Programa de Pós-graduação em Diversidade Animal
Universidade Federal da Bahia

Camilla Alves Souto

Sistemática da família Cassidulidae (Echinoidea: Cassiduloida) e considerações taxonômicas e paleobiogeográficas

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Dissertação apresentada ao Instituto de Biologia da Universidade Federal da Bahia para a obtenção do Título de Mestre em Zoologia pelo Programa de Pós-graduação em Diversidade Animal.

Orientadora: Profª Drª Carla Maria Menegola da Silva
Co-orientador: Dr. Rich Mooi

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Mestrando: Camilla Alves Souto
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De acordo com o regimento geral da UFBA e com o regimento interno deste programa de pós-graduação, foram iniciados os trabalhos da Comissão Examinadora, composta pelos professores Dra. Carla Menegola da Silva (presidente), Dra. Cynthia Lara de Castro Manso e Dra. Ângela Maria Zanata às 15 horas do dia 06 de Junho de 2012.
O mestrando fez a apresentação oral da dissertação durante 35 minutos. Após o encerramento das argüições, às 18 horas, a Comissão Examinadora pronunciou-se pela sua APROVAÇÃO, conforme parecer em anexo.
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Saraiva

Epígrafe

"If I run away,

I'll never have the strength to go very far"

Adaptado de Madonna

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Índice

Resumo

Os cassidulóides têm proporcionado grandes desafios aos taxonomistas que tentam classificá-los, provavelmente por se tratar de um grupo artificial. Estudos filogenéticos da ‘ordem’ resultaram em topologias com baixa resolução devido à falta de informação acerca de alguns táxons e sinais de exaustão de caracteres ao longo da evolução de suas famílias. Dentre elas, a família Cassiulidae é composta por cinco a seis gêneros e pouco se sabe sobre o relacionamento entre seus gêneros, visto que análises ao nível de ordem incluíram poucas espécies desta família. Neste trabalho foram realizadas análises cladísticas para propor uma hipótese de relações filogenéticas entre os gêneros da família Cassidulidae. A análise principal incluiu 16 cassidulídeos e 33 caracteres morfológicos. As análises seguintes tiveram como objetivo verificar a influência dos dados faltantes e da inclusão de táxons fósseis na topologia encontrada. Cada uma das três análises resultou em uma única árvore mais parcimoniosa, em geral, bem resolvida. As relações de parentesco foram: (*Eurhodia relicta* (demais *Eurhodia*) + ((*Australanthus* + *Cassidulus malayanus*) + (*Paralampas* (*Cassidulus* + *Rhyncholampas*)))). Tanto a quantidade de dados faltantes quanto a exclusão de espécies fósseis não afetaram negativamente a resolução da árvore. Os resultados obtidos indicaram a necessidade de estudar a taxonomia, principalmente, dos gêneros *Eurhodia*, *Cassidulus* e *Rhyncholampas* e a exclusão de *Cassidulus malayanus* e *Eurhodia relicta* dos seus respectivos gêneros. Possíveis ocorrências de processos heterocrônicos foram detectadas, a exemplo da evolução do gênero *Rhyncholampas* por peramorfose e do gênero *Paralampas* por pedomorfose. Os cassidulídeos provavelmente se originaram no Cretáceo Tardio e novidades não foram adicionadas à sua evolução. Como resultado, processos heterocrônicos devem ter desempenhado um papel importante na diversificação da família. Evidências de processos heterocrônicos obtidas a partir da análise atual foram discutidas. Finalmente, um cenário paleobiogeográfico dos cassidulídeos foi proposto, com origem Tetiana e dispersão inicial, seguida por expansão e vicariância.

Introdução geral

1. A ordem Cassiduloida

A ordem Cassiduloida A. Agassiz & Desor *sensu* Kier (1962), composta por 67 gêneros e cerca de 800 espécies fósseis e viventes, inclui os ouriços irregulares que apresentam pétalas, filódios e borrainas. Os registros mais antigos datam do Jurássico Inicial e o período de maior diversidade taxonômica foi o Eoceno (*ca.* 56 – 40 Ma), quando representaram cerca de 40% das espécies de equinóides (KIER, 1962). Subsequentemente, a ordem sofreu um forte declínio que pode ter sido resultante de diversos fatores, dentre os mais citados estão a competição com os clipeasteróides e espatangóides, o resfriamento climático decorrente da última glaciação do Fanerozóico e eventos estocásticos (KIER, 1962; SUTER, 1988; MCKINNEY & OYEN, 1989). Atualmente, a ordem restringe-se a apenas 3% da classe Echinoidea, com um total de 30 espécies viventes, a maioria considerada de incomum a muito rara (MOOI, 1990b). Seguindo a definição de Schopf (1984), Mooi (1990a) sugeriu a denominação de fósseis viventes para as espécies remanescentes, que seriam representantes pouco modificados morfologicamente de uma linhagem relativamente arcaica e com pouca representação recente.

Várias classificações já foram propostas para esta ordem (*e.g.*, DUNCAN, 1889; GREGORY, 1900; LAMBERT, 1918; HAWKINS, 1920; MORTENSEN, 1948a; KIER, 1962; KROH & SMITH, 2010), no entanto, nenhuma delas é considerada atualmente satisfatória ou, no caso das análises cladísticas, as relações de parentesco não possuem bom suporte. Historicamente, os cassidulóides têm sido considerados a "lata de lixo" dos Irregularia, por abarcar tudo o que não se encaixava nos grupos já estabelecidos. Latreille (1825) distinguiu os equinóides regulares dos irregulares, devido à migração do ânus que saiu do eixo principal do corpo[1], e, pouco mais tarde (1835 – 1889), quatro grandes ordens de equinóides irregulares foram propostas (figura 1), principalmente a partir do formato da carapaça: Holectypoida (formato globular e alto, lembrando os equinóides regulares), Spatangoida (formato cordiforme com um plastrão oral), Cassiduloida (formas diversas) e Clypeasteroida (forma

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[1] A evolução dos Irregularia passou por inúmeras modificações morfológicas voltadas para o hábito infaunal, pois viver enterrado no sedimento requer adaptações fisiológicas (*e.g.*, respiração) e comportamentais (*e.g.*, locomoção e alimentação). As principais modificações foram a especialização dos pódios ambulacrais, a redução dos espinhos e o deslocamento da boca (peristômio) para a região anterior do corpo (TELFORD & MOOI, 1996).

achatada e circular). Inicialmente, devido à posição do peristômio e ausência de uma Lanterna de Aristóteles nos adultos, os cassidulóides foram incluídos na mesma ordem dos espatangóides (DUNCAN, 1889; GREGORY, 1900), até ser considerada uma ordem plena e reconhecida por diversos autores (*e.g.*, HAWKINS, 1920; MORTENSEN, 1948a; KIER, 1962). No entanto, filogenias posteriores indicaram que cassidulóides eram mais relacionados com os clipeasteróides e que a ordem Cassiduloida era parafilética por não incluir a ordem Clypeasteroida (SMITH, 2001).

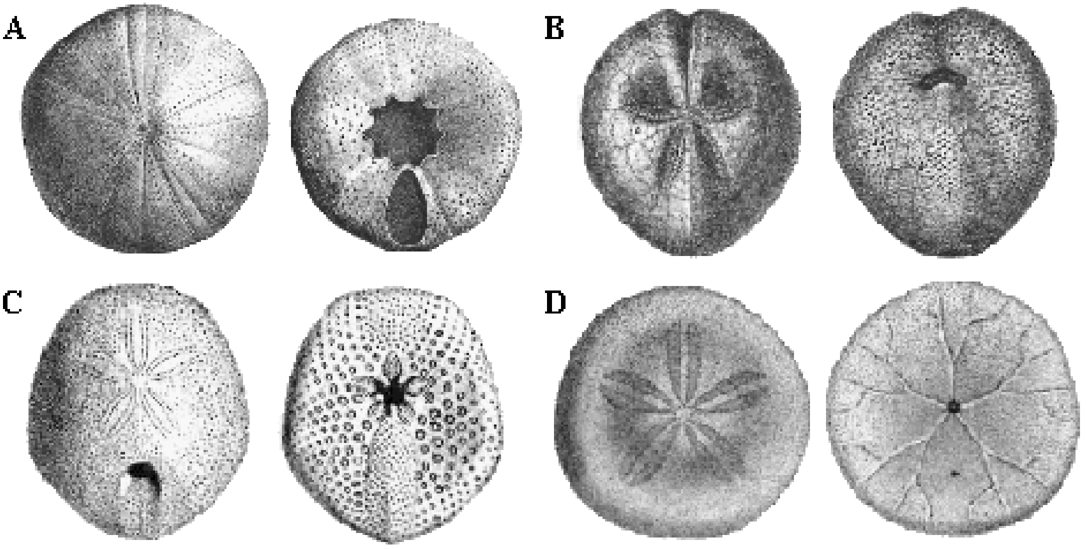

Figura 1. Representantes das quatro grandes ordens de Irregularia: A) Holectypoida, B) Spatangoida, C) Cassiduloida e D) Clypeasteroida. Atualmente, outras ordens são aceitas (*e.g.*, Holasteroida) ou foram propostas (*e.g.*, Echinoneoida). As imagens foram retiradas de Mortensen (1948a, b; 1951).

Ao contrário dos clipeasteróides, os cassidulóides formam um grupo conservador, do ponto de vista morfológico, e mostram sinais de exaustão de caracteres[2], sendo que a maior parte da sua história evolutiva envolve a modificação de caracteres em detrimento de novas aquisições (SMITH, 2001). Dentre as aquisições mais pontuadas (*e.g.*, MORTENSEN, 1948a; KIER, 1962) estão a modificação do sistema apical (de tetrabasal para monobasal), o surgimento de poros bucais e a redução do número de poros nas placas ambulacrais após as pétalas (de dois para um). Mortensen (1948a), por exemplo, utilizou a modificação do sistema apical, mesmo enfatizando que se tratava de uma classificação provavelmente artificial, para distinguir três famílias de cassidulóides: Echinobrissidae

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[2] A exaustão (ou saturação) de caracteres ocorre quando o número de estados de caracter distinguíveis é esgotado; ou seja, quando a mudança em um caracter é mais propensa à ocorrência de homoplasia do que do surgimento de uma novidade evolutiva (Wagner, 2000).

(tetrabasal), Apatopygidae (tetrabasal nos juvenis e monobasal nos adultos) e Cassidulidae (monobasal, e por esta ter ficado com muitos representantes, fez uma nova divisão e criou a família Echinolampadidae). Kier (1962), por outro lado, baseou-se em outras características, a exemplo da redução de espinhos no interambúlacro 5 criando uma área nua e o desenvolvimento de borrainas, para classificar os cassidulóides. Nesta classificação, as modificações ressaltadas por Mortensen (1948a) se transformaram em uma série de paralelismos (figura 2). Como conseqüência, estudos filogenéticos realizados com a ordem Cassiduloida têm revelado que quase todas as famílias delimitadas nas grandes revisões da ordem são parafiléticas (SUTER, 1994a, b; WILKINSON *et al.*, 1996; SAUCÈDE & NÉRAUDEAU, 2006).

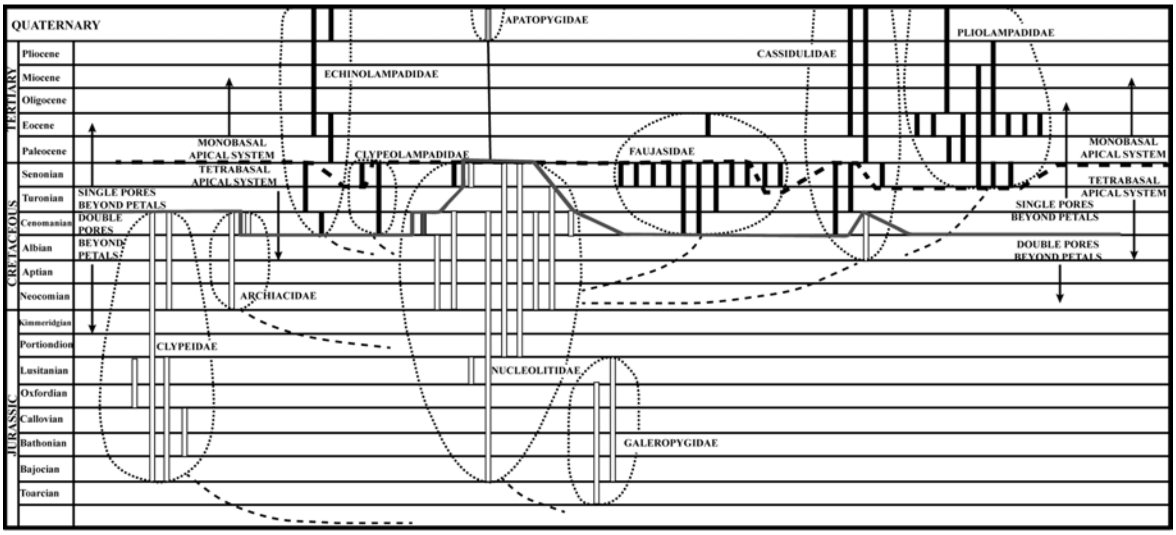

Figura 2. Evolução paralela dos cassidulóides (KIER, 1962 – Chart 1 adaptado). Cada barra representa um gênero e a sua amplitude representa o período geológico no qual registros foram encontrados. Os gêneros estão agrupados em dez famílias ligadas por linhas pontilhadas de acordo com a sua "evolução". Segundo Kier (1962), a família Apatopygidae (círculo pequeno no topo central), por exemplo, descendeu da família Nucleolitidae (círculo grande logo abaixo). A cor das barras representa mudanças evolutivas que ocorreram na ordem. Barras pretas, por exemplo, indicam os gêneros nos quais surgiram poros bucais e em que os poros após as pétalas passaram de dois para um; modificações estas que aconteceram diversas vezes na evolução da ordem, de acordo com esta representação. As linhas grossas horizontais também demonstram esse paralelismo. A linha pontilhada superior, por exemplo, indica a passagem de um sistema basal tetrabasal para monobasal.

Esses estudos, no entanto, apresentaram altas taxas de homoplasia para diversos caracteres, além de possíveis erros na codificação dos caracteres morfológicos, provavelmente resultantes de: descrições incompletas, visto que muitas delas são antigas e foram feitas quando certas estruturas não eram consideradas relevantes; desenhos inacurados, que não reproduziam a forma da carapaça e de suas estruturas com fidelidade; e da própria falta de estruturas, em decorrência de uma má preservação principalmente dos fósseis.

Após a constatação de que a ordem Cassiduloida compreendia um grupo artificial, algumas análises foram realizadas, a fim de desmembrá-la (SMITH, 1981; 2001; KROH & SMITH, 2010). A hipótese mais atual (KROH & SMITH, 2010) propôs a monofilia da ordem Cassiduloida, com a exclusão das famílias Apatopygidae e Echinolampadidae, além de diversos gêneros, que se posicionaram ao longo do cladograma, desde a origem dos Irregularia até o *stem group* da ordem Clypeasteroida (*e.g.*, *Faujasia* d'Orbigny e *Stigmatopygus* d'Orbigny). Segundo essa proposta, esta ordem deveria ser constituída apenas por duas famílias, Cassidulidae e Neolampadidae (incluindo os Pliolampadidae), datada do final do Cretáceo (Maastrichtiano) e incluindo apenas treze espécies viventes.

Os resultados encontrados por Kroh & Smith (2010) demonstraram, mais uma vez, que a ordem Cassiduloida *sensu* Kier (1962) compreendia diversos grupos não proximamente relacionados. A abundância de espécies fósseis em uma ordem cuja evolução foi marcada pela exaustão de caracteres certamente ajudou a confundir o trabalho dos taxonomistas, que produziram classificações com diversas incongruências taxonômicas. Incongruências estas já citadas por Mortensen (1948a) e Kier (1962), que ressaltaram que as famílias Cassidulidae e Pliolampadidae, por eles delimitadas, eram provavelmente artificiais.

2. A família Cassidulidae

A família Cassidulidae L. Agassiz & Desor é uma das duas famílias com representantes viventes da ordem Cassiduloida *sensu* Kroh & Smith (2010), com cinco ou seis gêneros e 40 espécies (MOOI, 1990b; SMITH & KROH, 2011). Dentre os gêneros, *Cassidulus* Lamarck, *Eurhodia* d'Archiac & Haime e *Rhyncholampas* A. Agassiz compõem mais de 90% das espécies. A família data do Cretáceo Tardio (Maastrichtiano) e atingiu o maior número de espécies no Eoceno, quando já apresentava alterações morfológicas decorrentes da ocupação de regiões infaunais mais profundas (assim como outros cassidulóides), a exemplo da redução no número de poros (de dois para um) nas placas que se seguem às pétalas, passagem de um sistema apical tetrabasal para monobasal, e o surgimento de poros bucais (KIER, 1962). De acordo com Suter (1994b), a monofilia da família é sustentada por quatro sinapomorfias: presença de um lábio sobre o periprocto, uma área nua ampla no interambúlacro oral 5, uma área nua no ambúlacro oral III, e presença de *pits* nestas áreas. No entanto, segundo Saucède & Néraudeau (2006), a única novidade evolutiva da família é a presença de *pits* na área nua do interambulacro oral 5.

Apesar de haver estudos taxonômicos robustos que incluíram a família Cassidulidae, a exemplo de Mortensen (1948a) e Kier (1962), ainda há muitas questões referentes às suas características diagnósticas e, desta forma, não se sabe ao certo o número de gêneros incluídos e suas respectivas espécies. Os únicos gêneros que foram descritos e permanecem a esta família, até o momento, são *Cassidulus* e *Rhyncholampas*. As espécies viventes de ambos estão aparentemente bem delimitadas, mas os limites entre as espécies fósseis não são bem definidos. Mesmo com fósseis relativamente bem preservados, muitas descrições são insatisfatórias e não incluem comparações com outras espécies simpátricas do gênero. Uma espécie encontrada no Eoceno Inicial da Flórida, por exemplo, é normalmente comparada apenas com espécies daquele período e Formação, como se não fosse possível que esta mesma espécie ocorresse no Eoceno da Venezuela, ou no Eoceno Tardio da Flórida. Apesar de Oyen & Portell (1996) terem afirmado que é raro uma espécie de equinóide ser encontrada em mais de uma unidade estratigráfica, é possível que a diversidade de espécies fósseis desses gêneros esteja superestimada, devido aos problemas já mencionados. Aliado a isso, não existem revisões destes gêneros e estas espécies ficaram esquecidas nos registros que contêm suas descrições originais, em sua maioria antigos.

Além das questões taxonômicas dentro de cada gênero há também a incerteza quanto à delimitação dos gêneros *Cassidulus* e *Rhyncholampas*. Devido às semelhanças existentes entre as espécies-tipos de ambos, *Cassidulus caribaearum* e *Rhyncholampas pacificus*, a segunda foi muitas vezes considerada como pertencente ao gênero *Cassidulus* (*e.g.*, MORTENSEN, 1948a; KRAU, 1954) e vice-versa (A. AGASSIZ, 1869). Kier (1962) ressaltou que estes gêneros possuem fortes afinidades, observadas por características intermediárias presentes em algumas espécies, o que também foi observado por Verrill (1867), Carter & Beisel (1987), dentre outros. De fato, em todos os estudos filogenéticos que os incluíram, estes gêneros foram considerados grupos-irmãos (SUTER, 1994a, b; WILKINSON *et al.*,

1996; SMITH, 2001; SAUCÈDE & NÉRAUDEAU, 2006). O limite entre eles, no entanto, não é estabelecido e a monofilia do gênero *Cassidulus* já foi questionada (SUTER, 1994b).

3. O uso de fósseis na reconstrução filogenética

A utilização de fósseis em estudos evolutivos tem gerado diversos debates e, em meio às "dificuldades", a principal questão é se os fósseis agregam algum valor à reconstrução filogenética. Ou seja, será que vale a pena incluir fósseis em estudos filogenéticos?

Atualmente, três fontes independentes de evidências são utilizadas para auxiliar a calibragem dos eventos cladogenéticos de uma filogenia: caracteres morfológicos e moleculares, e dados estratigráficos (BENTON, 1995). Dados morfológicos são a base da sistemática tradicional e, apesar de alguns autores acharem o seu uso dispensável (*e.g.*, SCOTLAND *et al.*, 2003), estes dados são fundamentais para os estudos evolutivos (LEE, 2004; WIENS, 2004). Dados moleculares são um dos pilares da taxonomia integrativa e vêm sendo amplamente utilizados em estudos com praticamente todos os táxons, por oferecerem muitas vantagens, principalmente quando integrados aos dados morfológicos (HILLIS *et al.*, 1996; JENNER, 2004). Dados estratigráficos, por outro lado, não estão presentes nos pensamentos da maioria dos zoólogos, são frequentemente vistos como desvantajosos e pouco utilizados para reconstruir filogenias, apesar de serem poderosos quando bem explorados (SANTINI & TYLER, 2004).

Muito dessa rejeição tem uma base metodológica, mas pode também ter algo de cultural. Tradicionalmente, as espécies fósseis são objeto de estudo dos paleontólogos e, portanto, estão alocadas apenas nos departamentos de geologia. Ainda que trabalhem com o mesmo táxon, a integração entre pesquisadores é muitas vezes nula, dificultando ao zoólogo ter conhecimento sobre os fósseis e ao paleontólogo ter conhecimentos sobre sistemática. Metodologicamente, as principais questões são relacionadas a dados faltantes (táxons e caracteres) e à confiabilidade na datação das formações geológicas, que, em certos casos, ainda deixa a desejar.

Táxons faltantes — A preservação dos organismos ao longo do período geológico é dependente de diversos fatores físicos (*e.g.*, taxa de erosão e sedimentação), químicos (*e.g.*, recristalização) e biológicos (*e.g.*, decomposição por microorganismos), além da composição do próprio organismo (proporção entre partes moles e duras). Alguns organismos são compostos basicamente por partes moles (*e.g.*, holoturóides) e outros vivem em ambientes sob pressões diversas que dificultam a fossilização (*e.g.*, ambientes marinhos com alta hidrodinâmica); tais espécies talvez nunca sejam descobertas devido à dificuldade de serem preservadas (BENTON, 1995). Além disso, existem ainda os problemas de amostragem, pois muitas localidades ainda são inacessíveis, mesmo com os equipamentos modernos. Consequentemente, o registro fóssil está longe de ser completo, apesar de existirem alguns táxons bem amostrados, em geral, aqueles compostos por muitas partes duras (*e.g.*, equinóides – MOOI [2001]; bivalves, braquiópodos e moluscos – BEHRENSMEYER *et al.* [2005]).

Dados faltantes — Considerando os fósseis conhecidos, ainda há o problema relacionado à sua qualidade, ou seja, se as suas características morfológicas foram bem preservadas. Além disso, características internas podem ser preservadas, mas são muitas vezes inacessíveis, pois requerem a destruição do espécime. Esta incapacidade de codificar um caráter morfológico em função da má preservação do fóssil talvez seja o tema mais debatido quando se trata de dados estratigráficos (*e.g.*, PATTERSON, 1981; FUEPELL, 1994; PREVOSTI & CHEMISQUY, 2010). Paterson (1981), por exemplo, mencionou que fósseis não devem ser utilizados em análises filogenéticas, pois eles provêm menos dados do que as espécies viventes. Em abordagens moleculares, fósseis também são colocados de lado, visto que a sua análise molecular é muito difícil e onerosa. Desta forma, a inclusão de fósseis resulta em uma matriz repleta de "?" que irá resultar, provavelmente, em baixa resolução filogenética.

Datação das formações geológicas – Apesar do aperfeiçoamento dos métodos de datação, ainda não podemos ter alta confiança na idade dos fósseis. As datações nunca são exatas e cada método tem um intervalo de erro. Além disso, muitas vezes os dados não são disponíveis e algumas espécies são referidas como, por exemplo, do Eoceno, que possui uma amplitude de mais de 20 milhões de anos. Dados estratigráficos são utilizados para escolher uma topologia entre árvores mais parcimoniosas (*e.g.*, SUTER, 1993) e datações errôneas podem levar a uma escolha inadequada.

Felizmente, o conhecimento sobre o registro fóssil tem aumentado consideravelmente (BENTON, 1995), e, por acreditar que a utilização de fósseis pode contribuir significativamente em estudos evolutivos, muitos pesquisadores estão discutindo todas essas questões e propondo análises que propiciem a agregação destes dados (SMITH & LITTLEWOOD, 1994; WIENS, 2003). Fósseis são essenciais para análises filogenéticas, pois eles possuem uma combinação única de caracteres plesiomórficos e apomórficos que fortalecem muitas relações de parentesco (DOYLE & DONOGHUE, 1987; GAUTHIER *et al.*, 1988). Além disso, a incompletude do registro fóssil não pode ser confundida com ausência de informação (BENTON, 1995) e, se bem analisados, alguns dados certamente os fósseis irão prover.

Para a polarização de caracteres via grupos externos, por exemplo, Huelsenbeck (1991) ressaltou que a adição de táxons fósseis próximos ao estado ancestral pode resolver uma filogenia melhor do que táxons viventes ou fósseis que viveram em um período próximo a estes. Há, no entanto, a desvantagem relacionada aos dados faltantes e, neste intuito, diversos métodos têm sido desenvolvidos para resolver esse problema (*e.g.*, WILKINSON, 1995; NORELL & WHEELER, 2003). E em muitos casos, apesar da grande quantidade de dados faltantes, muitos fósseis são informativos e valem a pena serem utilizados (DONOGHUE *et al.*, 1989; BENTON, 1995).

Índices para comparar a idade do aparecimento dos fósseis com os eventos cladogenéticos presentes em uma filogenia também têm sido propostos (*e.g.*, HUELSENBECK, 1994; BENTON, 1995; BENTON *et al.*, 2011). No entanto, Pol & Norell (2005) ressaltaram que alguns deles ignoram os erros inerentes a cada método de datação e utilizam tais datações como exatas, o que pode acarretar resultados errôneos. Mas, ainda assim, mesmo que existam os métodos moleculares para calibrar o período de divergência entre as espécies, eles requerem calibração externa que, geralmente, vem das evidências fósseis (WIENS, 2004).

Concluindo, apesar de terem consciência de todos os problemas atrelados à utilização de fósseis na reconstrução filogenética, muitos pesquisadores estão na busca de métodos que permitam a incorporação destes dados em estudos evolutivos. E não podemos esquecer que táxons e dados faltantes também são uma realidade quando trabalhamos com táxons viventes. Ainda estamos longe de conhecer toda a biodiversidade existente (MORA *et al.*, 2011) e, mesmo quando a conhecemos, muitas espécies são raras e, por isso, excluídas de análises morfológicas e moleculares (WIENS, 2004). Muitos espécimes viventes também são sujeitos à má preservação que resulta em matrizes com dados faltantes, sem falar nos dados inaplicáveis, bastante comuns em grupos muito derivados e que normalmente são tratados como "?".

4. A heterocronia e a evolução dos equinóides

A evolução dos organismos ocorre através de mecanismos que podem atuar em diferentes momentos da ontogenia e em diversos níveis biológicos (*e.g.*, gene, célula, organismo). Dois destes mecanismos, heterocronia e heterotopia, surgiram a partir das idéias de Ernst Haeckel e até hoje geram grande discordância entre os pesquisadores, principalmente quanto às suas definições e aos seus limites (MCNAMARA, 2002). Em linhas gerais, heterocronia pode ser definida como uma mudança no tempo de desenvolvimento dos organismos, que resulta em alterações de forma e tamanho (GOULD, 2000), e heterotopia é uma mudança no padrão espacial das estruturas, durante o desenvolvimento (MCNAMARA, 2002). Sendo assim, a heterocronia revela um paralelismo entre ontogenia e filogenia, já que os descendentes se parecem com os ancestrais, mas em estágios de desenvolvimento diferentes; heterotopia, por outro lado, resulta em alterações que geram dessemelhanças entre os ancestrais e seus descendentes (ZELDITCH & FINK, 1996).

McNamara & McKinney (2005) revisaram esses conceitos e adotaram a visão de que a heterocronia não deveria ser limitada apenas às modificações em forma e tamanho, mas abranger mudanças nas seqüências deste desenvolvimento, incluindo assim as taxas com que elas ocorrem. Quando há mudanças diferenciais na taxa de desenvolvimento de certa estrutura entre as espécies, as posições relativas dessas estruturas também vão mudar; sendo assim, heterocronia representa a causa das modificações e heterotopia o seu efeito (MCNAMARA, 2002).

Os equinodermatólogos, em geral, adotam este conceito e, atualmente, consideram a heterocronia como um dos mecanismos mais importantes na geração da diversidade dos equinóides (MCKINNEY, 1984; CIAMPAGLIO & D'ORAZIO, 2007). Na maioria dos casos, as mudanças que ocorrem durante a ontogenia dos equinóides regulares envolvem taxas de produção das placas, enquanto que nos irregulares elas se relacionam à taxa de crescimento de cada placa, proporcionando, por exemplo, a variedade de formas encontradas nos espatangóides (McNamara, 1988).

Heterocronia pode envolver tanto o aumento (***peramorphosis***) quanto a redução (***paedomorphosis***) do desenvolvimento alométrico, resultando em alterações morfológicas entre os ancestrais e seus descendentes. Alberch *et al.* (1979) descreveram matematicamente seis processos existentes de peramorfose (que eles chamaram de recapitulação) e pedomorfose (recapitulação reversa) (figura 3), além de dois processos que resultam apenas em alteração de tamanho, sem modificação morfológica entre ancestrais e descendentes: o **nanismo** e o **gigantismo**.

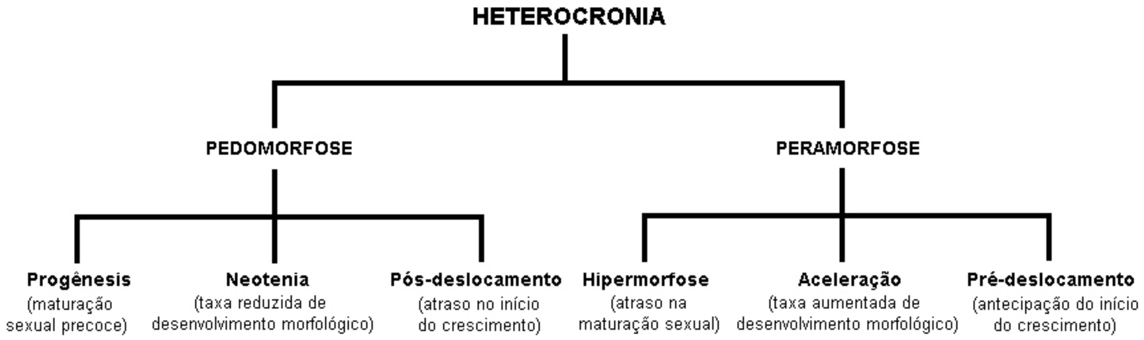

Figura 3. Classificação dos processos de heterocronia [retirado de McNamara (1986)].

Esses processos são fenômenos temporais que ocorrem ao nível específico, durante sucessivas gerações (McNamara, 1982a). Desta forma, quando os espécimes passam por um, ou diversos destes processos, se as modificações morfológicas geradas tiverem significado adaptativo favorável, haverá uma seleção preferencial pela fixação genética do morfotipo heterocrônico e uma nova espécie poderá se desenvolver (McNamara, 1986). Por viverem enterrados ou em contato direto com o fundo oceânico, uma das tendências evolutivas dos equinóides irregulares foi a adaptação morfológica a mudanças no tipo de sedimento. Em um estudo com espatangóides, por exemplo, McNamara (1985) demonstrou a ocorrência de especiação direcionada (evolução das placas dos filódios por peramorfose), produzindo adaptações voltadas para o enterramento e alimentação em sedimentos cada vez mais finos.

No entanto, o entendimento desses processos não é simples. Para identificar as formas ancestrais e indicar se os descendentes são pedomórficos ou peramórficos, há a necessidade de uma comparação com grupos-externos provenientes de períodos geológicos distintos (McNamara, 1986; Wiens, 2004), ou seja, o estudo de espécies fósseis é fundamental. Neste intuito, o estudo com equinóides é facilitado pela qualidade na preservação dos fósseis, mesmo os datados do Triássico Médio (245 Ma).

O crescimento dos equinóides é indeterminado e resultante da adição de placas coronais (carapaça, exceto placas peristomiais, do sistema apical e periprocto) a partir do sistema apical (Kier, 1974). Ao migrar no sentido aboral – oral, essas placas sofrem um crescimento periférico secundário, além de poder passar por um deslocamento meridional (McNamara, 1987). Segundo McNamara (1988), são essas mudanças heterocrônicas na taxa de produção, alometria e deslocamento das placas que controlam grande parte da diversificação dos equinóides; e as rápidas modificações passadas pelos equinóides irregulares mencionadas por Kier (1982) devem ser resultantes de processos heterocrônicos associados a pequenas mudanças genéticas, que alteraram o padrão de produção e crescimento subseqüente dessas placas, resultando na alteração da forma.

Em um grupo com sinais de exaustão de caracteres, a exemplo dos cassidulóides, esta alteração na forma pode ser crucial para explicar a origem de tamanha diversidade. Formas completamente distintas podem ser observadas, por exemplo, entre os gêneros *Conolampas* (Echinolampadidae), *Rhyncholampas* (Cassidulidae) e *Neolampas* (Neolampadidae), cada um adaptado a um tipo de ambiente, seja epifaunal, infaunal de águas rasas, ou infaunal de águas mais profundas, respectivamente. Infelizmente, o número de espécimes disponíveis para estudo normalmente é baixo e pouco se sabe sobre o hábito de vida dessas espécies.

5. Objetivos

5.1. Objetivo geral: analisar a história evolutiva da família Cassidulidae a partir de dados morfológicos de espécies fósseis e viventes.

5.2. Objetivos específicos

- Verificar a relação entre os gêneros da família Cassidulidae;

- Discutir questões taxonômicas resultantes da hipótese de relacionamento entre os táxons;
- Verificar a ocorrência de processos heterocrônicos na evolução dos cassidulídeos;
- Propor uma hipótese paleobiogeográfica para explicar a distribuição dos cassidulídeos;

CAPÍTULO I

Este capítulo contém o artigo intitulado

“Cladistic analysis of the Cassidulidae (Echinoidea: Cassiduloida) with taxonomic and paleobiogeographical considerations”

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Cladistic analysis of the Cassidulidae (Echinoidea: Cassiduloida) with taxonomic and paleobiogeographical considerations

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Abstract

A cladistic analysis of 16 cassidulids (both fossil and extant), based on 94 morphological characters states across 33 characters, was performed to propose a phylogenetic hypothesis of relationship among the cassidulid genera. Alternative analyses were also performed to determine the sensitivity of the resulting clades to missing data and exclusion of fossil taxa. Our phylogenetic analyses resulted in a single and highly resolved most-parsimonious tree and the family Cassidulidae (including *Australanthus*) was supported by five synapormophies related to tuberculation patterns in the oral region and to the periproct. The reconstructed hypothesis of genera relationship was: (*Eurhodia relicta* (remaining *Eurhodia* species) + ((*Australanthus* + *Cassidulus malayanus*) + (*Paralampas* (*Cassidulus* + *Rhyncholampas*)))). The genus *Eurhodia* (excluding *E. relicta*) was supported by one synapomorphy (one complete and one half columns in each half ambulacrum of the phyllodes), the clade (*Australanthus* + *Cassidulus malayanus*) by four synapomorphies (concerning the periproct, interambulacrum V, phyllodes and bourrelets), and the clade (*Cassidulus* + *Rhyncholampas*) by six synapomorphies (concerning the petals, 'soft tissue' characters and the periproct). Both the amount of missing data and exclusion of fossil species did not negatively affect the resolution of the tree. Taxonomic implications of these results, discussed on the basis of the current and previous studies, indicate the necessity of reviweing the genera *Cassidulus*, *Eurhodia* and *Rhyncholampas*, and the exclusion of *Cassidulus malayanus* and *Eurhodia relicta* from their respective genera. The cassidulids probably originated in the Late Cretaceous (Maastrichtian) and novelties were apparently not added to their evolution. As a result, heterochronic processes may have played a major role in diversifying the family, and evidences from the current analyses are discussed. Finally, a paleobiogeographic scenario for the temporal and geographical distribution of the cassidulids is proposed, with a Tethyan origin and initial dispersal, followed by a worldwide expansion and later vicariance. An understanding of the evolution of the cassiduloids requires extensive morphologic studies focusing on the evolution of their great novelties (e.g. apical system, bourrelets and naked zone) and on the heterochronic processes that ruled after their addition.

Key words: Cassidulidae, Systematics, evolution, morphology, Tethyan origin.

Introduction

The cassiduloids have provided great challenges to the taxonomists who tried to classify them. Mortensen (1948a) reviewed these attempts and expressed the feeling that '*(...) the subdivision of the cassiduloids into families again offers great difficulties*'. Consequently, the classifications proposed up to date were composed of artificial families, sometimes even recognized as such by the authors (e.g. Cassidulidae and Echinobrissidae [Mortensen 1948a], and Pliolampadidae [Kier 1962]). Studies testing the monophyly of the families proposed by Kier (1962) revealed that not only the Pliolampadidae, but nearly all of the other nine families were artificial (Suter 1994a, b; Saucède & Néraudeau 2006).

In view of the lack of unambiguous synapomorphies, the monophyly of the order Cassiduloida (*sensu* Kier 1962) has not been supported either (Suter 1994a, b; Smith 2001). As a result, Kroh & Smith (2010) dismembered the order and proposed a new classification by the exclusion of several genera, which would compose the stem group of the Irregularia clades, and of the families Apatopygidae and Echinolampadidae, which were elevated to ordinal status. The order Cassiduloida *sensu* Kroh & Smith (2010) is then composed by only two families (*versus* ten proposed by Kier 1962): Cassidulidae and Neolampadidae (including some pliolampadids); however, there are still no convincing synapomorphies supporting it.

Historically, the order Cassiduloida has been the 'trash can' of the irregular echinoids since the four major orders were defined. The lack of unifying characteristics would make almost any unusual irregular echinoid species a cassiduloid. As a result, the cassiduloids comprise a huge fossil record accounting for 20% of all fossil echinoids, dating back to the Early Jurassic (Kier 1974). Moreover, the evolution of the cassiduloids shows signs of character exhaustion (Wagner, 2000), since the last addition was in the Late Cretaceous (Smith 2001). This may help explain the high levels of homoplasy found by Suter (1994a, b). However, how can we explain the great diversification of the cassiduloids during the Eocene, or the evolution of the family Cassidulidae which probably originated in the K/T boundary?

McKinney (1984) and McNamara (1987, 1988) have shown the major role of heterochronic processes (*sensu* McNamara 2002) in echinoid evolution by changing the timing of development of pre-existing characters instead of evolving new ones (Ciampaglio & D'Orazio 2007). Cassidulids and neolampadids, for instance, may have evolved through peramorphosis and pedomorphosis in response to selective pressures leading to shallow or deep water environments (Philip 1963; Smith 2001; Ciampaglio & D'Orazio 2007).

Another possibility that could have negatively affected previous previous hypotheses of relationship among the cassiduloids is the lack of information on the morphology of the cassiduloids. Some of the taxonomic descriptions are incomplete, since many characteristics were not considered important by some authors or the fossils were not well preserved, others are inaccurate. Also, three major changes in the cassiduloid evolution have never been deeply studied: the evolution of the apical system, the development of bourrelets and the origin of the naked zone. All of these intrigue the understanding of the evolution of the family Cassidulidae, the 'true cassiduloids', which needs taxonomic revision and whose diversity may be underestimated.

Character and taxa selection is very important to reconstruct phylogenies (Mooi 2001; Nylander 2001; Smith 2001; Wiens 2003), but adding random characters or taxa just to inflate the dataset can result in spurious hypotheses of relationships. In view of character exhaustion and the high level of homoplasy found in previous studies, we restricted our focus to the cassidulids and performed analyses with different number of characters and taxa to try to improve the resolution of the inferred phylogeny.

Cassiduloids certainly comprise key taxa for comprehending the evolution of the Irregularia, and the role heterochrony played within this group. Because of their rich and cosmopolitan fossil record dating back to the Jurassic, cassiduloids could also be models in studies of extinction events and paleobiogeography if better understood. As our first step towards this understanding, this study aimed to 1) propose a phylogenetic hypothesis of relationship among the cassidulid genera, 2) discuss the taxonomic implications resulting from the reconstructed phylogenies; and 3) propose a paleobiogeographic scenario for the evolution of the family Cassidulidae.

Material and Methods

Ingroup Taxa

The classification of the family Cassidulidae is unstable and there is not a widely accepted work to follow. As it retains the name of the family (and of the order Cassiduloida), *Cassidulus* Lamarck is the only genus that has always been classified as a cassidulid, together with *Rhyncholampas* A. Agassiz, sometimes considered its synonym. In addition to these, over 20 other genera have already been considered a cassidulid. Considering this instability, we combined the classifications proposed by the great cassiduloid revisions and recent papers (Table 1) with results from previous phylogenetic studies (Fig. 1) to select a group of species that are most similar to *Cassidulus*.

Phylogenetic reconstructions of the cassiduloids have agreed that the family Cassidulidae is supported by three synapomorphies, all related to the naked zone running along the oral midline of the test: presence of a naked zone in the (1) interambulacrum 5 and (2) ambulacrum III, (3) both being pitted (Suter 1994a, b; Smith 2001, Saucède & Néraudeau 2006). Furthermore, all included genera have a monobasal apical system (Suter [1994a] and Saucède & Néraudeau [2006] coded *Rhynchopygus* as monobasal, instead of tetrabasal, and this may have led to the inclusion of this genus within the cassidulids). Therefore, we narrowed down the ingroup to all genera previously classified as a cassidulid which possessed a monobasal apical system and a naked zone throughout the oral midline of the test.

This approach resulted in seven genera; nevertheless, two of these (*Glossaster* Lambert and *Hypsopygaster* Bajarunas) could not be included in the analysis due to unavailability of material, poor existing descriptions of their type species, and their unstable taxonomic status. The ingroup consisted of five genera (16 species – Table 2); their type and all extant species were included in the analyses. To check the status of the genera and propose diagnostic characters, additional fossil species were included, whenever possible.

Genus *Australanthus* Bittner — This genus is currently classified within the faujasiids because of its well developed bourrelets. Mortensen (1948a) considered it as a synonym of *Procassidulus* (within the family Cassidulidae), although *Australanthus* has a monobasal apical system. Species included: *Australanthus longianus* (Gregory, 1890).

Genus *Cassidulus* Lamarck — The family Cassidulidae (and order Cassiduloida) was based on this genus. In turn, many cassidulid-like species (or even cassiduloid-like ones) were misplaced in this genus (Souto *et al.* 2011b). In this regard, we avoided including species which could not be analyzed or have a recognized doubtful taxonomic status (e.g. *Cassidulus trojanus* Cooke, 1942). Species included: *Cassidulus caribaearum* Lamarck, 1801; *Cassidulus californicus* Anderson, 1905; *Cassidulus infidus* Mortensen, 1948b; *Cassidulus malayanus* (Mortensen, 1948b); *Cassidulus mitis* Krau, 1954.

Genus *Eurhodia* d'Archiac — Kier (1962) described the family Pliolampadidae and placed *Eurhodia* within it, probably due to the presence of a longitudinal peristome. Pliolampadids, however, do not have a naked zone in the oral interambulacrum 5 and Mooi (1990b) reclassified *Eurhodia* as a cassidulid. Species included: *Eurhodia morrisi* Haime in d'Archiac & Haime, 1953; *Eurhodia australiae* (Duncan, 1877); *Eurhodia calderi* d'Archiac & Haime (1854); *Eurhodia holmesi* (Twitchell *in* Clark & Twitchell, 1915); *Eurhodia relicta* Mooi, 1990a; and *Eurhodia rugosa* (Ravenel, 1848).

Genus *Paralampas* Duncan & Sladen — This genus is known only from two fossil species from the Pakistan. Smith & Jeffery (2000) considered *Paralampas* as a subgenus of *Petalobrissus* Lambert (Nucleolitidae), which has a tetrabasal apical system. Species included: *Paralampas pileus* Duncan & Sladen, 1882.

Genus *Rhyncholampas* A. Agassiz — This genus is considered the sister taxa to *Cassidulus* and some authors have considered them as synonyms. Kier (1962) mentioned that both genera have some species with intermediate characteristics and are difficult to classify. In this regard, we chose fossil species with a clear taxonomic status, in addition to its type and extant species. Species included: *Rhyncholampas pacificus* (A. Agassiz, 1863); *Rhyncholampas gouldii* (Bouvé, 1846); *Rhyncholampas mexicanus* (Kew, 1920).

Outgroup selection

Outgroups were considered as terminal taxa to verify the relationship among cassidulid genera (Nixon & Carpenter 1993). Five species, two fossils and three extant, were chosen to compose the outgroup taxa (Table 2). Fossil taxa were chosen from a time period corresponding to the early history of the cassiduloids (*Nucleolites scutatus* Lamarck, 1816; Middle Jurassic) and of the cassidulids (*Catopygus carinatus* [Goldfuss, 1826]; Late Cretaceous). We hoped thereby to minimize homoplasy and problems of character exhaustion (Huelsenbeck 1991; Wagner 2000), common within the cassiduloids. These species are not closely related to the cassidulids and were chosen by the good quality of material available, avoiding, therefore, high quantity of missing data.

The family Neolampadidae is closely related to the cassidulids (Kroh & Smith 2010) and was represented by two extant species: *Neolampas rostellata* A. Agassiz, 1869 and *Studeria recens* (A. Agassiz, 1879). Neolampadids live in deeper waters (Mooi 1990b) and probably evolved through paedomorphosis (Philip 1963), which resulted in poorly developed (or even absent) petaloids and a reduced number of gonopores. The third extant species was *Oligopodia epigonus* (von Martens, 1865), whose taxonomic status remains unstable. Some authors classified this species within the cassidulids (Mortensen 1948a; Mooi 1990b), others considered *O. epigonus* as *incertae sedis* (Kier & Lawson 1978; Smith & Kroh 2011). Phylogenetic hypotheses have also suggested that this genus is a cassidulid (Suter 1994a, b; Saucède & Néraudeau 2006); however, in these studies *O. epigonus* was coded as having a naked zone in the oral midline. According to Smith (2001), this species should be placed within the neolampadids.

Data Collection

Data were collected from direct observation of specimens and from the literature (Appendix 1). The data matrices (Appendix 4) were constructed in Mesquite version 2.75 (Maddison & Maddison 2011). Inapplicable characters were coded as '–', while unknown character states were coded as '?'.

Abbreviations

Institutional abbreviations. **(CAS)**, California Academy of Sciences, USA; **(EqMN)**, Museu Nacional, Universidade Federal do Rio de Janeiro, Brazil; **(MCZ)**, Museum of Comparative Zoology, Harvard University, USA; **(MNHN)**, Museum National d'Histoire Naturelle, France; **(MV)**, Museum of Victoria, Australia; **(MZSP)**, Museu de Zoologia, Universidade de São Paulo, Brazil; **(NHM)**, National History Museum, England; **(SMNH)**, Swedish Museum of Natural History, Sweden; **(UCMP)**, University of California, Museum of Paleontology, USA; **(UF)**, Florida Museum of Natural History, USA; **(UFBA)**, Museu de Zoologia, Universidade Federal da Bahia, Brazil; **(UFSITAB-ECH)**, Echinoderm Collection, Universidade Federal de Sergipe, Brazil; **(USNM)**, United States National Museum, USA; **(ZMUC)**, Zoological Museum, University of Copenhagen, Denmark; **(ZUEC)**, Museu de Zoologia, Universidade Estadual de Campinas, Brazil.

Other abbreviations used. **CI** and **ci**, consistency index; **HI** and **hi**, homoplasy index; **Mya**, millions of years ago; **MPT**, most parsimonious tree; **RC** and **rc**, rescaled consistency index; **RI** and **ri**, retention index; **TL**, test length; **TNT**, Tree analysis using New Technology; **TW**, test width.

Character and Coding

The matrix comprised 33 morphological characters from test shape (3), apical system and aboral ambulacra (10), periproct (4), interambulacrum 5 and tuberculation (5), peristome and phyllodes (8), and ‘soft tissue’ (external appendages and plates on periproctal membrane – 3). Nineteen characters were binary and 14 multi-state, with a total of 94 character states (Appendices 2 and 3). Characters that could not be accurately categorized into discrete states and uninformative characters were not included.

At first, we hoped to include more characters from the pedicellariae to strengthen resolution within the extant species; however, we abandoned this idea because the pedicellariae presented a high intraspecific variability. Moreover, they were unavailable on fossil and some extant species (e.g. *E. relicta* and *S. recens*), and present high levels of homoplasy in comparison to skeletal structures (Coppard *et al.* 2012).

Phylogenetic analyses and group support estimation

Three cladistic analyses were conducted using the software TNT 1.1 (Goloboff *et al.* 2008). In all of them, a parsimony analysis was carried out using the implicit enumeration algorithm (exhaustive search), under the collapsing rule 1 (‘ambiguous’, which collapses every node with a minimum length of 0) to eliminate unsupported groups. All characters were treated as unordered and equally weighted.

Analysis 1 included all ingroup (16) and outgroup taxa (5), all 33 characters (94 states), and trees were rooted in *Nucleolites scutatus*. To verify the effect of missing data on the resulting topology, characters coding for ‘soft tissue’ structures were excluded from Analysis 2 (30 characters and 87 states); other parameters were maintained. Analysis 3 aimed to verify the *bias* toward relationships blurred by the absence of fossil taxa on the topology of the cassidulids. This analysis included only the nine extant taxa (6 ingroup and 3 outgroups), 26 characters (66 states – uninformative characters were removed), and trees were rooted in *Oligopodia epigonus*. For characters included in each analysis, illustrations of specimens and character indices see Appendices 2, 3 and 7, respectively.

Bootstrap resampling (1000 heuristic replicates; Felsenstein 1985) and absolute Bremer support (or branch support [searching sub-optimal trees of up to 15 steps longer than the shortest trees and saving a maximum of 10000 trees in each step]; Bremer 1994) were calculated to assess support for individual nodes. Character changes were optimised on the MPT tree using Winclada (Nixon 1999), under the ‘delayed transformation' (DELTRAN) option. DELTRAN optimizations favour parallelisms over reversals and as the cassiduloids evolved through a slow rate (Suter 1994a), we traced the character state evolution using this strategy.

Results

Phylogenetic hypothesis (Analysis 1)

The parsimony analysis 1 resulted in a single MPT of 90 steps (CI = 0.678, RI = 0.814, RC = 0.552, HI = 0.322). Overall, the phylogetic relationships were resolved, except for those within the genus *Rhyncholampas* (Fig. 2); relationships within the genera were, however, beyond the scope of the current analyses.

Seven synapomorphies supported the post-Maastrichtian cassiduloids; three of them were related to the last great modifications of this 'order' (i.e. reduction in the number of ambulacral pores beyond the petals, transition to a monobasal apical system, and the development of buccal pores). The others concern the reduction and modification of the phyllodes (adoral pores arranged in one column plus scattered pores between them, up to five pores in the inner column and five to seven in the outer column) and the orientation of the peristome (longitudinal).

Clade A (sister group of the cassidulids) was fairly supported (BS = 2; BP = 69), and although *O. epigonus* has many similarities with the cassidulids, this species was the sister taxon to the neolampadids (*S. recens* + *N. rostellata*). Four synapomorphies supported this clade: concerning the petals (linear shape and with pore-pairs separated by a small interporal partition), a maximum of nine plates between basicoronal plate 5 and the end of the periproct, and ophicephalous pedicellariae with numerous fine teeth on an open-U and running down on the edges of the neck. Three other synapomorphies supported the neolampadids (a knobbed oral interambulacrum 5, three gonopores, and interambulacral plates surrounding periproctal opening projecting vertically inside the test).

Monophyly of the family Cassidulidae (clade B) was highly supported (BS = 5; BP = 71) and corroborated by five synapomorphies related to tuberculation patterns in the oral region (presence of a naked zone in oral ambulacrum III and interambulacrum 5, and oral tubercles greater than adorals — all of these are derived states found in all taxa of this clade) — and to the periproct (transversal orientation and development of a slight lip).

Homoplastic characters were shared with *O. epigonus* (naked zone pitted) and *S. recens* (bourrelets projecting upwards).

A basal dichotomy split *E. relicta* from the remaining cassilulids (including the remaining species of the genus *Eurhodia*), and two homoplastic characters were shared between this species and the neolampadids + *O. epigonus* (see Appendix 5). The genus *Eurhodia* was, therefore, paraphyletic. This genus is usually recognized by its longitudinal and pentagonal peristome, both homoplastic conditions shared with *S. recens*. In addition to these, many other homoplastic characters were present within its species, showing the great diversity of forms that have been included in the genus *Eurhodia*. The remaining *Eurhodia* species, including its type species (*E. morrisi*), composed the clade C (BS = 2; BP = 24) which was supported by only one synapomorphy: one complete and one half columns in each half ambulacrum of the phyllodes. Although the relationships within this clade were resolved, bootstrap values were very low and branch support was ‘1’. The evolution of this clade showed the development of the phyllodes towards a plesiomorphic condition: an increasing number of pores, common in pre-Paleogene genera.

A transversal peristome was the only exclusive synapomorphy shared by all other cassidulids (clades D + E). Clade D was composed by *A. longianus* and *C. malayanus* showing the paraphyly of the genus *Cassidulus*. This clade was supported four synapomorphies and high values of branch support (5) and bootstrap (97%). Regarding the evolution of the cassiduloids, these species present plesiomorphic traits, such as a longitudinal periproct located in the aboral surface of the test and a great number of plates between basicoronal plate 5 and the periproct. Conversely, this clade was supported by two derived character states: up to four pores in the outer column of the phyllodes and strongly developed bourrelets, characteristic commonly found in the faujasiids.

Clade E (BS = 2; BP = 47) was supported by only one synapomorphy: developed bourrelets projecting up- and inwards. In addition, the character states ‘strong aboral lip above periproct’ and ‘interambulacral plates do not extend inside periproctal opening’ shall clearly distinguish the genera *Cassidulus* and *Rhyncholampas* from *Eurhodia*.

Paralampas pileus was the sister taxon to the clade F (*Cassidulus* + *Rhyncholampas*) and was the only cassidulid without pits in the naked zone. Clade F was supported by a high branch support (4) and bootstrap value (88%), and shared six derived states concerning the petals (petal III with a wide perradial zone and narrow row of pore-pairs, and columns of podia in posterior petals differing by more than one pore-pair), ‘soft tissue’ characters (plates on periproctal membrane arranged in two rows of large plates and few small plates, and many ossicles on tip of phyllopodia) and a strong lip above the periproct. This clade split in two other small clades: clade G (BS = 2; BP = 50) was composed by a monophyletic *Rhyncholampas* and clade H (BS = 1; BP = 48) included species of the genus *Cassidulus*. There were no exclusive synapomorphies supporting these clades. Within them, the only synapomorphies are three character states that supported *C. caribaearum* and *C. infidus* as sister taxa; all of them concerning the phyllodes (pores and phyllopodia).

Clades B (Cassidulidae), D (*A. longianus* + *C. malayanus*) and F (*Cassidulus* + *Rhyncholampas*) were supported by high values of branch support (BS = 4–5) and reasonable bootstrap percentages (BP = 71–97). Other major clades within the cassidulids did not have high support; nevertheless, they did not collapse, and in spite of the problems with character exhaustion we shall consider '2' a high value of branch support for clades C (*Eurhodia*) and (*P. pileus* + (*Rhyncholampas* + *Cassidulus*)); and '1' a good value of branch support for the remaining clades.

Character coding. Nineteen characters (57.6%) displayed a null rate of homoplasy (hi = 0), and those coding for aboral ambulacra and 'soft tissue' showed the best congruence and phylogenetic signal. Conversely, characters coding for test shape, periproct and phyllodes were usually homoplastic. Consistency index lower than 0.5 was found in less than 25% of the characters: inflation of the test, length of apical system in TL, shape of pore-pair rows in petal III, periproct orientation, pits on naked zone, and peristome shape.

Analysis 2. Effect of missing data on the topology

When soft tissue characters were removed, the analysis recovered a single MPT of 86 steps (CI = 0.663, RI = 0.805, RC, 0.534, HI = 0.337). Relationships within the cassidulids and the branch supports were unchanged (Fig. 2); bootstrap values showed only slight variations. Therefore, missing data resulted from the inclusion of 'soft tissue' characters had no negative impact in recovering the cassidulid phylogeny. In Analysis 1, these characters displayed a null rate of homoplasy (hi = 0) and were synapomorphies for clades A, F and (*C. caribaearum* + *C. infidus*). These clades, however, were also supported by at least 2–4 other synapomorphies and their support remained high.

Analysis 3. Phylogeny of the extant species

The parsimony analysis 3 (excluding fossil species) resulted in a single MPT of 45 steps (CI = 0.889, RI = 0.902, RC = 0.802, HI = 0.111). In comparison to the previous analyses, the monophyly of the cassidulids was better supported (BS = 5; BP = 96). The relationship among the three major branches remained unchanged. The node including the three Atlantic *Cassidulus* species and *R. pacificus* was supported by ten synapomorphies (BS = 6; BP = 98), and although it resulted in an unresolved trichotomy, the branches leading to *R. pacificus* and *C. caribaearum* + *C. infidus* were supported by three autapomorphies/synapomorphies each.

The two measurements of support were high for all branches (Fig. 3), and most of the characters included displayed a null rate of homoplasy (84.62%; hi = 0). The four homoplastic characters were: length of apical system in relation to the TL (ci = 0.33), shape of peristome (ci = 0.5), bourrelet projection (ci = 0.75), and maximum number of plates on interambulacrum 5b between the basicoronal plate and the end of the periproctal opening (ci = 0.8).

Taxonomic implications

The genus *Eurhodia*

***Eurhodia relicta*.** According to the results of the phylogenetic analysis performed herein and comparative morphological examination of *E. relicta*, we suggest that this species should not be included in the genus *Eurhodia*. Although the species previously included in *Eurhodia* share some characteristics, for instance, a longitudinal peristome, periproct with a slight aboral lip, and interambulacral plates extending horizontally inside the periproctal opening; they also have many characteristics that set them apart. *Eurhodia* is characterized by well developed phyllodes, composed by two columns in each half ambulacrum (the inner column can be reduced, but it is still a clear column), and many pores in the inner and outer columns; well developed petals with deeply conjugated pores; 10 to 11 plates between basicoronal plate 5 and the end of the periproct (*vs.* 8 in *E. relicta*); and a pentagonal peristome (*vs.* oval in *E. relicta*). *Eurhodia relicta* also present many similarities with *O. epigonus*, as Mooi (1990b) emphasized. These may, however, be a result of a tendency toward neoteny, fairly common within the extant cassiduloids (see further discussion below).

In addition to differences in morphology, there is a temporal incongruence between the stratigraphic range of the fossil species of *Eurhodia* (up to the Late Eocene; *ca.* 34 Mya) and of *E. relicta* (extant). In this regard, this species may belong to a new genus; however, further examination of its type specimens is necessary.

The fossil species. The assignment of *E. relicta* to *Eurhodia*, and possibly of other species, was probably due to its longitudinal peristome. This characteristic has been used to diagnose this genus, distinguishing it from *Cassidulus* and *Rhyncholampas*. The fossil species of *Eurhodia* analyzed herein were closely related and well supported; however, we cannot promptly indicate whether each branch of the cladogram should be treated as a taxonomically separate major taxon (e.g. genus or subgenus), as it has been suggested by Mortensen (1948a) and by our taxonomic examination. Given the great number of dissimilarities among them (e.g. test and petal shape, periproct orientation), which is very uncommon within closely related cassiduloids, we suggest a taxonomic revision of the genus *Eurhodia*. Furthermore, although two other genera possessing a longitudinal peristome were described (*Gisopygus* Gauthier *in* Fourtau and *Ravenelia* McCrady), they were synonymized with *Eurhodia* (see Mortensen [1948a], Kier [1962] and Roman & Strougo [1994]) based on poor descriptions and ambiguous illustrations.

Additional taxa. The genus *Glossaster* (not included in this analysis) also shares many characteristics with *Eurhodia* (e.g. test shape, petal development and periproctal traits), especially with *E. australiae* which has a longitudinal periproct, and should be included in a future phylogenetic analysis. *Eurhodia amygdala* (Desor, 1853) and *Cassidulus santolayae* Sillero *in* Santolaya & Sillero, 1994 also have longitudinal peristome and periproct, and could be closely related to *E. australiae*.

Cassidulus malayanus **and the genus** ***Australanthus***

Suter (1994a) had already suggested that *C. malayanus* could not belong to *Cassidulus*. However, the absence of additional fossil species to his analysis also showed that the genus *Cassidulus* could be monophyletic if *R. pacificus* were included in this genus. The current analysis clearly indicates that *C. malayanus* does not belong to the genus *Cassidulus*. The reversal of the position of the periproct to the aboral surface has occurred in other cassiduloids (Saucède & Néraudeau 2006) and it is of generic significance. *Australanthus longianus* and *C. malayanus* differ mainly in test shape (*A. longianus* is almost rounded) and size of pits in the naked zone (greater in *C. malayanus*). The size and depth of pits in the naked zone can vary greatly within a species (personal observation) and the difference in shape between these species may not be of generic significance. A careful taxonomic analysis with more specimens may indicate if *C. malayanus* should be placed within *Australanthus* or compose a new genus of its own.

Genera *Cassidulus* and *Rhyncholampas*

Although Analysis 3 left the relationship between *Cassidulus* and *Rhyncholampas* unresolved, Analysis 1 indicated the presence of two distinct genera. The presence of fossil species for both genera was very important to establish this relationship and to show that *R. pacificus* and the extant *Cassidulus* species are separated by at least 40 millions of years.

Because of problems with character exhaustion, it is indeed very difficult to diagnose these genera; therefore, we have to be aware of the modes of evolutionary changes occurring among them, which have resulted in slight but important modifications. Overall, *Rhyncholampas* have a larger test with more plates between the basicoronal 5 and the end of the periproct than *Cassidulus* (6 *vs.* 8), besides having more developed petals and phyllodes. In addition, specimens of *Rhyncholampas* take longer to become sexually mature (TL > 25 mm) than specimens of *Cassidulus* (TL < 15 mm). This may also be related to the ratio between apical system length and TL (greater in *Cassidulus*). In this regard, we support the separation of both genera, although a morphological analysis of those intermediate species mentioned by Kier (1962) is needed in order to allocate them to its correct genus or even to define a new genus to accommodate them.

Discussion

Huelsenbeck (1991) suggested the inclusion of species close to the ancestor in time to improve phylogenetic resolution. Considering the origin of the family Cassidulidae dating back to the Maastrichtian (Kroh & Smith 2010), we included a species *ca.* 20 My older (*C. carinatus*, Cenomanian) and another *ca.* 75 My older (*N. scutatus*, Late Jurassic). These are not so close to the ancestor time, nevertheless, considering the slow evolution of traits within the cassiduloids, just adding outgroups with plesiomorphic states was enough to resolve the phylogeny.

The phylogenetic hypothesis proposed by the current analyses does not conflict substantially with previous works (see Fig. 1), however, some differences occur. It differs from Smith (2001) in the position of *Paralampas*, considered as sister taxon to (*Cassidulus* + *Rhyncholampas*), and both agree in the placement of *O. epigonus* closer to the neolampadids. It differs from Suter (1994a) in that *E. morrisi* is closer to the clade (*Cassidulus* + *Rhyncholampas*) than *A. longianus*, and that *O. epigonus* was placed within the cassidulids. However, we do not agree with several characters states attributed to this species by Suter (1994a); for instance, the presence of an aboral lip above the periproct, a naked zone in oral interambulacrum 5 and ambulacrum III, and a pentagonal peristome. In addition, the apical system of *Rhynchopygus marmini* (L. Agassiz *in* Agassiz & Desor, 1847) was considered as monobasal, whereas it is tetrabasal. Saucède & Néraudeau (2006) modified the data matrix provided by Suter (1994a), but these inaccuracies were repeated.

Similarly to Suter (1994b), the current analysis with only extant taxa (Analysis 3) resulted in an unresolved trichotomy involving the genera *Cassidulus* and *Rhyncholampas*. Overall, both phylogenies are equivalent, but they differ in the resolution of the clade (*C. caribaearum* + *C. infidus*) provided by all the three analyses. Despite their high support, the topologies including only extant taxa did not add much to our knowledge on the relationship among the cassidulid genera, probably because of the low quantity of terminal ingroup taxa. Accordingly, the inclusion of fossil species was important to provide better resolution of phylogenetic relationships and detect taxonomic inconsistencies that have not been accessed before (e.g. involving *E. relicta* and *C. malayanus*).

Albeit the resolution of the current analysis has not been diminished by the amount of missing data, the negative effect of missing data in phylogenetic resolution usually prevents the inclusion of fossil taxa in evolutionary studies (Donohgue *et al.* 1989). As observed herein, the amount of missing data may be diluted if more characters are added (Wiens 2003; Prevosti & Chemisquy 2010); nevertheless, caution must be taken when choosing new characters. The addition of random characters with lack of phylogenetic signal may in turn increase the levels of homoplasy, especially within the cassiduloids which have not evolved novelties since the Late Cretaceous (Smith 2001). In such groups, it is more problematic to filter relevant information than to collect data (Mooi 2001; Nylander 2001).

Characters coding for aboral ambulacra usually show high level of homoplasy within the cassiduloids (e.g. Suter 1994b; Saucède & Néraudeau 2006). We probably minimized this level by measuring all involved structures, avoiding *biases* caused by ambiguous character states such as 'broad *versus* narrow', and analysing only adult specimens. The rate of development of the petals differs among the cassidulids specimens; for instance, the shape of the outer pores is usually round in juveniles of some species, getting elongated during their growth; the shape of the petals and conjugation of the pore-pairs may also change with individual growth. Homoplastic characters found by Suter (1994a, b), Saucède & Néraudeau (2006), and the current analyses were peristome shape (oval *vs.* pentagonal) and periproct orientation (longitudinal *vs.* transversal). These shifts are found throughout all cassiduloid groups and their meaning has not been studied yet.

Agreeing with Kier (1962), Saucède & Néraudeau (2006) attributed the high level of homoplasy, and consequently low phylogenetic resolution, to the parallel evolution within the cassiduloids. They also added that '*this renders cassiduloid phylogeny a difficult topic to investigate by procedures of parsimony*'. In fact, parallelism and reversals are frequent among irregular echinoids which evolved to live in similar environments (e.g. Kier 1974; Saucède *et al.* 2003); however, we disagree with their findings and believe that by understanding the evolution of the cassiduloid novelties, e.g. naked zone in oral midline and apical system modification, we can recover at least the radiation of the cassiduloid families. These great novelties are usually coded for presence *vs.* absence or tetrabasal *vs.* monobasal, respectively, and by not studying their evolution we may be missing important parts of this story. The apical system in *Apatopygus* Hawkins (tetrabasal in young and monobasal in adults), for instance, is a great example of our ignorance in this matter.

Another important issue is whether to rely or not in the literature to reconstruct the cassiduloid phylogeny. Many fossil and extant cassiduloids are difficult to find or obtain, however, excluding some taxa may be more useful than including incorrect data in the analysis. As Mortensen (1948a) pointed out '*it is a deplorable fact that in very many cases authors do not give exact information about the character of the apical system*', and this is certainly true to other characteristics as well.

Role of heterochrony in cassidulid evolution

We have proposed that examining the evolution of the major cassiduloid novelties shall be sufficient to define the major families. Recovering relationships within the Tertiary families, however, may depend on a different approach. Character exhaustion and heterochronic changes (see McNamara 1988) have resulted in a diversification of similar forms within the cassiduloids (e.g. *E. relicta* and *O. epigonus* [Mooi 1990b]), making it difficult to assign these organisms to a genus or even a family. The role heterochrony played in echinoid evolution has been fairly studied (Philip 1963; McKinney 1984; McNamara 1987; Ciampaglio & D'Orazio 2007) and its processes may be the key to understand the modifications within the cassidulids. For instance, our results suggest the occurrence of both peramorphosis [1] and pedomorphosis [2] in the evolution of the family Cassidulidae:

Size and sexual maturation. A great difference in size and timing of sexual maturation is observed within the cassidulids. An increase in size (i.e. acceleration [1]) and delayed sexual maturation (i.e. hypermorphosis [1]) were observed in the genus *Rhyncholampas,* while *Paralampas* presented a decrease in size (i.e. neoteny [2]) and precocious sexual maturation (i.e. progenesis [2]).

Differential development between columns of pore-pairs in paired petals. One of the synapomorphies that supported the clade F (*Cassidulus* + *Rhyncholampas*) was the amount of pores between the columns of pore-pairs, especially in petals I and V. This difference in number of pore-pairs was greater in *Rhyncholampas*, however, we could not find specific breaks (gaps) to distinguish between both genera. Albeit not found in other cassidulids, unequal petals can also be observed in echinolampadids (Suter 1994a), and is possibly a result of a delayed onset of growth of the inner column of pores (i.e. post-displacement [2]).

Position of the periproct. Saucède & Néraudeau (2006) detected a reversal of the periproct position towards the aboral surface in *Nucleopygus* Gauthier and attributed this shift to an early offset of migration of the periproct [2]. The same explanation could be extended for the reversal of the periproct detected in clade D (*A. longianus* + *C. malayanus*).

Number of interambulacral plates from the basicoronal 5 to the end of the periproct. As pointed out by Kier (1974), the number of plates tends to decrease with time within cassiduloids (although it may rise again latter in evolution). Overall, cassidulids had *ca.* 12 plates between basicoronal 5 and the end of the periproct, but this number decreased in some branches (e.g. *E. relicta*) and increased in others (e.g. clade D). This amount of interambulacral plates is conservative within a species and is ruled by the timing of development of the periproct since plates cannot be added after its offset of growth. Therefore, the early onset of periproct development may be explained by pre-displacement (i.e. [1]) and results in fewer plates; conversely, if its onset is delayed (i.e. post-displacement) more plates will be added in this region.

These processes are particularly important to explain the separation of the species *Cassidulus* and *Rhyncholampas*. Regarding this trait, *Cassidulus* evolved through pedomorphosis (*ca.* 10 plates) and *Rhyncholampas* through peramorphosis (*ca.* 12 plates).

Geographical distribution of the cassidulids and palaeobiogeographical considerations

Fossil evidence indicates that the family Cassidulidae has a Tethyan origin dating back to the Late Cretaceous when the oceans were connected by the Tethys and Central American seaways, providing a warm circum-equatorial current system (Bush 1997). Early cassidulids colonized the Indian subcontinent and the northern part of Africa at the time of an extensive epicontinental transgression at the Maastrichtian (Fig. 4A, B). Similarities among the fauna from North Africa, Middle East and India during the Paleocene and Eocene are also found in other marine invertebrates (Adegoke 1977; Luger 2003).

The distribution ranges of some species in the American continent during the Early Eocene, especially of *C. californicus* in California (Fig. 4C), suggest that this family undergone a rapid diversification during the beginning of the Tertiary. This expansion was favoured not only by the circum-equatorial current but also by a marine trough connecting Tethys and South Atlantic Oceans (through the Trans-Saharan seaway) (El-Nady *et al.* 2008).

Marine regression and a northward movement of the Gondwana continents resulting in the collision of Eurasia and Africa caused the interruption of this current system, and the marine fauna was then divided into Indo-Pacific (east) and Atlantic–eastern Pacific assemblages (west) (Vargas 2010). The Indo-Pacific clade (*A. longianus* + *C. malayanus*) has been isolated since then, and the remaining cassidulids were basically restricted to the west. After a long period of dispersal, vicariance probably took place.

Extant species of *Cassidulus* and *Rhyncholampas* were separated by the formation of the Isthmus of Panama (Fig. D) (*ca.* 3 Mya; Woodring 1966), and present current systems have probably isolated the extant *Cassidulus* species (e.g. Cabo Frio upwelling). Therefore, recent distribution of the cassidulids shows a high level of endemism with no overlap, indicating that the speciation mode is predominantly allopatric (Williams & Reid 2004). The closer species are *C. caribaearum* and *E. relicta*; however, they live in different water depths (1–10 m *vs.* 57–112 m, respectively; Mooi 1990b). The Indo-Pacific *C. malayanus* is the only known modern cassidulid that does not live in the American continent. This lack of geographical connection between the genus *Cassidulus* and *C. malayanus* reinforces the incorrect placement of this species. Cassidulids are, however, difficult to find, and their endemism and disjunct distribution could be due to the lack of collecting.

The biogeographical scenario accounting for the distribution of the cassidulids recovered from fossil evidence suggests an initial and rapid expansion in the Eocene followed by a secondary and slow dispersal in the Oligocene–Miocene, and by vicariance (Pliocene). Decreasing numbers in richness indicate that the family Cassidulidae is in decline, together with all cassiduloids (Kier 1974; Suter 1988), nevertheless, difficulties in collecting specimens and problems with classification may be leading us to *biased* conclusions.

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Table 1. Classification of the cassidulids according to previous studies. Genera included in only one of these studies and the reason they were not considered as ingroup in the present paper are mentioned as footnote. Abbreviations used are ‘C’, family Cassidulidae; ‘syn.’, synonym.

Genera	**Mortensen (1948a) ***	**Kier (1962) ****	**Mooi (1990b)**	**Smith & Jeffery (2000)**	**Smith & Kroh (2011)**
Australanthus	C (syn. *Procasidulus*)	Faujasiidae	–	–	Faujasiidae
Cassidulus	C	C	C	C	C
Eurhodia	C	Pliolampadidae	C	C	C
Glossaster	C (syn. *Procassidulus* ?)	C (syn. *Cassidulus*)	–	–	C
Hypsopygaster	C (syn. *Studeria*)	C	–	–	Neolampadidae
*Oligopodia****	C	–	C	–	‘gitolampadids’
Paralampas	C	C (syn. *Rhynchopygus* ?)	–	Nucleolitidae	C
Rhyncholampas	C (syn. *Cassidulus*)	C	C	C	C
*Studeria****	C	Pliolampadidae	C	–	Neolampadidae

* Mortensen (1948a) — genera with a tetrabasal apical system: *Astrolampas* Pomel, *Fauraster* Lambert & Thiery, *Lefortia* Cossman, *Procassidulus* Lambert, *Pygurostoma* Cotteau & Gauthier, *Stigmatopygus* d’Orbigny, *Vologesia* Cotteau & Gauthier. Genera lacking a complete naked zone running along the oral midline of the test: *Clypeanthus* Cotteau, *Ilarionia* Dames, *Galerolampas* Cotteau, *Gitolampas* Gauthier, *Haimea* Michelin, *Neocatopygus* Duncan & Sladen, *Oligopygus* de Loriol, *Pliolampas* Pomel, *Zuffardia* Checchia-Rispoli. Others: *Echinanthus* Leske (*nomen dubium*), *Microlampas* Cotteau (syn. *Echinolampas*), *Protolampas* Lambert (poorly known taxon).

** Kier (1962) — genera with a tetrabasal apical system: *Rhynchopygus* d’Orbigny, *Nucleopygus* L. Agassiz, *Ochetes* Pomel.

*** Absence of a naked zone.

Table 2. Taxa examined for morphological analyses of cassidulids, stratigraphic range, distribution, and museums where voucher specimens are lodged. All genera were represented by their type species, except *Studeria*. Species were listed alphabetically after the type species of each genus. Wherever type specimens were examined, this is indicated in parentheses as follows: ‘H’, holotype; ‘N’, neotype; ‘P’, paratype; ‘S’, syntype. E, M, L: Early, Middle, Late; ‘Pac.’, Pacific Ocean.

Outgroups	Stratigraphic range	Distribution	Museums
Catopygus carinatus	L Cretaceous	France and Germany	NHM, CAS
Neolampas rostellata	Recent	West Indies	CAS, MCZ, USNM
Nucleolites scutatus	M–L Jurassic	Western Europe and England	CAS, MNHN (S)
Oligopodia epigonus	Recent	Western Indian to South Pac.	MCZ, NHM, UF, USNM
Studeria recens	Recent	Indo-Pacific	MNHN
Ingroup Taxa	**Stratigraphic range**	**Distribution**	**Museum**
Australanthus longianus	L Eocene	Australia	MV, NHM (S), UCMP
Cassidulus caribaearum	Recent	West Indies	CAS, NHM, USNM
Cassidulus californicus	L Eocene	California	UCMP (N)
Cassidulus infidus	Recent	Brazil (Bahia)	SMNH (H), UFBA, UFSITAB-ECH
Cassidulus malayanus	Recent	Indonesia (Kei Island)	ZMUC (S)
Cassidulus mitis	Recent	Brazil (Southeast)	CAS, EqMN, UFBA, MZSP, ZUEC
Eurhodia morrisi	Paleocene to E Eocene	India	NHM, CAS, UCMP
Eurhodia australiae	L Eocene	Australia	UCMP
Eurhodia calderi	Eocene	Pakistan	UCMP
Eurhodia holmesi	M–L Eocene	USA (West Coast)	CAS
Eurhodia relicta	Recent	Venezuela and Suriname	USNM (H, P)
Eurhodia rugosa	M–L Eocene	USA (West Coast)	CAS, UCMP
Paralampas pileus	L Paleocene	Pakistan	UCMP
Rhyncholampas pacificus	Recent	Tropical Eastern Pac.	CAS, NHM, USNM
Rhyncholampas gouldii	M–L Oligocene	USA (West Coast)	CAS, UCMP
Rhyncholampas mexicanus	Pliocene	Baja California	UCMP (H)

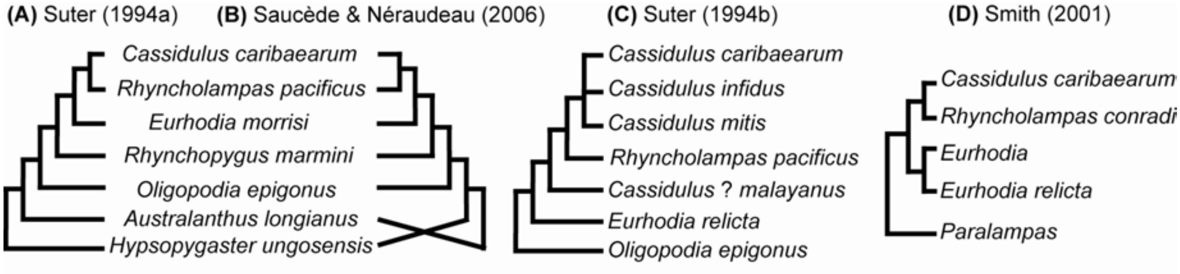


Figure 1. Hypotheses of phylogenetic relationship among cassidulids, based on morphological characters. (A) Suter (1994a), (B) Saucéde & Néraudeau (2006), (C) Suter (1994b), (D) Smith (2001).

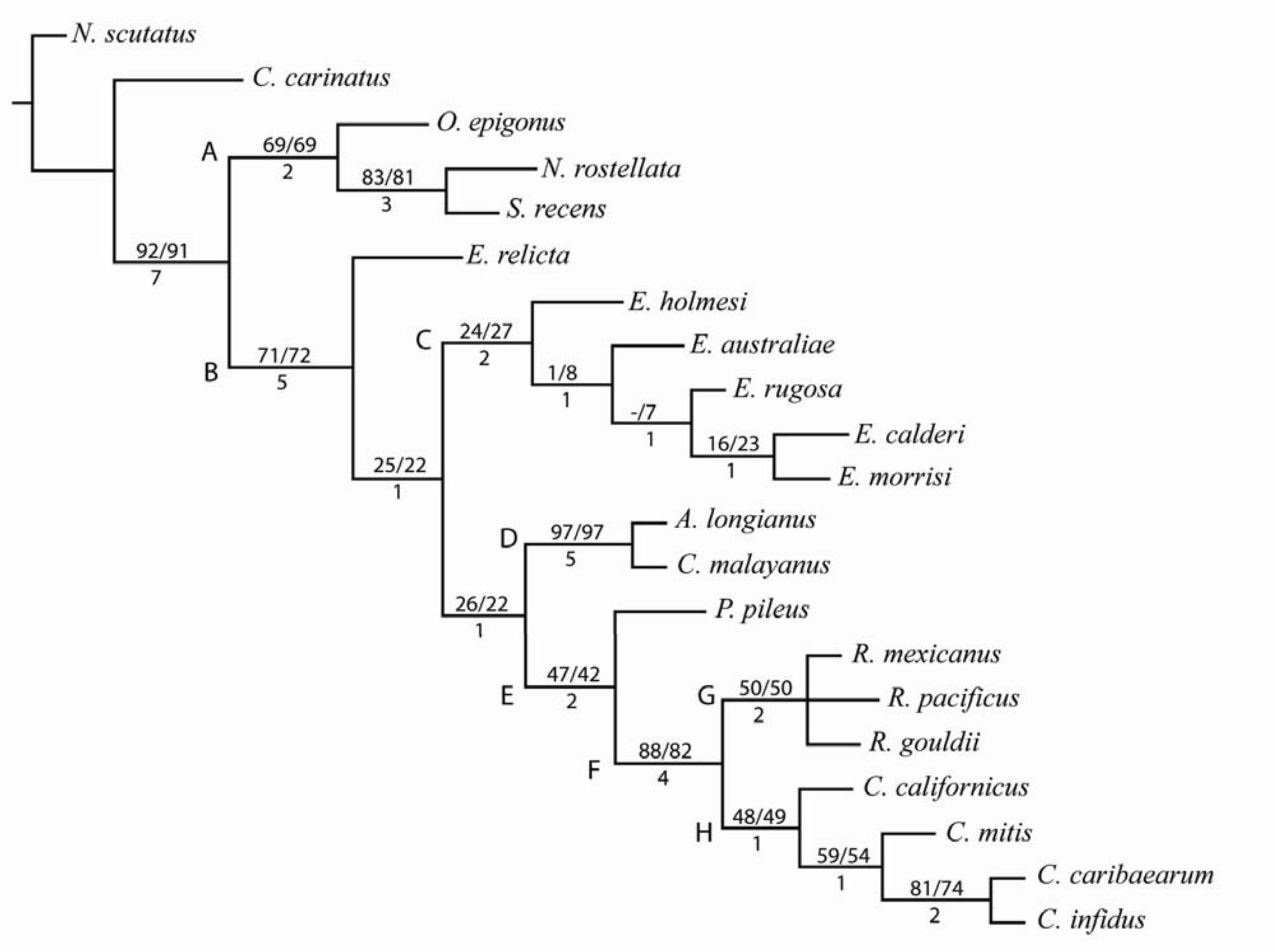


Figure 2. The single MPT ([1] 90 steps, CI = 0.678, RI = 0.814; [2] 86 steps, CI = 0.663, RI = 0.805) recovered by the analyses with all taxa. Boostrap values (1000 replicates) from analysis 1 (all data) and 2 (without 'soft tissue') are shown above the nodes (1/2); Bremer support values are shown below. Clades discussed in the text are indicated by capital letters.

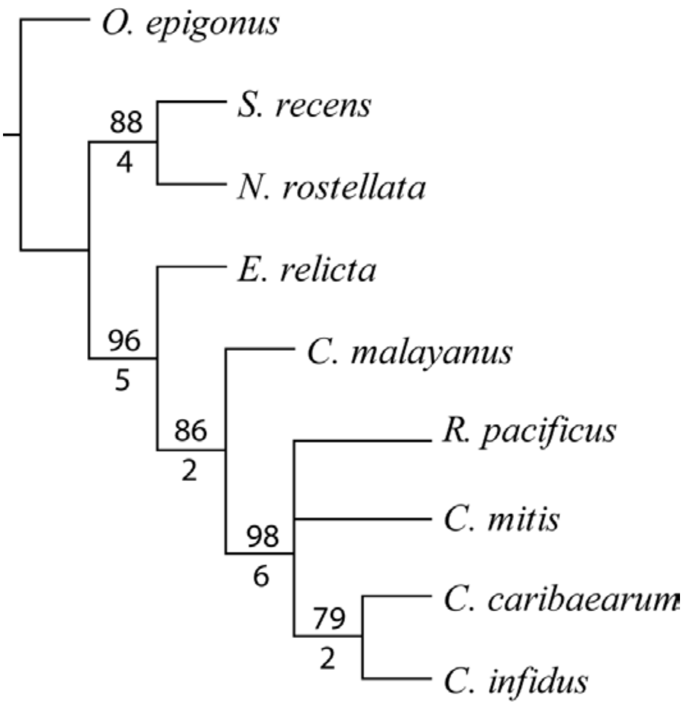
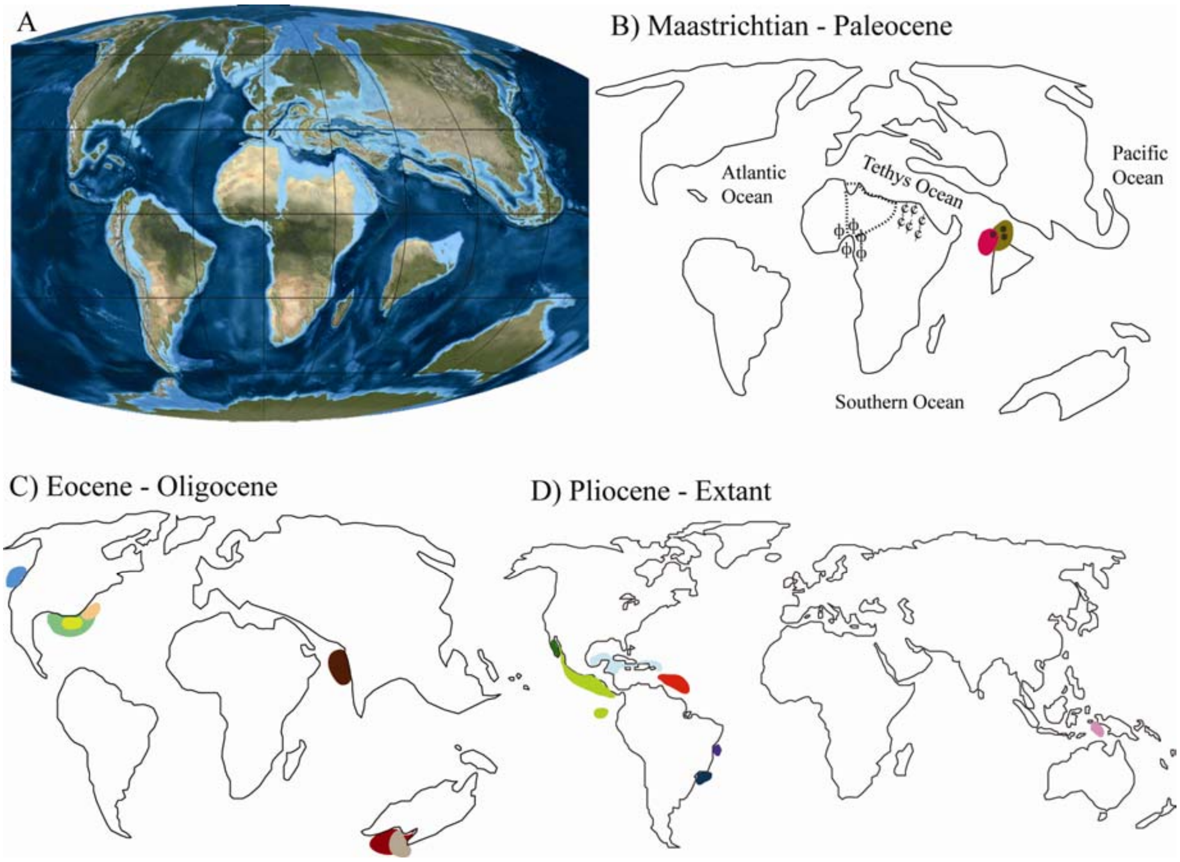


Figure 3. The single MPT (45 steps, CI = 0.889, RI = 0.902) recovered by the current analysis with extant species. Boostrap values (1000 replicates) are shown above the nodes; Bremer support values shown below.


A
B) Maastrichtian - Paleocene
Atlantic Ocean
Tethys Ocean
Pacific Ocean
Southern Ocean
C) Eocene - Oligocene
D) Pliocene - Extant

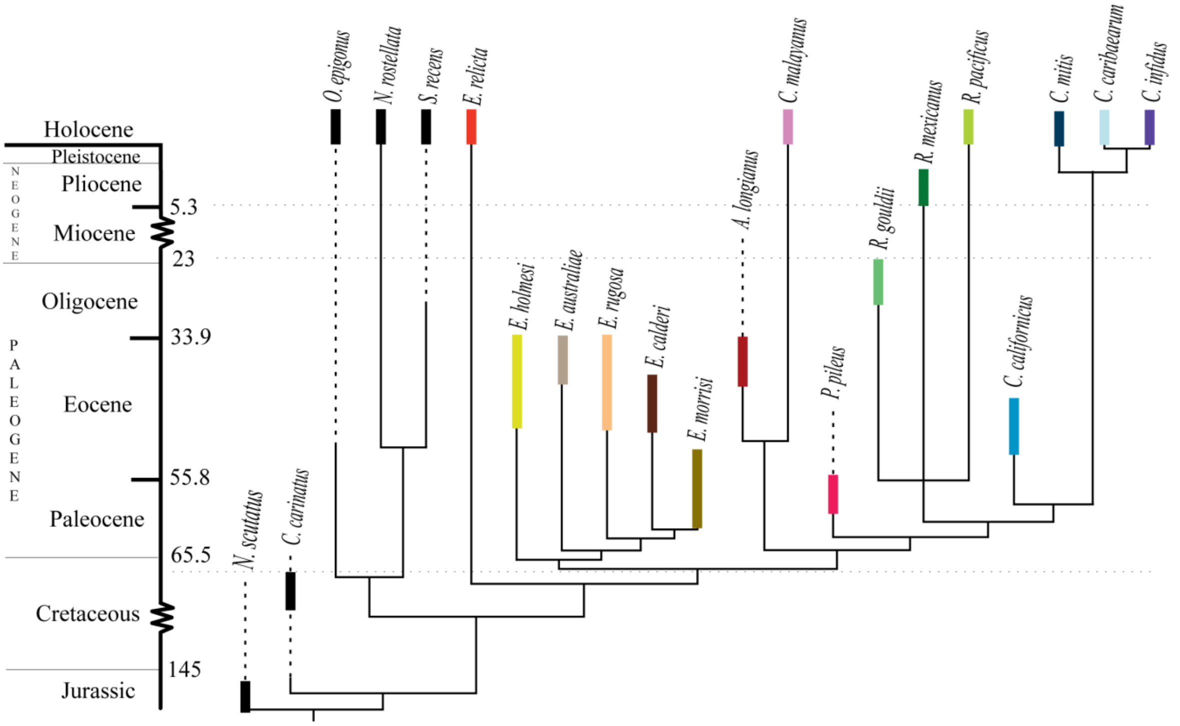

Holocene
Pleistocene
NEOGENE
Pliocene
5.3
Miocene
23
Oligocene
33.9
PALEOGENE
Eocene
55.8
Paleocene
65.5
Cretaceous
145
Jurassic
N. scutatus
C. carinatus
O. epigonus
N. rostellata
S. recens
E. relicta
E. holmesi
E. australiae
E. rugosa
E. calderi
E. morrisi
A. longianus
C. malayanus
P. pileus
R. gouldii
R. mexicanus
R. pacificus
C. californicus
C. mitis
C. caribaearum
C. infidus

Figure 4. Temporal and geographic distribution of the cassidulids included in the analyses. Below: evolutionary tree plotted from the single MPT retrieved from the parsimonious Analysis 1 (with all data). Solid bars represent known ranges of the species (colors other than black are labels for the maps) and longitudinal dashed bars represent known ranges of their genera. Above: A) map recovering the conditions of the Upper Cretaceous; and (B–D) maps from distinct time periods indicating the distribution range of the cassidulids included in the evolutionary tree (each color represents a species). In the Maastrichtian–Paleocene map (B), dashed line indicates the Trans-Saharan seaway, and symbols represent the known range of the oldest known species of the genus: ‘ф’ *Cassidulus* (*C. kieri* Adegoke, 1977), ‘¢’ *Rhyncholampas* (*R. ammonis* [Fourtau, 1913] and *R. strougoi* Azar & Elattaar, 1999), and ‘❋’ *Glossaster* (*G. ellipticus* Duncan & Sladen, 1882). Maps were based on (A) Blakey (2012), (B) Moussa *et al*. (2001), (C–D) Scotese (1997).

Appendix 1. Examined material

Family Cassidulidae L. Agassiz & Desor. *Cassidulus californicus*: UCMP 11348 (neotype). *Cassidulus caribaearum*: CAS 118368, 112632, 112633, 112637, 112638, 112640, 112683; NHM 87.6.27.7; USNM E13765, E18703, E18705, E36119, E36150; Mortensen (1948a), Kier (1962). *Cassidulus infidus*: SMNH-type-4859 (holotype); UFBA 314, 757; UFSITAB-ECH 123; Souto *et al.* (2011a). *Cassidulus malayanus*: ZMUC 236 (syntypes); Mortensen (1948a). *Cassidulus mitis*: CAS 116110; EQMN 3673, 3674; UFBA 756; ZUEC 11, 12; Krau (1954).

Eurhodia australiae: UCMP (loc. D73, slab 12532). *Eurhodia calderi*: UCMP (loc. C3631, slab 12516; loc. C3649, slab 12526; loc. C3651, slab 12528; loc. C3651, slab 12529); Duncan & Sladen (1882–1886). *Eurhodia holmesi*: CAS 67852, 68450. *Eurhodia morrisi*: NHM E741a; CAS 33195.1 (1sp.); UCMP (loc. C3632, slab 12832; loc. C3189, slab 12821); Duncan & Sladen (1882–1886); Kier (1962). *Eurhodia relicta*: USNM E20480 (holotype), E12971 (paratype); Mooi (1990a). *Eurhodia rugosa:* UCMP (loc. 3632, slab. 12832; loc. 3304, slab 12761); CAS 67860, 68447, 68449; Kier (1962).

Paralampas pileus: UCMP (loc. 3637, slab. 12518; loc. C3649, slab 12525); Duncan & Sladen (1882–1886).

Rhyncholampas gouldii: UCMP (loc. D452, slab 12737; loc. D3407, slab 12449; loc. D5465, slab 12453); CAS 67775.1, 67903.1–11. *Rhyncholampas pacificus*: CAS 90704, 90705, 90706, 90707, 90709.1, 106651, 106653; NHM 41110; USNM 6988, 8750, E51848, E3561; Mortensen (1948a). *Rhyncholampas mexicanus*: UCMP 11357 (holotype).

Family Faujasiidae Lambert. *Australanthus longianus*: MV P19225; NHM E42428 (syntype); UCMP (loc. B2035, slab 11053).

Family Neolampadidae Lambert. *Neolampas rostellata*: CAS (not deposited); USNM E20529; MCZ 8464, 2739; Mortensen (1948a).

Studeria recens: MNHN (not deposited).

Family Nucleolitidae L. Agassiz & Desor. *Catopygus carinatus*: NHM E2042; CAS 67300.00; Kier (1962).

Nucleolites scutatus: CAS 67305, 67306, 67307, 67308, 67542; MNHN B49337 (syntype); Kier (1962).

Incertae sedis. *Oligopodia epigonus*: MCZ 2697, 2757; NHM 59.1.31.13; UF2490, USNM 16309, E35684; Mortensen (1948a).

Appendix 2. Character list

This list is applied to all three analyses. Characters excluded from Analysis 2 (A2) and 3 (A3) were highlighted, their numbers were maintained in Appendices 5–7, but their characters states were reorganized.

1. Test shape (Appendix 3, Fig. 1A–D): subquadrate [0]; round (TW > 0.90 TL) [1]; oval (TW 0.75–0.90 TL) [2]; elongate (TW < 0.75 TL) [3]. A subquadrate test has its width nearly homogeneous throughout its length. Cassiduloids are usually round to oval, but species of *Nucleolites* are subquadrate and *Eurhodia* are elongate. Not included in A3.

2. Inflation of the test: slightly inflated (Appendix 3, Fig. 1F) [0]; strongly inflated (Appendix 3, Fig. 1E) [1]. This character coded for the relationship between test height and test width: a slightly inflated test increases in height as it diminishes in width and a strongly inflated test increases in height as it maintains its width.

3. Oral interambulacrum 5 shape: flat to concave (Appendix 3, Fig. 1F) [0]; convex [1]; knobbed (Appendix 3, Fig. 1E) [2]. Many cassiduloids have a flat or concave oral interambulacrum 5 running throughout the midline of the test; others (e.g. neolampadids) have knobs in this area, although the peristome may be in a slight concavity. Character state 1 was removed from A3 (*flat to concave [0]; knobbed [1]*).

4. Apical system (Mooi 1990b: fig. 1): tetrabasal [0]; monobasal [1]. Not included in A3.

5. Length of apical system in relation to the test length: large (over 6.5 in TL) [0]; small (up to 6.0 in TL) [1]. Only mature specimens were measured, i.e. with all gonopores well developed. The gonopores were not included in the measurements to avoid biases caused by sexual dimorphic species, whose females have larger gonopores than males (see Philip 1963: Text-Fig. 1d–e). Measurements were then taken from the anterior to the posterior region of the genital plate 2 (or from the midpoint between genital plates 2 and 3 in species with a tetrabasal apical system).

6. Number of gonopores: four [0]; three [1]. Cassiduloids usually have four gonopores, but this quantity was reduced in some species (i.e. *N. rostellata*) that have three or even two gonopores.

7. Aboral pores or pore-pairs: pore-pairs conjugated by a furrow [0]; pore-pairs with a small interporal partition [1]; rudimentary pores only [2]. Neolampas rostellata does not have developed petals and its ambulacral system is reduced to single and rudimentary pores, except for the phyllodes which are well developed. Characters 6–8 coded for features of the petals and, therefore, were treated as not applicable to this species. The level of the conjugation was not considered because of the intraspecific variation observed.

8. Petal III (Appendix 3, Fig. 2A) — width of perradial zone: narrow ($We < 0.45 Wp$) [0]; wide ($We > 0.45 Wp$) [1].

9. Petal III (Appendix 3, Fig. 2A) — width of pore-pair rows: wide ($2Wr > 0.5 Wp$) [0]; narrow ($2Wr < 0.5 Wp$) [1].

10. Petal III (Appendix 3, Fig. 2A) — shape of pore-pair rows: straight [0]; bowed [1].

11. Shape of anterior paired petals, considering the proportion of their components (Appendix 3, Fig. 2A–F): oblong [0]; linear [1]; tulip [2]; lanceolate [3]; oval [4]; elliptical [5]. Oblong and linear petals have nearly the same width throughout their length, but oblong petals have a wider perradial zone ($Wm > 0.5 Wp$). Tulip petals have bowed, thin ($2Wr < 0.5 Wp$) and open columns of pore-pairs ($We > 0.7 Wm$). Lanceolate and oval petals are strongly bowed and their columns of pore-pairs taper at the end; they differ by the position of the greatest width (first third *versus* on the half, respectively). Elliptical petals are less bowed and thinner than oval petals ($Wp < 0.4 Lp$). Character states 0 and 5 were removed from A3 (*linear [0]; tulip [1]; lanceolate [2]; oval [3]*).

12. Length of columns of respiratory podia in posterior petals: equal or differ by one pore-pair [0]; differ by more than one pore-pair [1]. Most cassiduloids have columns of pore-pairs of the same size; however, in a few species the number of pore-pairs may be significantly different within a species (i.e. *R. pacificus*, whose columns may differ in three to seven pore-pairs). This condition appears early in the life of the echinoid because of different timing in the development of both columns and, therefore, should not be influenced by the size of the specimen.

13. Ambulacral pores beyond petals: double [0]; single [1]. The number of pores in each ambulacral column reduced from two to one, probably during the Late Cretaceous. *Nucleolites scutatus* has full-sized pores and *C. carinatus* has the oral-most pore reduced. Not included in A3.

14. Periproct position on test surface considering the location of the periproctal membrane: on aboral surface (Appendix 3, Fig. 1A, C) [0]; marginal (Appendix 3, Fig. 1B, D, E, F) [1]. The marginal position was not divided into supramarginal and inframarginal because these are affected by the shape and height of the test, and also by the orientation of the periproct. Not included in A3.

15. Periproct placement within the test: in a wide groove (Appendix 3, Fig. 1A) [0]; in a narrow groove (Appendix 3, Fig. 1C) [1]; in a sulcus (or tubelike invagination) (Appendix 3, Fig. 1E) [2]; under a slight aboral lip (Appendix 3, Fig. 1D) [3]; under a prominent aboral lip (Appendix 3, Fig. 1B) [4]. The aboral lip is a projection of the test common among some cassidulids. This projection is very inconspicuous in *Eurhodia*, but usually prominent in *Cassidulus* and *Rhyncholampas*. Character state 0 was removed from A3 (*in a sulcus [0]; in a narrow groove [1]; under a slight aboral lip [2]; under a prominent aboral lip [3]*).

16. Periproct orientation: strongly longitudinal (width < 0.6 length) [0]; weakly longitudinal (width = 1.0 – 0.6 length) [1]; transverse (width > 1.0 length) [2].

17. Plates on periproctal membrane (Mooi 1990a: fig. 4): one row of large plates and many small plates [0]; two rows of large plates and few small plates [1]. Not included in A2.

18. Interambulacral plates surrounding (orally and laterally) periproctal opening (Appendix 3, Fig. 1E–G): project horizontally inside the test forming a subanal shelf [0];

project vertically inside the test [1]; do not project inside the test [2]. In *S. recens*, the plates project vertically inside the periproct forming a tubelike invagination (cone-shaped) where the periproctal membrane is attached. This structure may occur in other species, especially within the neolampadids, but further studies are necessary.

*19. Maximum number of plates on interambulacrum 5b, between the basicoronal plate and the end of the periproctal opening (Lovén 1874: Pl. XXII, fig. 179): 20 (0); 13 (1); 12 (2); 11 (3); 10 (4); 9 (5); 8 (6).*This character coded for the rate of skeletal growth until the formation of the periproct. The presence of several plates may suggest a rapid addition of plates at the apical system or late development of the periproct. The number of plates may suffer a slight variation within a species (usually by only one plate), but it does not vary with the size of the specimens. This number is also not related to the size of the species; for instance, *R. mexicanus* (TL = 70 mm) and *P. pileus* (TL = 20 mm) have the same number of plates. Within a genus, the number of plates may vary a lot between its species (i.e. *Eurhodia*) or may be very conservative (i.e. *Cassidulus*). Character states 0 and 3 were removed from A3 (*8 [0]; 9 [1]; 10 [2]; 12 [3]; 13 [4]*).

20. Naked zone running along the oral interambulacrum 5: absent [0]; distinct [1]. The naked zone is referred herein as an area free of primary tubercles that runs throughout the test, until its posterior edge. Some irregular echinoids possess only a random reduction of tubercles in this area which could be resulted by the presence of the interradial suture or just an impression caused by the presence of a dense tuberculation on the lateral edges of the test (because of its flatness) and bourrelets.

21. Naked zone running along the oral ambulacrum III: absent [0]; distinct [1]. This character is independent from character 20, although they were scored identically. Some taxa have a well-developed naked zone in the oral interambulacrum 5, but not in the oral ambulacrum III.

22. Pits on naked zone: absent [0]; present [1]. Species of *Eurhodia* usually have large and deep pits (except for *E. morrisi*); however, their size bears intraspecific variation within species of other genera (i.e. *Rhyncholampas*). The distribution of the pits is also very variable, not following any pattern.

23. Peristome orientation (Appendix 3, Fig. 3A–C): equant (width = 0.9 – 1.1 length) [0]; transversal (width > 1.1 length) [1]; longitudinal (width < 0.9 length) [2]. Character state 0 was removed from A3 (*longitudinal [0]; transversal [1]*).

24. Shape of peristome (Appendix 3, Fig. 3A–D): (sub)pentagonal [0]; oval [1]. The peristome in some cassiduloids (i.e. *C. infidus*) develops from a circular to a pentagonal shape, passing through a subpentagonal stage.

25. Bourrelet projection: poorly developed or flush (Appendix 3, Fig. 3A) [0]; well-developed and slightly projecting in- and up-wards (Appendix 3, Fig. 1B) [1]; developed and projecting upwards only (Appendix 3, Fig. 1C) [2]; strongly projecting into the peristome (Appendix 3, Fig. 1D) [3].

26. Buccal pores: absent [0]; present [1]. Not included in A3.

27. Arrangement of adoral pores in the lateral paired phyllodes (in each half ambulacrum): V-shaped with two columns [0]; two complete and parallel columns (Appendix 3, Fig. 3E) [1]; one complete and one half column [2]; one column and scattered pores [3]; only one column (Appendix 3, Fig. 3F) [4]. In the examined species, the lateral paired phyllodes were usually more developed than the others. Character states 0–2 were removed from A3 (*one column and scattered pores [0]; only one column [1]*).

28. Pores in the inner column of phyllodes: ten or more [0]; six to nine [1]; up to five [2]; absent [3]. Because the oral plates are the first to be formed, the phyllodes develop very early and are complete even in small specimens. As a result, this number varies little with size. Character state 0 was removed from A3 (*absent [0]; up to 5 [1]; six to nine [2]*).

29. Placement of sphaeridial pits: near buccal pores only (Appendix 3, Fig. 3F) [0]; throughout the phyllodes (Appendix 3, Fig. 3E) [1]. Some species of *Eurhodia* have many sphaeridial pits that may reach the distal end of the phyllodes. These pits may be confused with the inner column of pores and because of this, we can often find a description of *Eurhodia* stating that this species has only one column of pores in each half-ambulacrum. Not included in A3.

30. Maximum number of pores in the outer column of lateral paired phyllodes: eight or more [0]; five to seven [1]; up to four [2]. Not included in A3.

31. Oral tubercles with enlarged areoles and bosses displaced from center: no [0]; yes [1]. Species with enlarged areoles have larger spines on the oral region of the test that aid in their locomotion.

32. Ossicles on tip of phyllopodia: many (around six) [0]; few (around three) [1]; rare to absent [2]. Cassidulus caribaearum and *C. infidus* have few and thin ossicles on tip of their phyllopodia which dissolve quickly in sodium hypochlorite; *Cassidulus mitis* and *R. pacificus* have many ossicles, usually stronger than in the former species. Not included in A2.

33. Teeth on blade of ophicephalous pedicellariae: few coarse teeth on a semi-oval blade and running down in the middle of the neck (Souto et al. 2011a: fig. 7B) [0]; numerous fine teeth on an open-U blade and running down on the edges of the neck (Mooi 1990b: fig. 5a) [1]. The state [0] is present in *Cassidulus* and *Rhyncholampas* species and is quite variable within a species. Some specimens may have an almost oval foramen, which is not closed only because of the presence of the teeth running down along the neck. At the optical microscope these teeth may appear to be on the edges, but SEM images have shown that they are located on the neck. Not included in A2.

Appendix 3. Illustrations of some characters and character states.

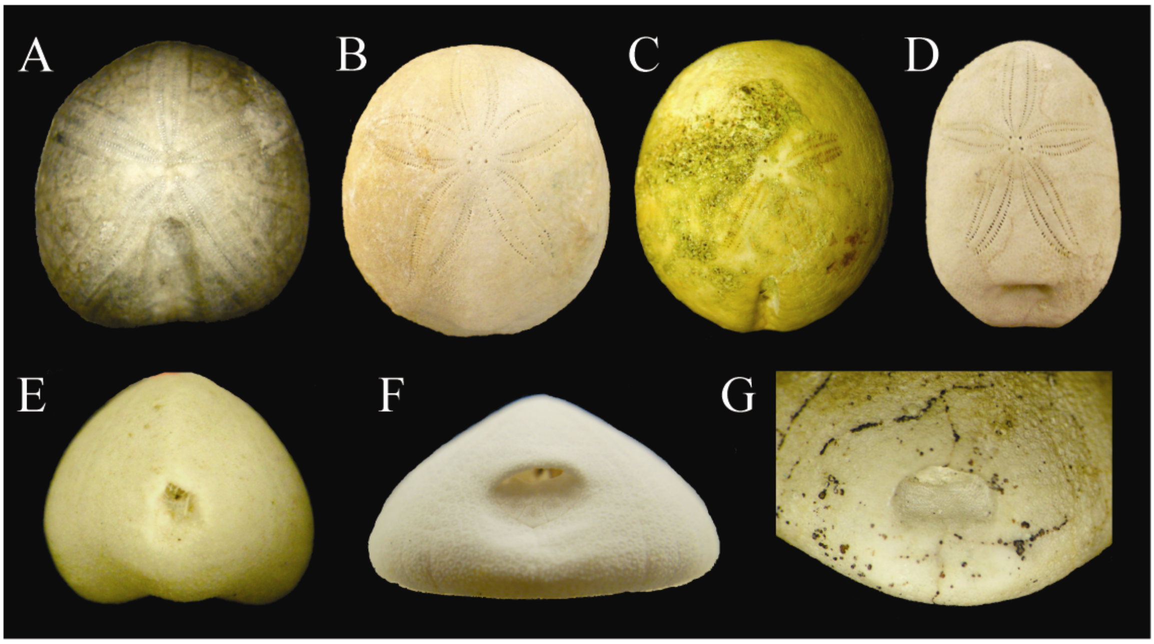


Figure 1. Aboral view of cassiduloids showing test shape — (A) subquadrate (*N. scutatus*), (B) round (*R. gouldii*), (C) oval (*A. longianus*), and (D) elongate (*E. rugosa*); and posterior view of test showing plates surrounding periproct opening — (E) extending vertically inside the test (*N. rostellata*), (F) not extending inside the test (*C. caribaearum*), and (G) extending horizontally inside the test (*E. rugosa*). Other characteristics are highlighted in Appendix 1.

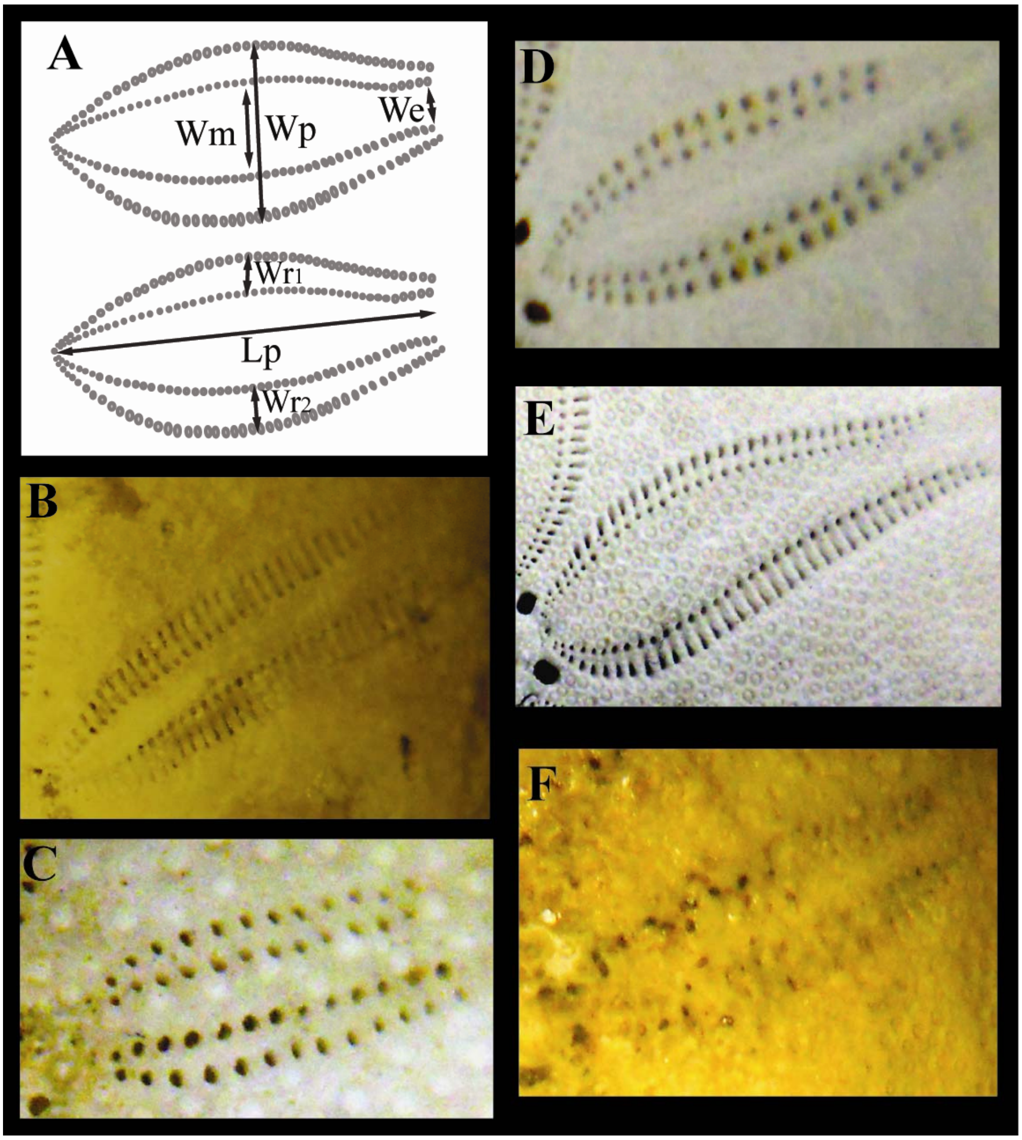


Figure 2. Petaloid characters and measurements (petal II in detail) — (A) drawing of the petal II of *E. morrisi* showing measurements: Wp (petal width), Wm (perradial zone width), We (opening width), Wr (pore-pair row width), and Lp (petal length). Petal shape oval, and the others (B) oblong (*N. scutatus*), (C) linear (*O. epigonus*), (D) tulip (*C. caribaearum*), (E) lanceolate (*R. pacificus*), and (F) elliptical (*E. australiae*).

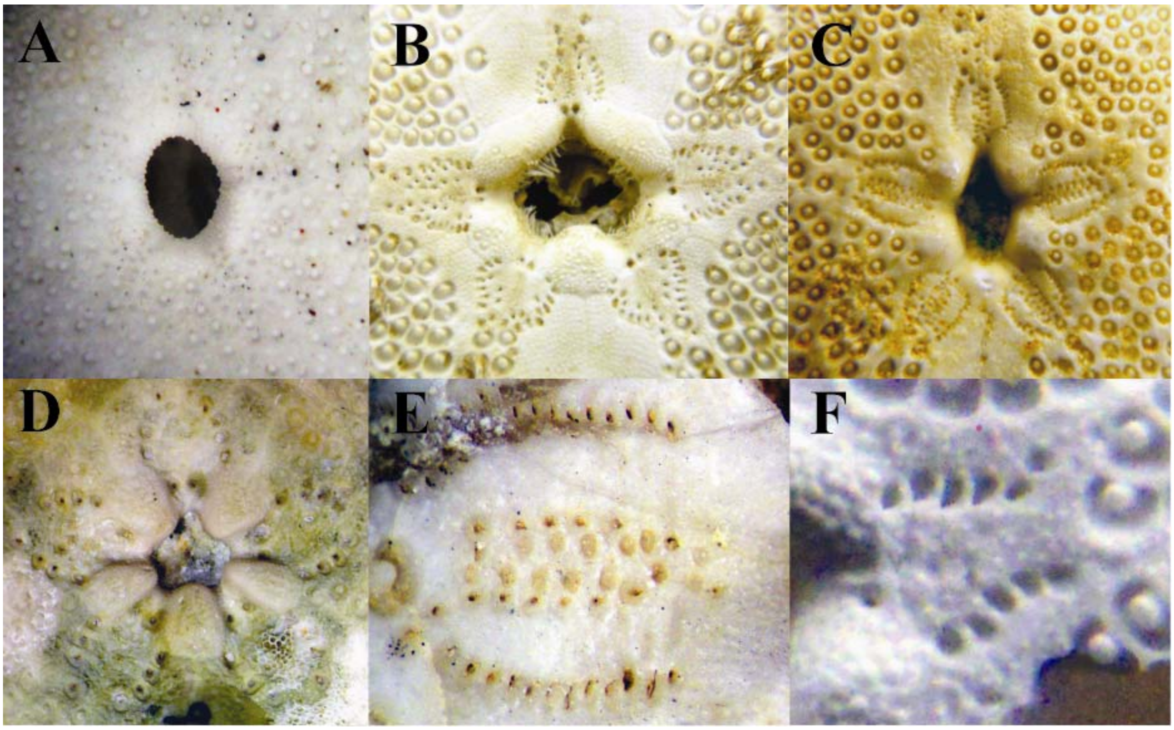


Figure 3. Peristome shape and orientation — (A) oval and longitudinal (*O. epigonus*), (B) pentagonal and transverse (*R. pacificus*), and (C) pentagonal and longitudinal (*E. morrisi*). (D) Detail of oral region of *A. longianus* showing strongly projecting bourrelets; phyllode 4 of (E) *E. morrisi* showing two parallel columns of pores, and of (F) *C. caribaearum* showing only one column. Other characteristics are highlighted in Appendix 1.

Appendix 4. Data matrices

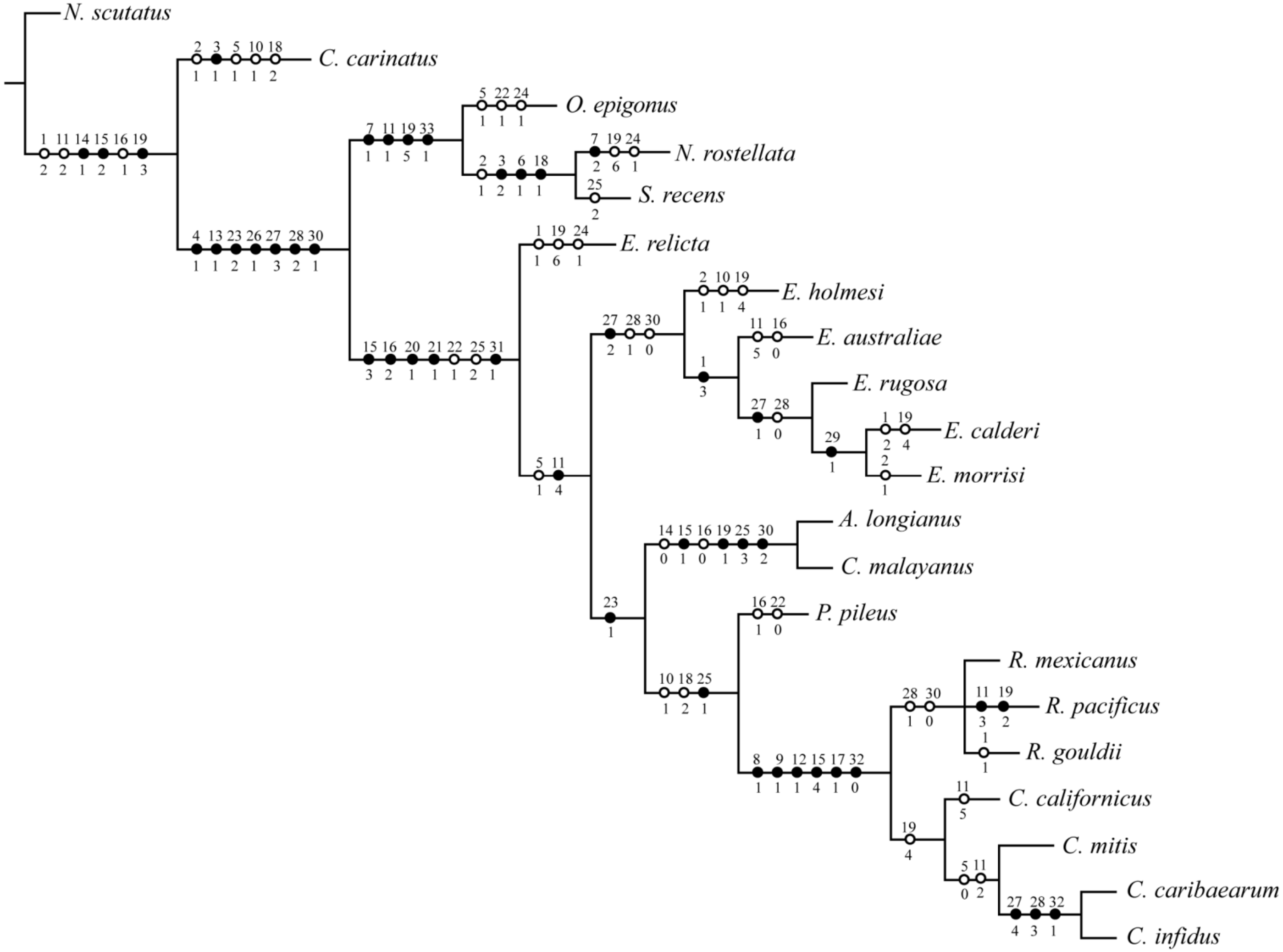
Main data matrix for character states of all species included in Analyses 1 and 2. Symbols used are: lacking observations in a taxon ‘?’; inapplicability of a character ‘-’.

Nucleolites scutatus	0000000000000000?00000000000000??
Catopygus carinatus	2110100001200121?23000000000000??
Oligopodia epigonus	200110100010112100500121013201021
Neolampas rostellata	2121012- - - - --12101600021013201021
Studeria recens	212101100010112101500020213201021
Australanthus longianus	2001100000401010?01211103132021??
Cassidulus californicus	2001100111511142?2421110113?011??
Cassidulus caribaearum	200100011121114212421110114301110
Cassidulus infidus	200100011121114212421110114301110
Cassidulus malayanus	200110000040101000121110313202120
Cassidulus mitis	200100011121114212421110113201100
Eurhodia australiae	3001100000501130?03211202121001??
Eurhodia calderi	2001100000401132?04211202110101??
Eurhodia holmesi	2101100001401132?04211202121001??
Eurhodia morrisi	3101100000401132?03211202110101??
Eurhodia relicta	10010000002011320061112121320112?
Eurhodia rugosa	3001100000401132?03211202110001??
Paralampas pileus	2001100001401131?23110101132011??
Rhyncholampas gouldii	1001100111411142?23211101131001??
Rhyncholampas mexicanus	2001100111411142?23211101131001??
Rhyncholampas pacificus	200110011131114212221110113100100

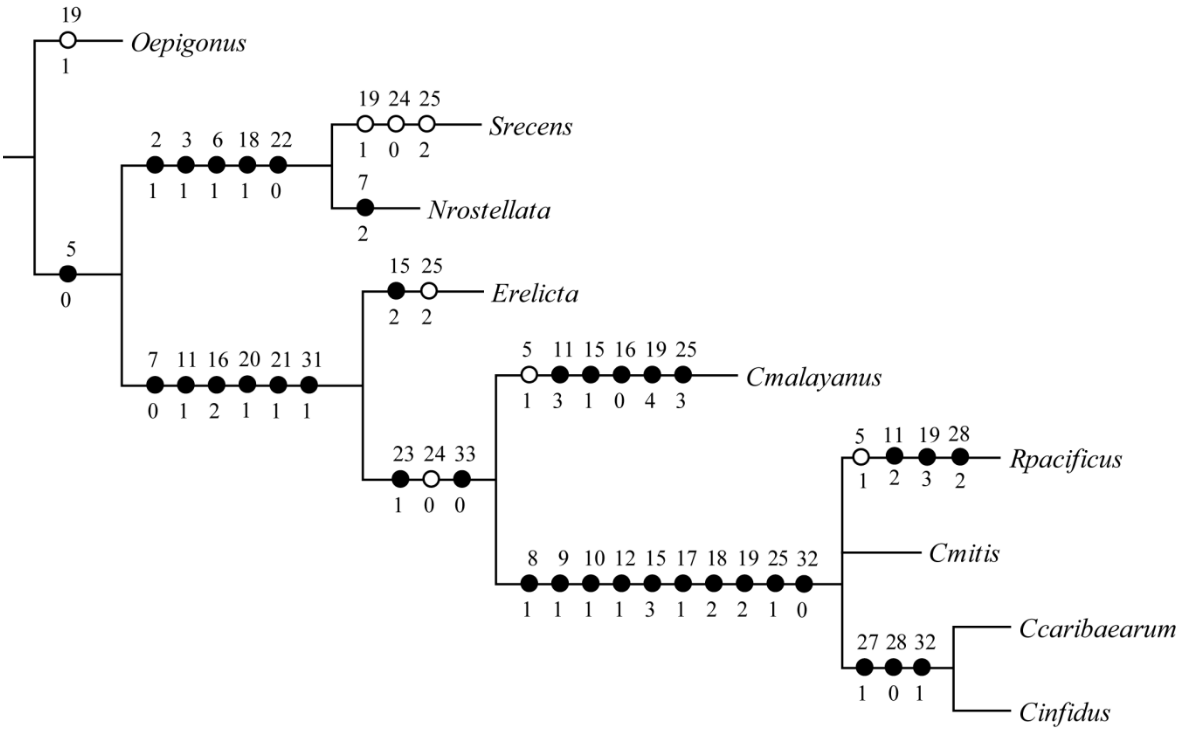
Data matrix for character states of extant species included in Analysis 3. Symbols used are: lacking observations in a taxon ‘?’; inapplicability of a character ‘-’.

Oligopodia epigonus	00101000000100100101001021
Neolampas rostellata	11012-- - - -0101000001001021
Studeria recens	11011000000101100000201021
Cassidulus malayanus	00100000301100411110301120
Cassidulus caribaearum	00000111113212211110110110
Cassidulus infidus	00000111113212211110110110
Cassidulus mitis	00000111113212211110101100
Eurhodia relicta	0000000010220001110120110?
Rhyncholampas pacificus	00100111213212311110102100

Appendix 5. The MPT of the analysis 1 (all taxa), with DELTRAN optimization. Numbers above the circles represent characters and those below character states; black circles indicate non-homoplasious changes and white circles represent homoplasies.



Appendix 6. The MPT of the analysis 3 (extant taxa), with DELTRAN optimization. Numbers above the circles represent characters and those below character states; black circles indicate non-homoplasious changes and white circles show homoplasies.



Appendix 7. Indices calculated for each character/parsimonious analysis: consistency index (ci), retention index (ri), homoplasy index (hi), and rescaled consistency index (rc). Analysis 1 included all taxa and characters; Analysis 2 excluded soft tissue characters; Analysis 3 included only the extant taxa and uninformative characters were removed.

Characters	**Analysis 1**				**Analysis 2**				**Analysis 3**			
	ci	**ri**	**hi**	**rc**	**ci**	**ri**	**hi**	**rc**	**ci**	**ri**	**hi**	**rc**
1	0.60	0.33	0.40	0.20	0.60	0.33	0.40	0.20	-	-	-	-
2	0.25	0.25	0.75	0.06	0.25	0.25	0.75	0.06	1.00	1.00	0.00	1.00
3	1.00	1.00	0.00	1.00	1.00	1.00	0.00	1.00	1.00	1.00	0.00	1.00
4	1.00	1.00	0.00	1.00	1.00	1.00	0.00	1.00	-	-	-	-
5	0.25	0.50	0.75	0.13	0.25	0.50	0.75	0.13	0.33	0.00	0.67	0.00
6	1.00	1.00	0.00	1.00	1.00	1.00	0.00	1.00	1.00	1.00	0.00	1.00
7	1.00	1.00	0.00	1.00	1.00	1.00	0.00	1.00	1.00	1.00	0.00	1.00
8	1.00	1.00	0.00	1.00	1.00	1.00	0.00	1.00	1.00	1.00	0.00	1.00
9	1.00	1.00	0.00	1.00	1.00	1.00	0.00	1.00	1.00	1.00	0.00	1.00
10	0.33	0.78	0.67	0.26	0.33	0.78	0.67	0.26	1.00	1.00	0.00	1.00
11	0.71	0.67	0.29	0.48	0.71	0.67	0.29	0.48	1.00	1.00	0.00	1.00
12	1.00	1.00	0.00	1.00	1.00	1.00	0.00	1.00	1.00	1.00	0.00	1.00
13	1.00	1.00	0.00	1.00	1.00	1.00	0.00	1.00	-	-	-	-
14	0.50	0.50	0.50	0.25	0.50	0.50	0.50	0.25	-	-	-	-
15	1.00	1.00	0.00	1.00	1.00	1.00	0.00	1.00	1.00	1.00	0.00	1.00
16	0.40	0.57	0.60	0.23	0.40	0.57	0.60	0.23	1.00	1.00	0.00	1.00
17	1.00	1.00	0.00	1.00	-	-	-	-	1.00	1.00	0.00	1.00
18	0.67	0.89	0.33	0.59	0.67	0.89	0.33	0.59	1.00	1.00	0.00	1.00
19	0.67	0.63	0.33	0.42	0.67	0.63	0.33	0.42	0.80	0.5	0.20	0.40
20	1.00	1.00	0.00	1.00	1.00	1.00	0.00	1.00	1.00	1.00	0.00	1.00
21	1.00	1.00	0.00	1.00	1.00	1.00	0.00	1.00	1.00	1.00	0.00	1.00
22	0.33	0.50	0.67	0.17	0.33	0.50	0.67	0.17	1.00	1.00	0.00	1.00
23	1.00	1.00	0.00	1.00	1.00	1.00	0.00	1.00	1.00	1.00	0.00	1.00
24	0.33	0.00	0.67	0.00	0.33	0.00	0.67	0.00	0.50	0.50	0.50	0.25
25	0.75	0.90	0.25	0.68	0.75	0.90	0.25	0.68	0.75	0.50	0.25	0.38
26	1.00	1.00	0.00	1.00	1.00	1.00	0.00	1.00	-	-	-	-
27	1.00	1.00	0.00	1.00	1.00	1.00	0.00	1.00	1.00	1.00	0.00	1.00
28	0.60	0.78	0.40	0.47	0.60	0.78	0.40	0.47	1.00	1.00	0.00	1.00
29	1.00	1.00	0.00	1.00	1.00	1.00	0.00	1.00	-	-	-	-
30	0.50	0.78	0.50	0.39	0.50	0.78	0.50	0.39	-	-	-	-
31	1.00	1.00	0.00	1.00	1.00	1.00	0.00	1.00	1.00	1.00	0.00	1.00
32	1.00	1.00	0.00	1.00	-	-	-	-	1.00	1.00	0.00	1.00
33	1.00	1.00	0.00	1.00	-	-	-	-	1.00	1.00	0.00	1.00

Conclusões gerais

1) A monofilia da família Cassidulidae, com a inserção do gênero *Australanthus*, foi sustentada por cinco sinapomorfias: a) periprocto transversal e b) localizado sob um pequeno lábio aboral; presença de uma área nua ao longo do c) interambúlacro oral 5 e d) ambúlacro oral III; e e) presença de tubérculos orais com aréolas alargadas e bases deslocadas do centro;

2) As relações de parentesco reconstruídas foram: (*Eurhodia relicta* (demais *Eurhodia*) + ((*Australanthus* + *Cassidulus malayanus*) + (*Paralampas* (*Cassidulus* + *Rhyncholampas*)))). Os gêneros *Eurhodia* e *Cassidulus* são parafiléticos;

3) Caracteres com dados faltantes foram diluídos e não geraram efeitos negativos na reconstrução filogenética da família;

4) A inserção de táxons fósseis foi fundamental para propor hipóteses de relacionamento entre os gêneros. Elas ajudam a polarizar o cladograma e calibrar dos eventos cladogenéticos. Além disto, a inserção de espécies fósseis ajudou na dectecção de problemas taxonômicos;

5) O estudo das últimas novidades evolutivas dos cassidulóides é necessário para verificar as relações entre as famílias desta ordem;

6) Sugerimos a ocorrência de processos heterocrônicos (peramorfose e pedomorfose) na evolução dos cassidulídeos e salientamos que o estudo destes processos é necessário a fim de verificar as relações inter e intragenéticas;

7) Registros fósseis indicam que a família Cassidulidae se originou no mar de Tethys, sofreu uma rápida expansão inicial (provavelmente no Eoceno) e vicariância posterior a partir do Plioceno.

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Anexos

Anexo 1. Normas da Revista

Journal of Systematic Palaeontology

Instructions for authors

Scope of the journal

The *Journal of Systematic Palaeontology* publishes papers which use systematics in ways that significantly advance our understanding of palaeogeography, palaeobiology, functional morphology, palaeoecology, biostratigraphy or phylogenetic relationships, as well as papers describing new or poorly understood fossil faunas and floras. Shorter contributions on technical or conceptual issues relating to systematic methodology and conservation issues are also welcome. However, papers that simply present systematic descriptions without attempting to explain their broader significance will not be published. Collections of thematic papers, such as those arising from symposia, are occasionally published, and these may have a more liberal remit.

Submission

As from 1/09/09, all manuscripts and revisions must be submitted using Manuscript Central. Please upload your manuscript following instructions given on the website:
http://mc.manuscriptcentral.com/tjsp
Please follow the style guide given below when preparing your text, figures and any supplementary material for submission.

Your paper will be sent out for review by at least two specialists and, based on their reports and the assessment of the Handling Editor and Editor-in-Chief, a decision on the suitability of the paper for publication will be made.

Copyright

Each author will be asked to sign a statement transferring full and exclusive rights to their article to the publisher *Taylor & Francis*, who will retain copyright.

Style Guide

General instructions

- Use a standard typeface, such as Times, Geneva or Helvetica, 12 pt typeface, 1.5 line-spacing with left justification for the text.
- Number all pages consecutively including the title page and references.
- List *Contents* on a separate page following the title page.

- Use British spelling throughout, but –ize and analyse. If necessary, have your text checked by someone with a good knowledge of English before submission.
- Material being described must be registered as part of a formal collection housed in a recognised institution so that it is accessible and available for study by subsequent researchers.

1. Title

The title should be short and informative. It should include reference to the taxonomic group being covered and the stratigraphical and/or geographical context of the paper. Left align the title in bold and type in lower case after the initial letter.

Each author should be listed on a separate line, followed by postal and email addresses.

2. Contents page

A complete list of headings used in the paper should be presented with subheadings indented appropriately. Do not use bold in this section.

First order heading……………………………………p. 000
Second order heading…………………………...…p. 000
Third order heading……………………….p. 000

List all taxa described in the text here.

3. Abstract

The Abstract is an extremely important part of the paper and care should be taken to make this concise and informative. This will be made available over the Internet as well as in the printed copy. Abstracts should be no longer than 300 words and should summarize the main results and conclusions of the paper. All new taxonomic names should be listed.

Provide four to six key words following the abstract.

4. Text

The text should be written in as clear and understandable a way as possible. Within the body of the text, paragraphs should follow on without a line-space, and with the first word indented. Use up to three levels of headings.
Please use single quotation marks throughout (any usage), or double if a quotation within a quotation.
Ensure any abbreviations used are explained on first usage.

(i) **Headings**

First order headings

Bold, 14 pt, left justified, initial capital then lower case and followed by a space of one line.

Second order headings

Bold, 12 pt, left justified, initial capital then lower case and with the text commencing on the following line.

Third order headings. Bold, 12 pt, left justified, initial capital then lower case followed by a full point and with the text commencing on the same line.

(ii) **Citing references**. References should be cited in the text as follows:
Gauthier (1902) or (Gauthier 1902) for single authors.
Cotteau & Triger (1855) or (Cotteau & Triger 1855) for two authors.
Skelton *et al*. (1990) or (Skelton *et al*. 1990) for multiple authors.
Lambert *in* Lambert & Thiery (1925) or (Lambert *in* Lambert & Thiery 1925) for subdivided publications.
Ali (1989, 1992a, b) or (Ali 1989, 1992a, b) for citing two or more publications.
(Ward & Cooper 1999; Keith 2001) for multiple references.
Note that when citing authors of taxonomic names, a comma should be placed between the author's name and the date of publication, e.g. *Terebellaria ramosissima* Lamouroux, 1821 or *Schizonema subplicatum* (Reed, 1917).

Page and figure numbers in other texts should be cited as follows:
Keith 2001, p. 27
Keith 2002, fig. 3

References for all taxonomic names should appear in the Reference section.

(iii) **Citing illustrations**. All figures must be referred to in the text, and should normally be numbered in the sequence in which they are cited. Use Fig. when referring to a single illustration or part of an illustration and Figs when referring to two or more separate illustrations.

(iv) **Abbreviating taxonomic names**. The first citation of taxonomic names in each paragraph should be in full, but can be abbreviated thereafter within the paragraph.

5. Taxonomic layout

In papers that include systematic descriptions, please use the following style guide.
The taxonomic section should always start with a first order heading.

Supraspecific taxa. Centred and with taxonomic name in bold but author/s and date of publication not in bold. Ensure that authors of higher taxa are included in the bibliography.

Successive paragraphs can then follow as necessary, with Type species, Diagnosis, Occurrence, Description, and Remarks as third order headings.

Species-level taxonomy. Species names should always be preceded by text indicating the supraspecific placement at generic level. Higher categories are optional, and the use of plesions and annotated hierarchical systems such as that of E.O. Wiley (1979. *Systematic Zoology* **28**, 308-337) is encouraged if appropriate.

• Species names should be in bold and italics and centred.
• References to figures should follow on the next line, also centred and in brackets.

- The synonymy list should list previous names as they were published, and in order of date of publication. The author of synonyms should be separated from the published name by a semicolon. Examples of synonymy entries are as follows:

1839 *Orthis semicircularis* Sowerby *in* Murchison: 639, pl. 21, fig. 7.
1987 *Dolerorthis sowerbyiana* (Davidson); Temple: 30, pl. 1, figs 11-18.
2008 *Triplesia girvanensis* Cocks: 81, pl. 6, figs 8-12.

- The annotation system recommended by S.C. Mathews (1973, *Palaeontology* **16**, 713-719) may be applied.
- Type and other material should be listed (ensure that abbreviations of collection repositories are explained somewhere in the text, e.g. in a Material and Methods section, or at the end of the Introduction).
- The following order should be used for species systematics after the synonymy list: Diagnosis, Derivation of name [for new species only], Material, Occurrence [stratigraphical and geographical], Description and Remarks.

6. References

- Authors' names should be given in full each time, in sentence case and bold.
- List authors alphabetically.
- Multiple publications by the same author should be listed chronologically.
- Use an ampersand (&) to link two or more authors of co-authored papers.
- Indent succeeding lines in each citation.

(i) Journals

- Journal titles should be given in full and italicised.
- The volume number should be in bold.
- Pagination should be given in full and separated from the volume number by a comma.
- Plates should only be listed if they are not included within the pagination of the paper.
- Only give part numbers of volumes when this is required to specify the paper, i.e. if each part in the volume is paginated from zero.

Bittner, A. 1892. Ueber Echiniden des Tertiars von Australien. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften Mathematisch-Naturwissenschaftliche Classe*, **101**(3), 331-371, pls 1-4.

Checcia-Rispoli, G. 1917. "*Zuffardia*," nuovo genere di Echinidi del Cretaceo superiore della Tripolitania raccolti dal cav. Ignazio Sanfilippo. *Giornale di Scienze Naturali ed Economiche di Palermo,* **30**, 14 pp., 1 pl.

Clark, H. L. 1923. Two new genera of sea-urchins. *Bulletin of the Museum of Comparative Zoology, Harvard,* **65**, 341-348.

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Gallemí, J., López, G., Martínez, R., Muñoz, J. & Pons, J.M. 1995. Distribution of some Campanian and Maastrichtian macrofaunas in southeast Spain. *Cretaceous Research*, **16**, 257-271.

Lambert, J. 1905. *In* Doncieux, A, Fossiles nummulitiques de l'Aube et de l'Herault. *Annales de la Université de Lyon,* **17**, 129-164, pl. 5.

(ii) **Books**

- Italicise the title of the book.
- Give publisher and city of publication followed by number of pages.
- For chapters within books follow the style guide below. Use (ed.) and (eds) to indicate editorship.

Bardack, D. 1997. Wormlike animals: Enteropneusta (acorn worms). Pp. 89–92 *in* D.W. Shabica, and A.A. Hay (eds) *Richardson's Guide to the Fossil Fauna of Mazon Creek.* Northeastern Illinois University, Chicago.

Benito, J. & Pardos, F. 1997. Hemichordata. Pp. 15-102 *in* F.W. Harrison & E.E. Ruppert (eds) *Microscopic anatomy of invertebrates. Volume 15, Hemichordata, Chaetognatha, and the invertebrate chordates*. Wiley-Liss, New York.

Carroll, S. B., Grenier, J. K. & Weatherbee, S. D. 2001. *From DNA to diversity: molecular genetics and the evolution of animal design.* Blackwell Science, Oxford, 214 pp.

Young, G. & Bird, J. 1828. *A geological survey of the Yorkshire Coast: describing the strata and fossils occurring between the Humber and the Tees, from the German Ocean to the Plain of York.* 2nd edition. Kirby, Whitby, iv + 367 pp., 19 pls.

7. Figures

All illustrations, whether line drawings or photographs, are specified as Figures. These may include composite illustrations in which the component parts are labelled using letter suffixes, e.g. A, B, C. This lettering and any other labelling should be at least 2 mm tall, and preferably in a standard sans serif font such as Helvetica. The maximum size for full-page illustrations is 175 mm x 235 mm, or 84 mm wide to fit a single column, and figures should be designed to make good use of the space, ensuring that background space between component parts of a figure is minimized.

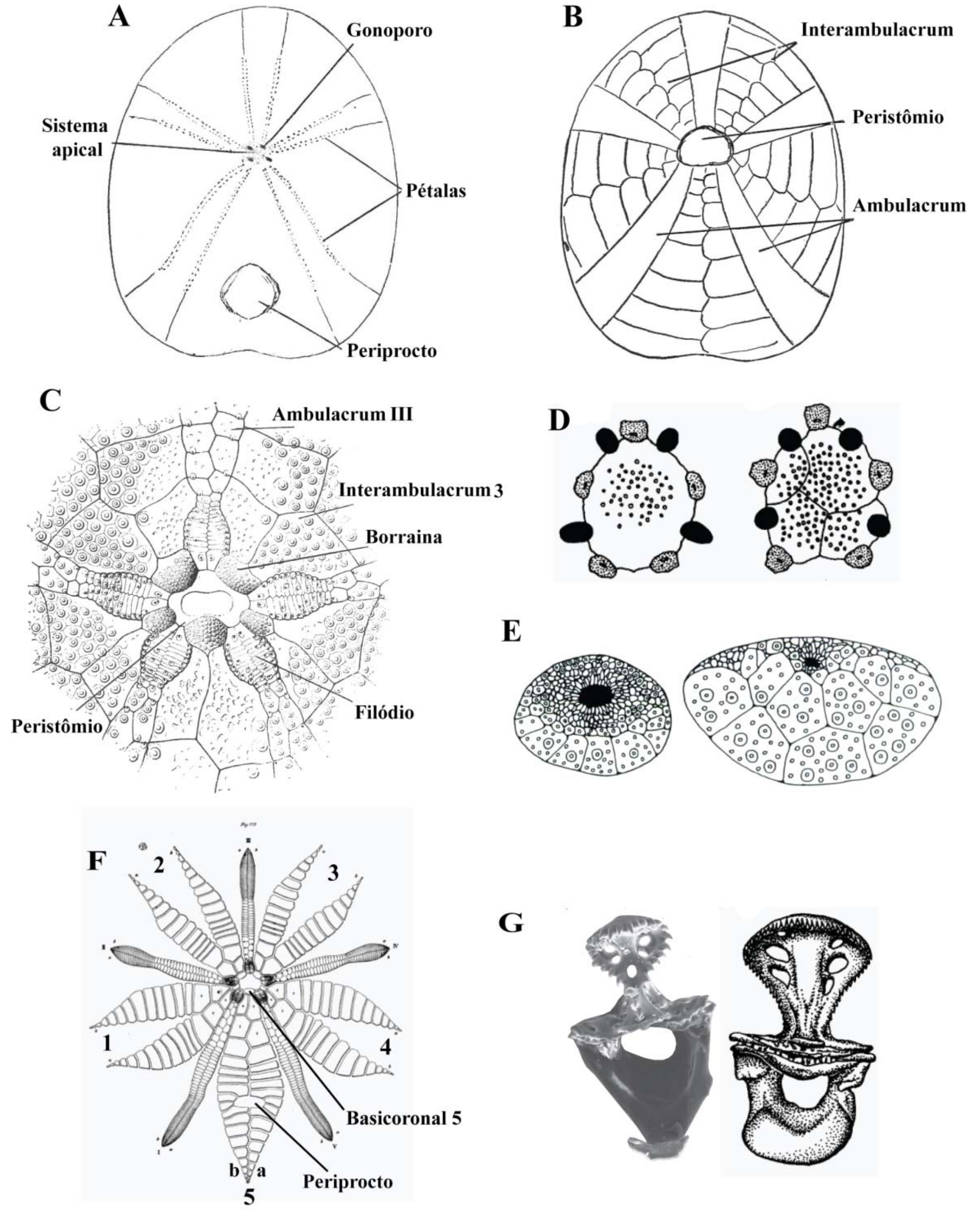
Figures can be prepared with either a white or black background, though the former is preferable.

Illustrations should be saved as TIFF or PICT files. Line drawings should be submitted at 600 dpi, digital images of halftones (photographs) at 300 dpi.

8. Appendices and Supplementary Material

Authors are encouraged to place data such as character lists into appendices, which will be printed after the References, or Supplementary Material available online. The editors may recommend moving secondary data into one of these two categories.

Anexo 2. Morfologia dos cassiduloides — (A) vista aboral, (B) vista oral, e (C) detalhe da região oral [imagens retiradas e modificadas de Hyman, 1955 – Figs. 229 e 230a); (D) sistema apical monobasal e tetrabasal, respectivamente [imagem retirada de Mooi (1990b) – Fig. 1]; (E) placas na membrana do periprocto com uma fileira de placas maiores *vs.* duas fileiras de placas maiores [imagem retirada de Mooi (1990a) – Fig. 4]; (F) desenho das placas interambulacrais (numeradas) e ambulacrais [imagem retirada de Lovén (1874) – Pl. XX, Fig. 179]; (G) valvas de pedicelárias oficéfalas de *Cassidulus infidus* e *Neolampas rostellata* [imagens retiradas de Souto *et al.*, 2011 – Fig. 7b; e Mooi (1990b) – Fig. 5a).



Anexo 3. Paleocorrentes do Paleoceno. Setas separando os hemisférios indicam a corrente circum-equatorial. Fonte: HAQ, B.U. & van EYSINGA, F.W.B. 1998. Geological Time Table, Elsevier.