and line art. The order in which material on cleavage is presented was reorganized to clarify relationships among principal topics of yolk amount and distribution, cleavage type, cleavage pattern, and subtopics of direct and indirect **development**, mosaic versus regulative **development**, and differences between protostomes and deuterostomes. Pag.XIV

General Properties of Living Systems The most outstanding general features that have arisen during life's history include chemical uniqueness; complexity and hierarchical organization; reproduction (heredity and variation); possession of a genetic program; metabolism; **development**; and environmental interaction. Pág.3

Development. All organisms pass through a characteristic life cycle. **Development** describes the characteristic changes that an organism undergoes from its origin (usually the fertilization of the egg by sperm) to its final adult form (Chapter 8). **Development** usually features changes in size and shape, and the differentiation of structures within the organism
pág.9

Among animals, the early stages of **development** are often more similar among organisms of related species than are later **developmental** stages.
Pág. 10

Characteristics of molecular biology, cell biology, organismal structure, **development**, and ecology are compared among related species to identify their patterns of variation
pag. 13

The most outstanding attributes of life include chemical uniqueness, complexity and hierarchical organization, reproduction, possession of a genetic program, metabolism, **development**, and interaction with the environment . Pág.20

A gene for eye color, for instance, may be the ultimate cause of eye color, yet at the same time it may be responsible for influencing the **development** of other characters as well.

Pág 86

The problem in **development** is to explain how, if every cell has a full gene complement, certain genes are “turned on” and produce proteins that are required for a particular **developmental** stage while the other genes remain silent. Pág 96

Systematics is the science of classification and reconstruction of phylogeny (evolutionary relationships) of organisms (Chapters 6 and 10). Systematics has traditionally depended on detailed analyses of morphology (structure) and **development** as criteria for distinguishing groups of organisms and for reconstructing phylogenies. Pág 100

In many instances sequence analysis has provided the only evidence for relationships between organisms because no evidence was provided by morphology and **development**.

Pag 100

Ontogeny is the history of the **development** of an organism through its entire life. Early **developmental** and embryological features contribute greatly to our knowledge of homology and common descent. Pág 115

Genetic changes that do not alter protein structure may alter patterns of protein synthesis during **development** and can be very important to an organism. Pag 129

During the last two decades the combination of genetics with modern techniques of cellular and molecular biology produced an avalanche of information that solved many questions. Causal relationships between **development** and evolution have also become the focus of research. We do at last appear to have a conceptual framework to account for **development**.

Pag.157

Early scientists and laypeople alike speculated at length about the mystery of **development** long before the process was submitted to modern techniques of biochemistry, molecular biology, tissue culture, and electron microscopy. Pág 157

An early and persistent idea was that young animals were preformed in eggs and that **development** was simply a matter of unfolding what was already there. Pág 157

Current ideas of **development** are essentially epigenetic in concept, although we know far more about what directs growth and differentiation Pág 157

Development describes the progressive changes in an individual from its beginning to maturity (Figure 8-2). In sexual multicellular organisms, **development** usually begins with a fertilized egg that divides mitotically to produce a many-celled embryo. Pag 157

At each stage of **development** new structures arise from the interaction of less committed rudiments. Each interaction is increasingly restrictive, and the decision made at each stage in the hierarchy further limits **developmental** fate. Pág 157

The initial event in **development** in sexual reproduction is fertilization, the union of male and female gametes to form a zygote. Fertilization accomplishes two things: it provides for recombination of paternal and maternal genes, thus restoring the original diploid number of

chromosomes characteristic of the species, and it activates the egg to begin **development**. However, sperm are not always required for **development**. Eggs of some species can be artificially induced to initiate **development** without sperm fertilization (artificial parthenogenesis), but in the great majority of cases the embryo will not be able to progress very far down the **developmental** path before lethal **developmental** abnormalities arise.

Pág. 158

In addition, eggs of most species contain morphogenetic determinants that will direct the activation and repression of specific genes later in postfertilization **development**. Pág 158

Fertilization also initiates an almost complete reorganization of the cytoplasm within which are morphogenetic determinants that will activate or repress specific genes as **development** proceeds. Pág 159

Movement of cytoplasm repositions the determinants into new and correct spatial arrangements that are essential for proper **development**. Pag 160

The best explanation for this feature of mammalian egg **development** is common ancestry with birds and reptiles. Reptiles, birds, and mammals share a common ancestor whose eggs were telolecithal. Pág 165

This is a derived condition that evolved in early vertebrates to accommodate large stores of yolk during **development**. Pag.168

If a blastomere is removed from an early embryo, the remaining blastomeres can alter their normal fates so as to compensate for the missing blastomere and produce a complete organism. This adaptability is termed regulative **development**. Regulative **development** occurs in most deuterostomes (excluding tunicates) (see Figure 8-9). Pág 168

Early embryonic **development** is directed by products synthesized during oogenesis and stored in the egg. Pag 168

The Homeotic Genes As **development** proceeds, gene expression must be regulated to ensure the orderly **development** of the embryo. Pag 169

Genes carrying the homeobox sequence are all expressed during **development**, suggesting that the homeobox performs a broadly essential function. Pág.169

In this way the homeodomain proteins switch subordinate genes on or off at specific times during **development**.Pág 169

Genes at the beginning of the cluster produce proteins that control the formation of the upper body; those farther along the cluster control **development** of the upper abdomen; and those at the end of the cluster control **development** of the lower abdomen (Figure 8-17).

Pág 169

Amphibian **development** provides an excellent example of how homeotic genes control **development**. In amphibians, one homeotic gene encodes a homeobox protein that controls expression of target genes that direct formation of the anterior spinal cord . pag 170

The portion of spinal cord that should have formed was missing altogether (Figure 8-18), because the genes that directed its **development** were not activated in the absence of the homeobox regulatory protein. Pág 170

A prominent outcome of the shared ancestry of vertebrates is their common pattern of **development**. This common pattern is best seen in the remarkable similarity of postgastrula vertebrate embryos (Figure 8-19). Pág 170

The likeness occurs at a brief moment in the **development** of vertebrates when the shared chordate hallmarks of dorsal neural tube, notochord, pharyngeal gill pouches with aortic arches, ventral heart, and postanal tail are present at about the same stage of **development**.
Pág 170

The important contribution of early vertebrate **development** to our understanding of homology and evolutionary common descent is described in Chapter 6 in the section on Ontogeny, Phylogeny, and Recapitulation, p. 115. pag 170-171

During **development**, certain parts of each cell's genome are expressed while the remainder are switched off. Genes expressed early in **development** produce proteins that regulate the expression of subordinate genes in the **developmental** hierarchy. Pag. 177

The postgastrula stage of vertebrate **development** represents a remarkable conservation of morphology when jawed vertebrates from fish to humans exhibit features common to all. As **development** proceeds, species-specific characteristics are formed. pag 177

Both evolutionary taxonomy and cladistics require that patterns of common descent among species be assessed before higher taxa are recognized. Comparative morphology (including **development**), cytology, and biochemistry are used to reconstruct nested hierarchical relationships among taxa that reflect the branching of evolutionary lineages through time. Pág 211

The evolutionary consequence of that **development** alone was enormous, however, for it is the type of symmetry assumed by all more complex animals. Pág 281

The considerable powers of regeneration in planarians have provided an interesting system for experimental studies of **development**. Pág 288

Development of the vertebrate head and paired sense organs was largely the result of two embryonic innovations present only in vertebrates: pag 499

Paedomorphosis, the displacement of ancestral larval or juvenile features into a descendant adult, can be produced by three different evolutionary-**development** processes: neoteny, progenesis, and postdisplacement. Pág 500

It clearly illustrates many shared derived characters of vertebrates that are obscured in the **development** of other vertebrates.
Pag 501

All other vertebrates have jaws, a major **development** in vertebrate evolution. Pág 535

From comparative studies of **development**, biologists believe that the kidney of the earliest vertebrates extended the length of the coelomic cavity and was composed of segmentally arranged tubules, each resembling an invertebrate nephridium pag 670

Coiling of the intestine is common among all vertebrate groups and reaches its highest **development** in mammals, in which the length of the intestine may exceed eight times the length of the body. Pag 715

Conversely, oversecretion of thyroid hormones causes precocious **development** in all vertebrates, although its effect is particularly prominent in fish and amphibians. Pag 761

RESTRICÃO

Biological research has consistently rejected vitalism, showing instead that all living systems operate and evolve within the **constraints** of the basic laws of physics and chemistry. pag10

Cancer cells originate from normal cells that lose their **constraint** on division and become dedifferentiated (less specialized) to some degree. pag100

Gene products of tumor suppressor genes act as a **constraint** on cell proliferation. One such product is called p53 (for “53-kilodalton protein,” a reference to its molecular weight) pag100

Despite the appearance of structural and functional adaptations for distinctive ways of life, the evolution of new forms always develops within the architectural **constraints** of the phylum’s ancestral pattern. pag180

Throughout their long history, protozoa have radiated to generate a bewildering array of morphological forms within the **constraints** of a single cell. pag312

Temperature therefore is a severe **constraint** for animals, all of which must maintain biochemical stability. pag676

Ectotherms partially free themselves from thermal **constraints** by seeking out habitats with favorable temperatures, by behavioral thermoregulation, or by adjusting their metabolism to the prevailing temperature through biochemical alteration. pag682

Nevertheless, despite these **constraints**, aggressive encounters on occasion can be true fights to the death. pag762

ESPECIAÇÃO

Organisms reproduce, sexually or asexually, to produce new organisms (Chapter 5). Populations can become fragmented to give rise to new populations, and species can give rise to new species through a process known as **speciation**. pag7

The criterion of reproductive compatibility has received the greatest attention in studies of species formation, also called **speciation**. pag116

Biological features that prevent different species from interbreeding are called reproductive barriers. The primary problem of **speciation** is to discover how two initially compatible populations evolve reproductive barriers that cause them to become distinct, lineages pag116

Speciation by gradual divergence in animals may require extraordinarily long periods of time, perhaps 10,000 to 100,000 years or more. pag116

Geographical isolation followed by gradual divergence is the most effective way for reproductive barriers to evolve, and many evolutionists consider geographical separation a prerequisite for branching **speciation**. pag116

Speciation that results from evolution of reproductive barriers between geographically separated populations is called allopatric **speciation** or geographic **speciation**. The separated populations evolve independently and generating reproductive barriers between them as a result of their separate evolutionary paths. Ernst Mayr (Figure 6-18) has contributed greatly to our knowledge of allopatric **speciation** through his studies of **speciation** in birds. pag116

Allopatric **speciation** begins when a species splits into two or more geographically separated populations. This splitting can happen in either of two ways: by vicariant **speciation** or by a founder event. Vicariant **speciation** is initiated when climatic or geological changes fragment a species' habitat, producing impenetrable barriers that separate different populations. pag117

Vicariant **speciation** has two important consequences. Although the ancestral population is fragmented, the individual fragments are usually left fairly intact. pag117

Indeed, the same geographic patterns are observed among closely related species in different groups of organisms whose habitats are similar. Such patterns provide strong evidence for vicariant **speciation**. pag117

The alternative means of initiating allopatric **speciation** is for a small number of individuals to disperse to a distant place where no other members of their species are present. pag117

Allopatric **speciation** caused by founder events has been observed, for example, in the native fruit flies of Hawaii. pag117

Unlike what happens in vicariant **speciation**, the new population initially has a very small size, which can cause its genetic structure to change dramatically from that of its ancestral population (see p. 126). pag117

Surprisingly, we often learn most about the genetics of allopatric **speciation** from cases in which formerly separated populations regain geographic contact following evolution of incipient reproductive barriers that are not absolute. pag117

Can **speciation** ever occur without prior geographic separation of populations? Allopatric **speciation** may seem an unlikely explanation for situations where many closely related species occur together in restricted areas that have no traces of physical barriers to animal dispersal. pag118

To explain **speciation** of fish in freshwater lakes and other examples like these, sympatric ("same land") **speciation** has been hypothesized. pag118

Supposed cases of sympatric **speciation** have been criticized, however, because the reproductive distinctness of the different populations often is not well demonstrated, so that we may not be observing formation of distinct evolutionary lineages that will become different species. pag118

In animals, however, **speciation** through polyploidy is an exceptional event. pag119

Punctuated equilibrium states that phenotypic evolution is concentrated in relatively brief events of branching **speciation**, followed by much longer intervals of evolutionary stasis (Figure 6-25). Speciation is an episodic event, having a duration of approximately 10,000 to 100,000 years. Because species may survive for 5 million to 10 million years, the **speciation** event is a “geological instant,” representing 1% or less of a species’ life span. pag121

The process of allopatric **speciation** by founder events provides a possible explanation for punctuated equilibria. Remember that founder-induced **speciation** requires the breaking of genetic equilibrium in a small, geographically isolated population. Such small populations have very little chance of being preserved in the fossil record. pag121

Founder-induced **speciation** cannot be the exclusive cause of punctuated equilibrium, however, because punctuated equilibrium may be observed in groups where **speciation** by founder events is unlikely. pag121

Peter Williamson, a British paleontologist working in fossil beds 400 m deep near Lake Turkana, documented a remarkably clear record of **speciation** in freshwater snails. pag121

The transitions occurred within 5000 to 50,000 years. In the few meters of sediment where **speciation** occurred, transitional forms were visible. pag121

Natural selection acting independently on geographically separated populations would cause them to diverge from each other, thereby generating reproductive barriers that lead to **speciation**. pag123

Speciation links macroevolution and microevolution. Major trends in the fossil record described earlier (see Figures 6-11 and 6-12) are clearly within the realm of macroevolution. pag129

The emergence of new adaptations and species, and the varying rates of **speciation** and extinction observed in the fossil record go beyond the fluctuations of allelic frequencies within populations. pag129

The second tier covers millions of years, the scale on which rates of **speciation** and extinction can be measured and compared among different groups of organisms. pag129

Rates of **speciation** and extinction vary among lineages, and lineages that have the highest **speciation** rates and lowest extinction rates produce the greatest diversity of living forms. pag130

The characteristics of a species may make it more or less likely than others to undergo **speciation** or extinction events. Because many characteristics are passed from ancestral to descendant species (analogous to heredity at the organismal level), lineages whose characteristics increase the probability of **speciation** and confer resistance to extinction should come to dominate the living world. pag130

This species-level process that produces differential rates of **speciation** and extinction among lineages is analogous in many ways to natural selection. It represents an expansion of Darwin’s theory of natural selection. pag130-131

We expect **speciation** rates to be enhanced by social systems that promote founding of new populations by small numbers of individuals. pag131

Effect macroevolution is similar to species selection except that differential **speciation** and extinction among lineages is caused by variation in organismal-level properties (such as specialized versus generalized feeding) rather than species-level properties (see p. 6).
pag131

Such geographic isolation could generate more frequent opportunities for **speciation** to occur throughout geological time. pag131

A lineage of specialized grazers that contains blesboks, hartebeests, and wildebeests shows high **speciation** and extinction rates; since the late Miocene, 33 extinct and 7 living species are found, representing at least 18 events of branching **speciation** and 12 terminal extinctions. pag131

In contrast, a lineage of generalist grazers and browsers that contains impalas shows neither branching **speciation** nor terminal extinction during this same interval of time. Interestingly, although these two lineages differ rates, and species diversity, they do not differ significantly in total number of individual animals alive today. pag131

Recognition of three or more distinct species of Homo does not necessarily imply the occurrence of branching **speciation** in this lineage; it is perhaps equally likely that we are observing phyletic change within a single species through time, and using the species names only to denote different grades of evolution. pag633

DERIVA

We now know that even random processes (genetic **drift**, p. 126) can produce sorting among varying organisms. pag123

In large biparental populations, allelic frequencies and genotypic ratios attain an equilibrium in one generation and remain constant thereafter unless disturbed by recurring mutations, natural selection, migration, nonrandom mating, or genetic **drift** (random sorting). pag124

Genetic equilibrium is disturbed in natural populations by (1) random genetic **drift**, (2) nonrandom mating, (3) recurring mutation, (4) migration, (5) natural selection, and interactions among these factors. pag125

This chance fluctuation in allelic frequency from one generation to the next, including loss of alleles from the population, is called genetic **drift**. pag126

Genetic **drift** occurs to some degree in all populations of finite size. Perfect constancy of allelic frequencies, as predicted by Hardy-Weinberg equilibrium, occurs only in infinitely large populations, and such populations occur only in mathematical models. pag126

All populations of animals are finite and therefore experience some effect of genetic **drift**, which becomes greater, on average, as population size declines. Genetic **drift** erodes the genetic variability of a population. pag126

Because inbreeding and genetic **drift** are both promoted by small population size, they are often confused with each other. pag127

Genetic **drift** changes allelic frequencies and consequently also changes genotypic frequencies. Even very large populations have the potential for being highly inbred if there is a behavioral preference for mating with close relatives, although this situation rarely occurs in nature. Genetic **drift**, however, will be relatively weak in very large populations
pag127

Migration prevents different populations of a species from diverging. If a large species is divided into many small populations, genetic **drift** and selection acting separately in the different populations can produce evolutionary divergence among them. pag127

Interaction of genetic **drift** and selection in different populations permits many different genetic combinations of many polymorphic genes to be tested against natural selection
pag127

Interaction of selection, genetic **drift**, and migration in this example produces evolutionary change that is qualitatively different from what would result if any of these three factors acted alone.
pag128

Natural selection, genetic **drift**, mutation, nonrandom mating, and migration interact in natural populations to create an enormous opportunity for evolutionary change; perpetual stability, as predicted by Hardy-Weinberg equilibrium, almost never occurs across any significant amount of evolutionary time. pag128

Some swim upright, others swim upside down, and many are delicate microscopic forms that **drift** as plankton in the oceans or in lakes. pag389

Much of the time they **drift** passively, but they can dart forward in swift spurts, using the caudal fin and longitudinal muscles— a fact that no doubt contributes to their success as planktonic predators.
pag481

After absorbing the remainder of its yolk supply, the young ammocoete, now about 7 mm long, leaves the nest gravel and **drifts** downstream to burrow in some suitable sandy, low-current area.
pag513

Mutation, isolation, genetic **drift**, and natural selection have operated for us as they have for other animals. pag633

MACROEVOLUÇÃO

Macroevolution refers to evolution on a grand scale, encompassing the origins of new organismal structures and designs, evolutionary trends, adaptive radiation, phylogenetic relationships of species, and mass extinction. pag124

Macroevolutionary research is based in systematics and the comparative method (p. 198). Following the evolutionary synthesis, both **macroevolution** and microevolution have operated firmly within the tradition of neo-Darwinism, and both have expanded Darwinian theory in important ways. pag124

Macroevolution describes large-scale events in organic evolution. Speciation links **macroevolution** and microevolution. Major trends in the fossil record described earlier (see Figures 6-11 and 6-12) are clearly within the realm of **macroevolution**. Patterns and processes of **macroevolutionary** change

emerge from those of microevolution, but they acquire some degree of autonomy in doing so. pag129

Effect **macroevolution** is similar to species selection except that differential speciation and extinction among lineages is caused by variation in organismal-level properties (such as specialized versus generalized feeding) rather than species-level properties (see p. 6). pag131

Sometimes, lineages favored by species selection or effect **macroevolution** are unusually susceptible to mass extinction. Climatic changes produced by the hypothesized asteroid bombardments could produce selective challenges very different from those encountered at other times in the earth's history. pag132

Natural selection, species selection, effect **macroevolution**, and catastrophic species selection interact to produce the **macroevolutionary** trends that we see in the fossil record. Studies of these interacting causal processes have made modern evolutionary paleontology an active and exciting field. pag132

HILDEBRAND

SELECÃO

Previously, it was thought that each of an animal's features is controlled by a different gene and was independently made perfect by natural **selection**. pag7

Thus, it is usually stated or implied that adaptive traits are structural or behavioral features that contribute to survival of the species through natural **selection**. pag7

The same **selection** process may produce different features in different populations, as on adjoining islands, and there may be no **selection** pressure, as for a vestigial organ. pag7

The cornerstones of Darwin's theory of organic evolution are variation, competition, differential reproduction, and natural **selection**. He recognized that for any feature that is heritable (structure, physiological response, behavior), variation exists in populations.
pag12

Finally, Darwin knew that in just a few generations, animal and plant breeders could artificially select for wanted variants and produce strikingly dissimilar descendants from a common ancestor (e.g., Great Dane and Chihuahua). He was fascinated by artificial **selection** and saw it as so integral to his thesis that he devoted the first chapter of *The Origin* to examples. He reasoned that in nature, a multitude of factors must be involved in selecting which variants will be maintained or lost through time. Darwin termed the process by which this occurs natural **selection**. pag13

Evolutionists agree that descendant species evolved from common ancestors and that natural **selection** has had an important role in guiding the direction of structural change. However, they are now less unified in their interpretation of the process than they were in the 1930s and 1940s, when a "modern synthesis" of Darwinian theory emerged that seemed generally acceptable. pag13

The traditional belief, called phyletic gradualism, is that evolutionary change results within a lineage from the slow and continuous accumulation of those mutations that are favored by natural **selection**. This causes descendant structures, and also species, to remain well adapted to gradually changing habitats; there is no sharp demarkation between an ancestral species and its descendant.
pag13

It is most advantageous for each species to remain about as it is, so natural **selection** tends to prevent change. Large habitats do move slowly in earth history (e.g., forests advance and recede), but most of the animals move with them, remain adapted, and change relatively little. pag13

Natural **selection** therefore tends to cause the animal to become a somewhat different kind of animal. If the habitat alters as a unit, the evolutionary change is in a more or less straight line and is said to be linear. If the old habitat sub-divides into different units, different parts of the original animal population become isolated from one another and adapt independently and evolution is branching.
pag13-14

As a habitat becomes less and less satisfactory, the force of natural **selection**, that is, **selection** pressure, for the old way of life weakens. If extreme variants in the population may be better suited for life in a new habitat than old, provided that one or several new habitats are physically available and not ali

occupied by effective competitors. **Selection** pressure then becomes strong and shifts from the old lifestyle toward the new. pag14

Natural **selection** may cover "that a structure that was useful in one way before can now be useful for another purpose. Such structures are said to have preadaptation. pag14

Such gradual changes are called evolutionary trends or morphoclines and, though not universal, have been usual for large populations evolving at moderate rates. Evolutionary trends are oriented and prolonged by **selection** pressure. The characteristic continues to develop because it continues to be advantageous. pag15

First, natural **selection** makes no provision for nature's senior citizens. It improves the fitness of breeders and potential breeders, but neglects individuals that are no longer productive. pag17

kangaroo rats and jerboas now to hot, sandy deserts; golden moles and marsupial moles to life in the soil. It is the effectiveness of natural **selection** that causes basically similar animals having nearly identical functional requirements to evolve similar structural adaptations. pag18

Since those remote days, each group has gone its own way, retaining some of the common features over the ages, but altering or deleting others and adding new structures in response to differing **selection** pressures. pag27

Only a fraction of the adult forms that can be imagined have ever evolved. Formerly it was believed that this is solely because **selection** pressure eliminates trends toward forms that do not occur. pag17

They conclude that these specializations reflect **selection** early in the evolution of the crocodylian lineage for high aerobic activity and the ability to run and breathe at the same time. pag234

Olfaction contributes to the recognition of familiar surroundings by homing pigeons, the avoidance of noxious insects by chickens, the **selection** of nest-building materials by starlings, the location of pelagic food by petrels, and the finding of carrion by vultures. pag349

Through natural **selection**, organisms are not "designed" to satisfy a goal, nor is natural **selection** mere engineering. Engineers tend to design structures for a single purpose; structures of organisms often serve several purposes. pag548

Selection at the filter is more or less fixed, yet may be influenced by filtration rate, water pressure, slight alteration of pore size (e.g., by degree of crowding of gill rakers), and by rate of cleaning. How fishes clean their filters and move food into the esophagus is poorly understood. Coughing (sudden, forceful reversal of the water stream) may contribute. pag556

GENE HOX

Important genes, called homeotic or **Hox genes**, control fundamental features such as polarity along an anterior-posterior axis and, in those forms possessing them, the segmental location and nature of appendages. Surprisingly. pag73

When a **Hox gene** is activated by "upstream" genes at different stages during development, it produces proteins, which in turn selectively activate numerous structural "downstream" genes responsible for executing the precise morphology of specific body segments. pag73

For example, a mutant fly could grow a pair of legs on the head segment where its antennae should be, the embryonic cells expressing their **Hox genes** behaving as if confused as to their location along the anterior-posterior axis of the embryo. pag73

In *Drosophila*, rather than just one **Hox gene** (the proposed early metazoan condition), there are eight located in tandem along a single chromosome. Together, the eight **Hox genes** form a cluster. This in-tandem arrangement on a single chromosome is an organization found in most non-vertebrates and is thought to be the result of duplication events of the single ancestral **Hox gene**. Evidence is mounting that the **Hox genes** of vertebrates (most studied in mammals, including mouse and human) possess a structural organization and function. pag73

The vertebrate condition, in which **Hox genes** are located in four clusters on four separate chromosomes (haploid state), is thought to have arisen by two duplication events and by fission. pag73

Within each **Hox gene**, there exists a sequence of base pairs (a homeobox) that is highly conserved from one gene to the next along the in-tandem series and across chromosomes. In any given species, it is the interactions of the multiple **Hox genes** that give rise to specific morphologies; the precise mechanism is a focal point for intense research. pag73

Evolutionary morphologists are studying the effects of **Hox genes** (and of other regulatory genes not found in these clusters). The techniques available (immunolocalization, in situ hybridization) allow for detection of both when and where these genes influence development. pag73

Do **Hox genes** evolve? If your interest is piqued, see the References. pag73

In other words, for all vertebrates having paired appendages, regardless of neck length, the cervical-thoracic junction and the emergence of the brachial plexus are expressions of homologous **Hox genes**. The findings suggest that evolutionary change in axial formulas is due to changes "upstream" in genes that control the **Hox genes** themselves, rather than "downstream" in genes that they control. This concept is useful where morphological boundaries between regions have been lost, as in caecilians and snakes. However, Galis cautions that the prediction of vertebral boundaries solely on the basis of the expression of **Hox genes** is made difficult by the multiple effects of surrounding developmental processes.

pag149

It might be anticipated that the differentiation of the regions of the spine also is strongly linked to homeotic genes. To address this question, Burke and colleagues compared **Hox gene** expression and vertebral development of a fish, an amphibian, two birds, and a mammal (see References). Of particular interest was the transition between the cervical and thoracic vertebrae. pag149

New fossils, advances in methods of phylogenetic analysis, attention to developmental processes, and discovery of the regulatory effects of **Hox genes** have provided new insights, but not yet consensus. pag151

Tabin, and Kemp stress the similarities of the pectoral and pelvic appendages in all major groups, and they believe that they are serial homologs that emerged at about the same time in Paleozoic fishes and that both sets of fins are under the control of a posterior series of **Hox genes**. pag151-152

How did the vertebrate brain evolve? Until recently, we could address this question only in a most general way because we had little data upon which to construct an informed hypothesis. With an understanding of **Hox genes**, realization of the power of phylogenetic analyses, and a better understanding of development, testable hypotheses are emerging.

pag338

Recall that the role of **Hox genes** in specifying brain organization is best documented for hindbrain segmentation (Comment 5.1 and figure on p. 116). Hox duplication resulted in the genesis of neural crests and neurogenic placodes (Table 5.1), two new features fundamental to the development of the skeletal elements of a new pharyngeal pump and, as particularly stressed by Northcutt, new receptors advantageous to a more active lifestyle

pag338-339

DESENVOLVIMENTO

Some structures and patterns of organization are best understood in terms of **development** and **developmental** mechanisms.

Biological Homology and the Conservation of Process Significant advances in our understanding of early **development** and molecular genetics have given rise to another view of homology.

Animals as different as a fruitfly and a bird, for example, possess clusters of virtually identical genes that dictate the early **development** of paired appendages.

The gradual **development** of tusks, antlers, and unusual beaks are examples. Other trends involve increase in specialization of parts, such as the formation of elaborate enamel patterns in the grinding teeth of horses. Pag 15

All chordates (as the name implies) have a notochord during early **development**. Cephalochordates and many vertebrates (but not urochordates) retain the notochord, or remnants thereof, as adults. Pag.24

It seems that some groups evolved from the larva, not the adult, of the preceding group. Sexual **development** is accelerated and the **development** of other organ systems is arrested, so the nonreproductive larval stage of the ancestor becomes the reproductive adult stage of the descendant. Pag 28

Before a description of **development**, however, it is desirable to review the basis for the long, important, and close relationship between embryology and morphology. Pag. 67

It is evident to the discerning student that the **development** of the individual from egg to adult (ontogeny) and the ancestry of the species (phylogeny) are closely related. Following the publication in 1859 of Darwin's *The Origin of Species*, the nature of the relationship became the subject of observation and speculation. Pág 67

Emphasis has shifted from product (the concern of de Beer) to process. Reciprocity is sought between the genetics of **development** and the mechanisms of morphogenesis. In some instances evolutionary theory is tested by direct experiment. Pag 70

There are several possibilities: (1) of the **development** of the somatic features (but not of the reproductive organs) of the descendant is accelerated, the result is recapitulation in the classical sense; that is, adult characters of the ancestor come to be juvenile characters of the descendant. Pág 70

If **development** is accelerated only for the reproductive system (a process called progenesis) or is retarded for one or more somatic features (a process called neoteny), the resulting condition is pedomorphosis (= child + form), or the retention of ancestral juvenile characters by adult descendants. pag 70

The **developmental** process puts constraints on adult form. Evolutionary change results only from alterations in **development**, and **developmental** mechanisms are both stable over time and channelized. Pags 70-71

Entry of the sperm into the egg restores the diploid number of chromosomes, and activates the egg both to become refractory to the entry of additional sperm and to initiate **development** of the embryo. pag.72

The **development** of a multi cellular organism requires that gene expression be regulated in each cell in the correct order and at the correct time pag 73

When a Hox gene is activated by "upstream" genes at different stages during **development**, it produces proteins, which in turn selectively activate numerous structural "downstream" genes responsible for executing the precise morphology of specific body segments. Pág 73

The techniques available (immunolocalization, in situ hybridization) allow for detection of both when and where these genes influence **development**. Pág 73

Long-standing questions about the origins and evolution of paired fins, branchial arches, vertebral differentiation, and brain **development** (see Figure 8.2, p. 116) are being reexamined. Pag 73

Consequently, **development** is slower there, blastomeres near the vegetal pole are larger than those near the animal pole, the blastocoel is displaced into the animal hemisphere, and cleavage is said to be unequal. Pág 73

Neural crests and these ectodermal placodes are alike in their origin from ectoderm. Their approximate time of **development**, their uniqueness to vertebrates, and their conservation among the classes. pag 78

Development and Structure of Hard Tissues The scales and non glandular integumentary appendages of fishes are largely of dermal origin, whereas those of tetrapods are largely of epidermal origin. The most complex derivatives of the integument of fishes are hard scales and denticles of various kinds. Pag 86.

There is, therefore, a basic similarity in the mechanism of **development** of teeth and all skin derivatives regardless of ultimate hardness and principal germ layer of origin pag 86

Only mammals have mammary glands, which secrete the milk to suckle the young. The first indication of the **development** of the glands is the appearance in the embryo of a pair of epidermal ridges, the milk lines, which extend lengthwise from the chest to the inguinal region. Pág 98

Horns and Antlers The various types of tetrapod horns and antlers serve for recognition, display, ritual fighting, and defense. They may be carried by males only or by both sexes, but sexual dimorphism is nearly universal, reflecting the hormonal control of their **development**. Pág 100

Attempts have also been made to construct a phylogeny of other integumentary structures, but the task is made difficult by multiple origins, evolutionary plasticity, parallelism, and convergence. Considerations of paleontology, **development**, innervation, and function have been of little help. Some morphologists believe that the various mucous glands of the aquatic vertebrates probably originated at various times, evolved along separate lines, and are not homologs of any glands of reptiles, birds, and mammals. Pág 101

The vertebrae of modern amphibians remain an enigma. The pattern of **development** gives no useful information about the homologies of vertebral elements. Their centra (which always consist of a single unit) are probably broadly homologous to each other and to those of other tetrapods. Pág 147

What determines the **development** of morphologically distinct vertebrae? How might this vertebral differentiation evolve? Pág 149

genes. To address this question, Burke and colleagues compared Hox gene expression and vertebral **development** of a fish, an amphibian, two birds, and a mammal (see References). Of particular interest was the transition between the cervical and thoracic vertebrae. Pág. 149

The skeletal patterns of the various tetrapod feet are derived from the primitive pattern by deletions and fusions that can usually be verified by embryonic **development**. Pág. 159

Shubin and Alberch (see References) used experimental and comparative embryology to clarify the **development** of limbs in a way that is consistent with the comparative anatomy of fossil and living lobe-finned fishes and tetrapods. Pág. 160

Facial muscles reach their highest **development** in human beings. The ancestral innervation by the seventh cranial nerve is retained. Pág. 191

Evolution of Lungs from Amphibians to Mammals Typical lungs of tetrapods differ from fish lungs in being paired, in having a higher surface-to-volume ratio, in joining the ventral side of the gut tube by a duct termed the trachea, in receiving blood of low oxygen content in vessels that are related in **development** to the sixth aortic arches, and in returning oxygenated blood directly to the heart without prior mixing with blood from other organs. Pág 229

Brainerd, Ditelberg, and Bramble studied lung ventilation in the urodele *Necturus* by cinevideography, measurement of pressure in buccal and pleuroperitoneal cavities, and electromyography of hypaxial musculature. Pending further comparative data about lung **development** and ventilatory motor patterns, they could not choose among hypotheses for the origin of mixed-air and unmixed-air mechanisms. Pág. 234

The pattern of circulation changes in **development** much as it must have changed in evolution, and it is fascinating to observe the sometimes marked changes in progress because the system functions continuously throughout. Pág. 240

In birds and mammals this problem is resolved by the **development** of a system of coronary vessels and fully separated ventricles, and their myocardium is not spongy. pag. 244

The organ varies from small (some rodents) to medium (carnivores, primates) to large (some ungulates), its **development** being inversely proportional to the excretory efficiency of the placenta. Pág. 275

In summary, trends in the evolution of the vertebrate kidney include the loss of nephrostomes and external glomeruli, the occurrence of more numerous and non segmental nephrons, and **development** from a progressively more posterior, and ultimately shorter part of the nephrotome. Pág. 275

All other vertebrates have two pairs of urogenital ducts that remain identical in the two sexes to the end of the indifferent stage of **development** and then are modified according to sex and taxon. Pág 289

Some mammals in at least five orders postpone **development** instead by delayed implantation of the blastocyst (corresponding to the blastula of other vertebrates). These mechanisms time birth with seasonal food, dormancy, or return to breeding grounds. Pág 296

The olivary nuclei arise from the alar plates, yet during **development** migrate down to the ventrolateral wall of the medulla. This complex of nuclei is present in all vertebrates. It is best developed in the most active representatives mammals, birds, and some fishes. Pág. 325

With an understanding of Hox genes, realization of the power of phylogenetic analyses, and a better understanding of **development**, testable hypotheses are emerging. Two recent reviews of the evolution of the vertebrate brain from that of cephalochordates (amphioxus) are in general agreement regarding the major events (see Butler and Northcutt in References). Pág. 338

There are structural as well as physiological and behavioral adaptations for living at high elevations, deep in the sea, and in caves. Some vertebrates are modified for walking on snow, mud, or floating vegetation. Adaptations for prenatal **development** and parturition include placental morphology, length and structure of the umbilical cord, and shape of the uterine cavity in relation to the shape, flexibility, and densities of different parts of the fetus. pág. 384

RESTRICÃO

Developmental **Constraints** on Form The developmental process puts **constraints** on adult form. Evolutionary change results only from alterations in development, and developmental mechanisms are both stable over time and channelized. pag70-71

Their investigation relates to emerging principles of broad application, including Hox genes, biological versus phylogenetic homology (see p. 4), developmental **constraints** (see p. 70, and the Wake and Roth book in References), and the interpretation of character-states in cladistic analysis (see p. 30). pag96

Morphological Correlates to Energy Conservation Investigators are sorting out the morphological and behavioral correlates of the costs of locomotion. For example, energy **constraints** impact on muscle architecture. pag551

POUGH

SELEÇÃO

Um século mais tarde, Charles Darwin e Alfred Russell Wallace explicaram a diversidade de plantas e animais como um produto da **seleção natural** e evolução. pag (01)

As idéias atuais sobre evolução, enfatizam a **seleção natural** que atua ao nível dos indivíduos como o mecanismo predominante na produção de mudanças ao longo do tempo.
pag (02)

Já que um macho utiliza os dentes para segurar, ou para estimular, a fêmea antes e durante a cópula, a **seleção sexual** pode entrar em ação. pag (115)

Uma última hipótese envolve a **seleção** específica. A produção de ovos e de larvas flutuantes, levados pela corrente, aumenta as chances de colonização de todas as manchas de habitats adultos em uma grande área. pag (143)

A história de vida de Liophiidae ceratióides dramatiza como a **seleção** adapta um vertebrado a seu habitat. pag (146)

Talvez, certos Sarcopterygii do Devoniano possuíssem nadadeiras que os permitiam rastejar de poços secos, passando pela terra e chegando a locais ainda com água. Poderiam milhões de anos de **seleção** sobre estes peixes, mais capazes de evitar a morte encontrando águas permanentes, produzir uma linhagem que apresentasse o aumento da habilidade na superfície? pag (202)

Essas tendências a maior dimorfismo sexual, exibições mais diversificadas e envolvimento mais ativo da fêmea na corte podem refletir a **seleção** sexual pelas fêmeas dentro dos gmos derivados. pag (239)

Esse tipo de **seleção** pelas fêmeas produziria uma população de machos, todos se exibindo vigorosamente, e aqueles que incluíssem novos componentes a corte, seriam mais atraentes às fêmeas do que seus rivais. pag (239)

A teoria da história de vida prediz que a **seleção** agiria no sentido de encurtar os períodos da vida em que uma espécie é mais vulnerável à predação; a velocidade do clímax metamórfico talvez seja uma manifestação desse fenômeno. pag (250)

Em outras palavras, a **seleção** para taxas metabólicas aumentadas durante atividade também leva a taxas de descanso aumentadas, e por fim taxas de descanso produziram calor suficiente para a termoregulação endotérmica. pag.(285)

Por outro lado, qual é o nível no qual a hipótese de capacidade aeróbia propõe que a **seleção** em formas incipiente mente endotérmicas teriam agido, assim a dificuldade em encontrar a relação entre as taxas metabólicas de atividade e descanso em um experimento poderiam falsear a hipótese. pag (286)

Com a **seleção** agindo em dezenas de milhões de anos, uma pequena ligação hereditária é tudo o que se precisa para a hipótese da capacidade aeróbia funcionar, e essa ligação pode ser muito

pouco para demonstrar em um experimento de laboratório com animais que já são ectotermos ou endotermos especializados. pag (286)

Ela sugere que se a termoregulação parental acelera o crescimento dos embriões e juvenis, a **seleção** pode ter agido primeiro para produzir endotermia durante o desenvolvimento em brionário (p. ex., enquanto os pais cuidam de seus ovos) e subsequentemente prolongar a endotermia para incluir o período enquanto os pais estão cuidando dos filhotes no ninho. pag (286)

Seleção de temperatura por girinos. Girinos de *Rana boylei* mudam de posição em uma poça de água em resposta a mudanças de temperatura durante o dia. pag (373)

Por outro lado, dado que a linhagem dos dromeossauros consistia de predadores terrestres, bípedes e cursores, é plausível invocar pressões de seleção arborícolas para a evolução do vôo nas aves? pag (422-423)

Os machos têm cores mais brilhantes do que as fêmeas e penas modificadas como resultado da **seleção** sexual. pag.(468)

À medida que aumenta a competição entre os machos por parceiras, a variação no sucesso reprodutivo dos machos aumenta individualmente e a **seleção** sexual tem tendência a tornar-se mais intensa. pag.(469)

Apesar de sua relativa raridade as espécies de aves, espécies poligâmicas de aves têm sido bastante estudadas, porque estes sistemas de acasalamento pouco usuais podem revelar muito acerca dos mecanismos de evolução e **seleção** sexual. pag (469)

A construção do ninho vai desde quase nada mais do que o trabalho de simples **seleção** de um galho, o qual apenas equilibra o ovo, aos ninhos comunitários de múltiplas câmaras usados por várias gerações. pag (472)

Embora os mamíferos possuam uma acuidade maior de audição do que os demais tetrápodes, e uma série de ossos parece amplificar a força da vibração até a orelha interna, a anatomia da orelha média dos mamíferos é mais um acidente evolutivo do que o resultado da **seleção** em favor de um aumento da capacidade auditiva. pag (530)

Portanto, um ruminante pode ser mais limitado quanto à sua **seleção** por espécies vegetais, enquanto um fermentador intestinal deve encontrar todos os aminoácidos essenciais em uma variedade maior de plantas. pag.(567)

Pernas mais longas teriam dado, aos carnívoros, um pouco mais de velocidade para perseguir os herbívoros, resultando na **seleção** de ungulados com pernas mais longas, para um escape mais rápido. pag (571)

Tal relação dentre os indivíduos provoca situações nas quais a **seleção** de parentesco pode ser um fator determinante do comportamento social dos búfalos africanos. pag.(616)

Este comportamento altruísta provavelmente representa a **seleção** parental, pois a estabilidade das fêmeas nos grupos de búfalos resulta em relações genéticas entre os indivíduos. pag.(616)

O comportamento altruísta, desse tipo, está geralmente associado à **seleção** parental, mas os indivíduos em grupos de antílopes, com dietas do tipo II, não são muito aparentados e, também, não demonstram outros tipos de comportamento altruísta, tais como a defesa dos mais jovens. pag (617)

Ligações de parentesco entre as fêmeas e a **seleção** de parentesco têm papéis importantes sobre os comportamentos das fêmeas em sistemas sem transferência das mesmas, pois as fêmeas de um grupo são aparentadas umas às outras pag (624)

Em outras palavras, um proto-hominídeo, ou um hominídeo primitivo, deve ter andado de forma bípede, inicialmente, de uma forma não eficiente, antes que a **seleção** pudesse agir sobre o esquelet pag.(652)

A fase de vida pós-reprodutiva expandida nos humanos é muito maior que a dos outros símios, mas a **seleção natural** não pode atuar diretamente nos caracteres que ocorrem nos indivíduos na fase pós reprodutiva pag.(655)

Pode ser que a presença de uma avó que auxilia suas filhas a criar seus jovens gerou a **seleção** para ampliar a fase pós-reprodutiva dos humanos. pag (655)

Apenas espécies que tenham sido avaliadas podem ser incluídas nessa categoria, e a **seleção** de uma espécie para ser avaliada indica que pode estar em risco; deste modo, a escolha entre Deficiente de Dados e Ameaçada é difícil. pag.(667)

Essa **seleção** causou um decréscimo de mais de 20 por cento na massa corpórea e comprimento do como dos machos de *Ovis ca nadensis* desde o início de 1970.

EVO-DEVO

Um a união da biologia evolutiva com nosso crescente e rápido conhecimento dos mecanismos genéticos, que controlam o crescimento e desenvolvimento, deu origem a uma nova especialidade biológica - biologia do desenvolvimento evolutivo - que é conhecida pela abreviatura em inglês, **Evo-Devo**. A evolução das penas tem sido esclarecida pelos estudos **Evo-Devo**, das ações de dois genes que são cruciais para o desenvolvimento dos membros dos vertebrados: Um gene chamado "sonic hedgehog" que produz uma proteína que induz a proliferação das células; e o gene "bone morpho genetic protein 2" que regula a proliferação celular e promove a diferenciação celular. Esses dois genes estão envolvidos no desenvolvimento das penas, e a ativação e desativação dos mesmo controla a duração e o padrão de desenvolvimento dessas estruturas (Prum 1999). Uma perspectiva **Evo-Devo** baseada na ação dos genes durante a evolução das penas, pode ser comparada com o crescente corpo de informação sobre a ocorrência de penas nos dinossauros fósseis (Figura17-5). pag444

Os fósseis não revelam todos os detalhes dos diversos passos da evolução das penas, que são previstas pelo modelo **Evo-Devo**, mais as duas propostas mostram um nível substancial de concordância. Fósseis de *Sinosauropteryx* são rodeados por traços que muitos paleontólogos interpretam como simples filamentos, correspondentes ao estágio 1 do modelo **Evo-Devo**, e *Caudipteryx* tem penas com vexilo sobre suas asas e caudas e tufo de barbas sobre o corpo.

Archaeopteryx é o primeiro registro de vexilos assimétricos, e esse tipo de pena também é encontrado em formas posteriores. pag444

DESENVOLVIMENTO

Dois grupos principais de vertebrados se distinguem no que se refere a uma inovação do **desenvolvimento** embrionário, o aparecimento de três membranas formadas por tecidos a partir do embrião (veja Capítulo 9). pag 3

A maneira pela qual o celoma se forma durante o **desenvolvimento** também difere entre protostômios e deuterostômios. pag 18

Os genes Hox não codificam características específicas diretamente: eles regulam a expressão e a hierarquia de outros genes que controlam o formato do corpo, especialmente o processo do **desenvolvimento** ao longo do eixo da região cranial para a região caudal.
pag (22)

Estudar embriões pode mostrar como os sistemas se desenvolvem e como a forma do adulto está relacionada com os constrangimentos funcionais e históricos durante o **desenvolvimento**. pag (24)

Os cientistas modernos não aderem mais rigidamente à lei biogenética de que "a ontogenia recapitula a filogenia", proposta por embriologistas do século dezenove, tais como von Baer e Haeckel (isto é, a idéia de que o embrião passa fielmente por seus estágios evolutivos ancestrais durante seu **desenvolvimento**). pag (25)

O **desenvolvimento** dos vertebrados, a partir de uma única célula fertilizada (o zigoto) até a condição adulta, será resumida brevemente. Esta é uma informação básica importante para muitos estudos, mas um tratamento detalhado está além do escopo deste livro. pag (25)

Outras peculiaridades são encontradas na extremidade rostral expandida da cabeça dos vertebrados, que possui um complexo padrão de **desenvolvimento** e não acompanha a simples segmentação do corpo (Northcutt 1990). pag (27)

Desde o século XIX, não se tem encontrado ovos fertilizados para que se pudesse estudar o **desenvolvimento** da anatomia das feiticeiras! pag (50)

Durante essa longa jornada, essas larvas encontram águas mais frias que as larvas americanas, e deste modo crescem mais lentamente. As taxas de crescimento e **desenvolvimento** são fenômenos separados, de qualquer maneira, temperatura fria retarda mais a taxa de crescimento do que a taxa de **desenvolvimento**. pag (132)

Streisinger reconheceu o potencial impar do "zebrafish" como um modelo laboratorial para a pesquisa genética e do **desenvolvimento**. pag (151)

Diversos níveis de **desenvolvimento** das estruturas de apreensão de alimentos e de locomoção caracterizam a evolução dos Actinopterygii. As radiações destes níveis são representadas, hoje, por um pequeno número de espécies que são relitos de gmpos que gmpos antes tinham muito mais espécies: os Cladistia ("bichirs" e "reedfishes"), condrósteos (esturjões e peixe-espátula) e os Neopterígeos primitivos ("gars" e "bowfin", *Amia*). pag (155)

Entretanto, somente uma das linhagens terrestres dos tetrápodes da Era Paleozóica fez a próxima grande transição na história dos vertebrados, que foi o **desenvolvimento** de membranas embrionárias que definem os vertebrados amnióticos. (196)

Uma nova perspectiva evolutiva foi dada por estudos sobre o **desenvolvimento** embrionário (Shubin e Alberch 1986). pag (204)

Os Amniota possuem músculos maiores e mais diferenciados do que os não amniotas, e a noção de criação de espaço foi, originalmente, a explanação evolutiva preferida. Todavia, Frazzetta (1968) apontou que a razão evolutiva *inicial* para o **desenvolvimento** destes orifícios foi, de certa forma, diferente. Pág 216

Cretáceo na China, e essa evidência da ocorrência de penas tem sido suplementada com estudos sobre o crescimento e **desenvolvimento** das penas nas aves atoais (Quadro 17-1).
Pág 439

U m a união da biologia evolutiva com nosso crescente e rápido conhecimento dos mecanismos genéticos, que controlam o crescimento e **desenvolvimento**, deu origem a uma nova especialidade biológica - biologia do **desenvolvimento** evolutivo - que é conhecida pela abreviatura em inglês, Evo-Devo. Pág 440

A evolução das penas tem sido esclarecida pelos estudos, Evo-Devo, das ações de dois genes que são cruciais para o **desenvolvimento** dos membros dos vertebrados:pág 440

Esses dois genes estão envolvidos no **desenvolvimento** das penas, e a ativação e desativação do mesmo controla a duração e o padrão de **desenvolvimento** dessas estruturas (Prum 1999).Pág 440

O estágio 1 representa uma nova característica evolutiva e de **desenvolvimento** no momento em que o placode forma um tubo alongado que é o germe da pena. Pág 440

As predições Evo-Devo, baseadas nos estudos do **desenvolvimento** e crescimento das penas das aves atuais, têm uma boa correspondência com a presença de penas associadas aos fósseis de dinossauros não aves e de aves. pág 440

A bolsa escrotal, provavelmente, evoluiu de maneira convergente nos marsupiais e nos eutérios, pois o controle de seu **desenvolvimento** é diferente nos dois grupos
pág 555

A maioria dos eutérios apresenta um útero bipartido em parte, ou por toda a sua extensão; o que pode ocorrer com os humanos como uma anormalidade no **desenvolvimento** .
pág 555

Alguns eutérios (p. ex., roedores e insetívoros) nascem em um estado altamente altricial, no qual são apenas um pouco mais desenvolvidos do que os filhotes de marsupiais; outros nascem em estágios de **desenvolvimento** mais avançados, se estendendo a um estado altamente precoce (a maioria dos ungulados), no qual o filhote pode correr após algumas poucas horas de seu nascimento. pág 557

GENE HOX

Dois aspectos embrionários podem ser responsáveis por muitas das diferenças entre vertebrados e outros cordados. Um é o Complexo do **gene Hox** (genes homeobox) que caracteriza os animais. pag (22)

Os **genes Hox** não codificam características específicas diretamente: eles regulam a expressão e a hierarquia de outros genes que controlam o formato do corpo, especialmente o processo do desenvolvimento ao longo do eixo da região cranial para a região caudal. pag (22)

Medusas (e possivelmente também esponjas) têm um ou dois **genes Hox**, o ancestral comum dos protostômios e deuterostômios provavelmente tinha sete, e metazoários mais derivados tinham até treze. Entretanto, vertebrados são únicos em conseguir a duplicação do complexo **Hox** inteiro. pag.(22)

Parece que houve um evento de duplicação no início da evolução dos vertebrados: o anfioxo tem um único agrupamento **Hox**, enquanto os vertebrados sem mandíbulas viventes têm dois. pag (22)

Os caracteres que distinguem os vertebrados de outros cordados parecem estar relacionados com duas inovações embrionárias críticas: uma duplicação do complexo do **gene Hox** e o desenvolvimento do tecido da crista neural. pag (42)

Assim como a transição de Chordata não-vertebrados para vertebrados foi caracterizada por uma duplicação do complexo do **gene Hox**, a transição entre vertebrados agnatos para gnatostomados pode ter envolvido um segundo evento de duplicação (Monastersky 1996). pag (56)

Peixes de nadadeiras raiadas têm características únicas, altamente derivadas, tais como a duplicação adicional do **gene Hox**, descrito no Capítulo 2. pag (126)

genes Hox na formação dos membros dos Tetrapoda, são revisados por Shubin et al. (1997) e por Coates e Cohn (1998). pag (205)

Os **genes Hox** determinam o padrão cranio-caudal no embrião Vertebrata. pag (205)

Todos os vertebrados mandibulados possuem quatro diferentes agrupamentos de **genes Hox**, chamados de HOXA-XOXD. pag (205)

O desenvolvimento dos membros dos vertebrados envolve os **genes 5'Hox**, os quais são expressos na parte final destes quatro agrupamentos de **genes Hox**, mas as similaridades de expressão gênica entre os peixes e os tetrápodes se estendem somente à parte proximal (mais próxima ao corpo) do membro. pag (205)

Os genes expressos nos membros distais dos tetrápodes (mãos e pés) parecem ter sido, inicialmente, derivados do agrupamento **HOXA**, com uma associação posterior com o agrupamento **HOXD**. pag (205)

RESTRICÇÃO

O fator tempo é a principal **restrição** ao número de fêmeas que um macho é capaz de cortejar e o sucesso no acasalamento costuma ser o mesmo para todos os machos de um coro. pag.(239)

Acima de tudo, a permeabilidade do tegumento à água limita a maioria dos anfíbios a microhabitats onde possam controlar ganho e perda de água. Parece uma séria restrição, mas no microhabitat de quando os anfíbios utilizam a permeabilidade da pele para alcançar alto grau de independência da água existente. pag.(262)

Porque o volume de sangue no circuito pulmonar é muito menor do que o volume no circuito sistêmico, essa restrição pode limitar o fluxo de sangue ao corpo. pag.(278)

Anexo 13 – Normas para submissão de trabalhos ao periódico científico: Ciência e Educação

Diretrizes para Autores

Ciência & Educação publica artigos científicos e de revisões de literatura resultantes de pesquisas empíricas ou teóricas originais sobre temas relacionados à Educação Científica (Ciências, Física, Química, Biologia, Geociências, Educação Ambiental, Matemática e áreas afins) incluindo críticas, defesas e comentários sobre artigos publicados na própria revista.

APRESENTAÇÃO DOS TRABALHOS

Ciência & Educação aceita colaborações em português, espanhol e inglês. Os originais devem ser enviados com texto digitado em Word for Windows ou softwares compatíveis, fonte Times New Roman, corpo 12, espaço simples, com até 15 laudas. O tamanho do papel é A4 e as margens devem ser configuradas: 3 cm para as margens superior e esquerda e 2 cm para as margens inferior e direita.

ARTIGO ORIGINAL

Todos os originais submetidos à publicação devem conter resumo em língua vernácula e em inglês (abstract), bem como até cinco palavras-chave alusivas à temática do trabalho, em português ou espanhol e inglês.

Os padrões de referências e de citações seguem as normas mais atualizadas da Associação Brasileira de Normas Técnicas (ABNT), NBR6023 e NBR10520, respectivamente.

Na *folha de rosto* devem constar o título do trabalho (em português ou espanhol e inglês) e afiliação completa de todos os autores na seguinte ordem: **última formação** (graduado em..., graduando em... especialista em..., mestre em..., doutor em..., mestrando em..., doutorando em...), **função** (docente, pesquisador, coordenador, diretor...), **departamento** ou **unidade** (por extenso), **universidade** (sigla). **Cidade, estado, e-mail** e endereço do primeiro autor, para correspondência.

Na *primeira página do texto* devem constar o título completo do artigo em português ou espanhol e inglês, resumo em português ou espanhol e abstract, com até 150 palavras. Também devem ser atribuídas até cinco palavras-chave em português e em inglês (key words), separadas por ponto final. Esses descritores (palavras-chave/key words) devem refletir da melhor maneira possível o conteúdo abordado no artigo, de forma a facilitar a pesquisa temática dos usuários.

TABELAS

Tabelas devem ser representadas segundo as normas de apresentação tabular do Instituto Brasileiro de Geografia e Estatística (IBGE, 1993). A identificação da tabela deve figurar na parte superior da mesma, em algarismo arábico, precedido da palavra tabela, seguida pelo título, item obrigatório, todos em fonte menor do que a do texto. Toda tabela deve citar a fonte, inscrita a partir da primeira linha de seu rodapé, para identificar o(s) responsável(is) pelos dados numéricos. A identificação deste(s) deve ser precedida da palavra Fonte ou Fontes.

Toda tabela deve ter cabeçalho para indicar o conteúdo das colunas. A moldura de uma tabela **não** deve ter traços verticais que a delimitem à esquerda e à direita. Recomenda-se que uma tabela seja apresentada em uma única página e que tenha uniformidade gráfica nos corpos e tipos de letras e números, no uso de maiúsculas e minúsculas e no uso de sinais gráficos.

ILUSTRAÇÕES

Ilustrações de quaisquer tipos (desenhos, fotos, esquemas, fluxogramas, gráficos, mapas, organogramas, plantas, quadros etc.) devem ter extensão .jpeg, com resolução mínima de 400 dpi. Quando se tratar de gráficos e imagens coloridas, os autores devem enviar gráficos e imagens em versão colorida e em versão preto e branco ou tons de cinza. A versão on-line disponibilizará a versão colorida.

A ilustração deve ainda ser inserida o mais próxima possível do texto a que se refere. A identificação é em algarismo arábico, seguida do título e/ou legenda (parte inferior, em fonte menor).

NOTAS DE RODAPÉ

Numeradas em algarismos arábicos, devem ser sucintas e usadas somente quando estritamente necessário. Além disso, devem estar em fonte menor e alinhadas à esquerda, no final da página.

TRANSCRIÇÕES

Devem ser colocadas entre aspas e em itálico (por exemplo: transcrição de entrevista, de discurso etc.).

CITAÇÕES

As chamadas de citações por sobrenome de autor e data devem ser em letras maiúsculas e minúsculas e, quando entre parêntesis, devem ser em letras maiúsculas. Devem ser citados até três autores, com sobrenomes separados por ponto e vírgula. Para mais de três autores, usar o sobrenome do primeiro e a palavra et al.

1. Citações diretas ou literais no texto: devem subordinar-se à forma: (sobrenome de autor, data, página). Com até três linhas, as citações devem ficar entre aspas e **sem itálico**. Com mais de três linhas, as citações devem seguir o seguinte padrão: recuo de 4 cm na margem, fonte menor, sem aspas e **sem itálico**.

2. Citações indiretas: quando o autor for citado no texto, colocar sobrenome do autor e ano (entre parêntesis).

Exemplos:

- Seu caráter interdisciplinar compreende "[...] uma área de estudos onde a preocupação maior é tratar a ciência e a tecnologia, tendo em vista suas relações, conseqüências e respostas sociais" (BAZZO; COLOMBO, 2001, p. 93).
- Na mesma perspectiva, Peixoto e Marcondes (2003) discutem visões equivocadas da ciência presentes nas interpretações de alunos inscritos em um programa especial de formação de professores de química para o Ensino Médio.

3. Citações de diversos documentos de um mesmo autor publicados no mesmo ano são distinguidas pelo acréscimo de letras minúsculas, em ordem alfabética, após a data e sem spacejamento.

- Reside (1927a)
- Reside (1927b)

4. Todos os autores citados devem constar das referências listadas no final do texto, em ordem alfabética, segundo as normas.

REFERÊNCIAS

Livro

- SILVA, F. **Como estabelecer os parâmetros da globalização**. 2. ed. São Paulo: Macuco, 1999.
- MINAYO, M. C. S. **O desafio de conhecimento**: pesquisa qualitativa em saúde. 7. ed. São Paulo; Rio de Janeiro: Hucitec-Abrasco, 2000.

Capítulo de livro

Regra 1: Autor do livro igual ao autor do capítulo

- SANTOS, J. R. dos. Avaliação econômica de empresas. In: _____. **Técnicas de análise financeira**. 6. ed. São Paulo: Macuco, 2001. p. 58-88. (páginas inicial e final do capítulo são obrigatórias)

Regra 2: Autor do livro diferente do autor do capítulo

- ROSA, C. Solução para a desigualdade. In: SILVA, F. (Org.). **Como estabelecer os parâmetros da globalização**. 2. ed. São Paulo: Macuco, 1999. p. 2-15. (páginas inicial e final do capítulo são obrigatórias)

Regra 3: Quando o autor for uma entidade:

- BRASIL. Ministério da Educação e do Desporto. Secretaria de Educação Fundamental. **Parâmetros curriculares nacionais**: meio ambiente e saúde. 3. ed. Brasília: SEF, 2001. v. 9.

Regra 4: Quando houver mais de um autor, separá-los com ponto-e-vírgula:

- MERGULHÃO, M. C.; VASAKI, B. N. G. **Educando para a conservação da natureza**: sugestão de atividades em educação ambiental. São Paulo: EDUC, 1998.

Nota: quando existirem mais de três autores, indica-se apenas o primeiro, acrescentando-se a expressão et al. (sem itálico). Exemplo:

- SANZ, M. A. et al. **Ciencia, tecnología y sociedad**. Madrid: Noesis, 1996.

Regra 5: Séries e Coleções

- MIGLIORI, R. **Paradigmas e educação**. São Paulo: Aquariana, 1993. 20 p. (Visão do futuro, v. 1).

Regra 6: Livro em meio eletrônico

- ALVES, C. **Navio negroiro**. [S.l.]: Virtual Books, 2000. Disponível em: <<http://.....>>. Acesso em: 04 mar. 2004 (*dia, mês abreviado, ano*).

Periódico

A regra para autores segue a mesma orientação de livros.

Regra 1: Artigos de revistas

- VILLANI, A.; SANTANA, D. A. Analisando as interações dos participantes numa disciplina de física. **Ciência & Educação**, Bauru, v. 10, n. 2, p. 197-217, 2004.

Em meio eletrônico:

- RODRIGUES, R. M. G. Tarefa de casa: um dos determinantes do rendimento escolar. **Educação e Filosofia**, v. 12, n. 24, p. 227-254, jul./dez. 1998. Disponível em: <http://.....>. Acesso em: 04 mar. 2004. (*dia, mês abreviado, ano*)

Teses e Dissertações

BOZELLI, F. C. **Analogias e metáforas no ensino de física**: o discurso do professor e o discurso do aluno. 2005. 234f. Dissertação (Mestrado em Educação para a Ciência)- Faculdade de Ciências, Universidade Estadual Paulista, Bauru, 2005.

Nota: quando o trabalho for consultado on-line, mencionar o endereço eletrônico: Disponível em: <http://.....>. Acesso em: 04 mar. 2004. (*dia, mês abreviado e ano*)

Trabalho apresentado em evento

(Atas, anais, proceedings, resumos, entre outras denominações)

ZYLBERSZTAJN, A. Resolução de problemas: uma perspectiva Kuhniana. In: ENCONTRO DE PESQUISA EM ENSINO DE FÍSICA, 6., 1998, Florianópolis. **Anais...** Florianópolis: SBF, 1998. 1 CD-ROM.

Nota: quando o trabalho for consultado em material impresso colocar páginas inicial e final do mesmo. Se o evento estiver publicado em meio eletrônico, especificar a descrição física do documento (CD-ROM, disquete etc). Para consultas on-line mencionar o endereço eletrônico e a data de acesso. Disponível em: <http://.....>. Acesso em: 04 mar. 2005. (*dia, mês abreviado e ano*)

ORDENAÇÃO DAS REFERÊNCIAS

Todos os documentos citados no texto devem constar na lista de referências, que, por sua vez, deve estar ordenada de acordo com o sistema alfabético e alinhada à esquerda da página.

Referências de mesmos autores podem ser substituídas por um traço sublinear (equivalente a seis espaços) e ponto, desde que apareçam na **mesma página**.

Exemplos:

- RUBBA, P. A.; HARKNESS, W. L. Examination of preservice and in-service secondary science teachers' beliefs about science technology-society interactions. **Science Education**, v. 77, n. 4, p. 407-431, 1993.
- _____; SCHONEWEG, C.; HARKNESS, W. L. A new scoring procedure for the views on science-technology-society instrument. **International Journal of Science Education**, London, v. 18, n. 4, p. 387-400, 1996.

Obras com mesmo autor e título, mas de edições diferentes:

- FREIRE, G. **Sobrados e mucambos**: decadência do patriarcado rural no Brasil. São Paulo: Ed. Nacional, 1936. 405 p.
- _____. _____. 2. ed. São Paulo: Ed. Nacional, 1938. 410 p.

Nota: cabe ao(s) autor(es) verificar se os endereços eletrônicos (URL) citados no texto e/ou referências estão ativos.

Condições para submissão

Como parte do processo de submissão, os autores são obrigados a verificar a conformidade da submissão em relação a todos os itens listados a seguir. As submissões que não estiverem de acordo com as normas serão devolvidas aos autores.

1. A contribuição é original e inédita, e não está sendo avaliada para publicação por outra revista; não sendo o caso, justificar em "Comentários ao Editor";
2. Os arquivos para submissão estão em formato Microsoft Word versão 6.0 ou superior ou software equivalente;
3. Todos os endereços "URL" no texto (ex.: <http://pkp.sfu.ca>) estão ativos
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7. A identificação do autor foi removida da primeira página do texto, para viabilizar a avaliação por pares cega;
8. Sistema de chamada autor-data para citações e notas de rodapé, com a lista de referências no final do artigo;
9. Remoção do nome do autor em "Propriedades", na opção do menu "Arquivo" do MS Word ou software similar.

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Anexo 14 – Normas para submissão de trabalhos ao periódico científico: IENCI Investigação em Ensino de Ciências

Normas para submissão de trabalhos (IENCI/EENCI)

O artigo deve ser enviado de duas formas:

1) por meio eletrônico para ienci@if.ufrgs.br, para a IENCI, ou eenci@if.ufrgs.br, para a EENCI. O artigo deve estar no formato .doc (compatível com Winword 97/2000/XP/2003) ou em formato RTF (Rich Text Format);

2) impresso (três cópias), acompanhado de uma breve mensagem de encaminhamento.

Endereço para envio: Marco A. Moreira - Instituto de Física – UFRGS, Caixa Postal 15051, Campus do Vale, 91501-970 Porto Alegre/RS, Brasil.

A ordem de apresentação dos elementos iniciais do artigo e a formatação correspondente devem seguir o exemplo abaixo, ocupando apenas a primeira página:

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Original title translated to English

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Nome do Segundo Autor Quando Pertencente à Mesma Inst.

[emailautor2@nonono.nono.br]

Instituição a qual pertencem

Endereço da instituição

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Resumo

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Palavras-chave: Lorem ipsum; Libero; Magna tincidunt.

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Abstract

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Keywords: Lorem ipsum; Libero; Magna tincidunt.

46

- A segunda página do trabalho submetido deve ser uma cópia da primeira (em que aparece o título, resumo, abstract, etc.), porém sem dados que possam identificar o autor. A primeira página ficará com os editores e da segunda em diante, será enviada aos árbitros.
- Referências bibliográficas que permitam identificar os autores do trabalho devem ser substituídas pelo código: Autor X1....Autor Xn, onde 1 ≤ n ≤ número de citações distintas que permitem identificação.

- Tamanho da folha: A4.
- Margens esquerda, direita, superior e inferior: 2,0 cm.
 - Tabulação: 1,5 cm da margem esquerda.
 - Espaço entre linhas simples e após o parágrafo 10 pt.
- Em todo o texto: espaço entre linhas simples e após o parágrafo 10 pt (no Winword, estas opções são apresentadas no menu 'Formatar => Parágrafo').
 - Alinhamento do corpo do texto: justificado;
- Fonte: Times New Roman 12 pt, para títulos e corpo de texto, e 10 pt para notas de rodapé e citações longas recuadas;
- As notas de rodapé devem ser numeradas continuamente e em algarismos arábicos;
- Tabelas, gráficos, figuras ou imagens devem ser inseridas no lugar apropriado do texto. Não é necessário enviá-las separado;
- A legenda das tabelas deve ser posta acima das mesmas e dos gráficos, imagens, e/ou figuras, abaixo.
- No final artigo deve constar uma lista completa das referências bibliográficas citadas ao longo do texto. Esta lista deve estar em ordem alfabética e seguir o modelo apresentado na seção 'Referências bibliográficas' das presentes normas.

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47

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Livros no todo

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