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Rudist classification for the revised Bivalvia volumes of the 'Treatise on Invertebrate Paleontology'

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ABSTRACT. An updated phylogenetic classification of rudist bivalves is proposed for the revised Bivalvia volumes of the 'Treatise on Invertebrate Paleontology'. Already formalised as Order Hippuritida Newell, rudists are divided between two new monophyletic suborders established herein, Requieniidina, comprising all taxa attached by the left valve, and Radiolitidina, encompassing all those attached by the right valve. The Requieniidina contains one superfamily, Requienioidea Kutassy, consisting of a small paraphyletic family, Epidiceratidae Renngarten, and a larger derivative family, Requieniidae Kutassy. The Radiolitidina contains two superfamilies re-defined herein, Radiolitoidea d'Orbigny and Caprinoidea d'Orbigny. The paraphyletic Radiolitoidea includes a small basal family. Diceratidae Dall, together with a major clade that encompasses the paraphyletic Monopleuridae Munier Chalmas and a large descendent family, Radiolitidae d'Orbigny, as well as a smaller descendent family, Polyconitidae Mac Gillavry, which, in turn, is considered the root stock for the families Plagioptychidae Douvillé, Hippuritidae Gray, Caprotinidae Gray, Caprinulidae Yanin, and Trechmannellidae Cox. The monophyletic Caprinoidea d'Orbigny, comprises the monophyletic Family Caprinidae d'Orbigny and paraphyletic Family Caprinuloideidae Damestoy, from which probably arose both the families Ichthyosarcolitidae Douvillé and Antillocaprinidae Mac Gillavry. This classification covers at least 158 genera (including a few currently being described), leaving 8 poorly known genera as incertae sedis. A glossary of morphological terms is appended.

Key words: Bivalvia, Rudists, Phylogenetic classification, Order Hippuritida, Suborder Requieniidina, Suborder Radiolitidina.

1. INTRODUCTION

The suprageneric classification of rudists set out below is proposed for the revised Bivalvia volumes of the 'Treatise on Invertebrate Paleontology', currently in preparation. It is a revision of that given in Carter et al. (2011) following presentation of the latter scheme by the author at the 9th International Congress on Rudists, held in Kingston, Jamaica, in June 2011, and subsequent discussion at the meeting and thereafter. It includes previous nomenclatural corrections by Bouchet et al. (2010) according to the articles of the International Commission on Zoological Nomenclature (ICZN; Ride et al., 1999).

Most of the suprageneric taxa presented here monophyletic, according to current are phylogenetic analyses (e.g., Skelton and Masse, 1998; Chartrousse, 1998a; Skelton and Smith, 2000; Masse, 2002; Scott et al., 2010). The establishment of such taxa is the main goal of phylogenetic systematics because they unambiguously reflect the hierarchy of inferred evolutionary branching events (Smith, 1994). When classifying fossil organisms according to the Linnean system, however, novel grade-groupings

and their ancestral 'stem groups' that lack the diagnostic shared derived characters (synapomorphies) of the former are unavoidably assigned to different higher taxa of equivalent rank (Carter et al., 2011) – as in the analogous vertebrate case of birds and reptiles. Taxa considered to include the ancestors of other named taxa of equivalent rank are, by definition, paraphyletic, and are indicated here by '!' after the taxon name, following the convention used in Carter et al. (2011). In order to optimise the phylogenetic informativeness of the classification set out here, paraphyletic families of stem group genera have been kept as small as current phylogenetic resolution allows – although scope certainly remains for further pruning with more probing phylogenetic analysis. Polyphyletic taxa, which misrepresent evolutionary relationships by pooling together taxa of independent ancestry, have been avoided, as far as present understanding allows.

Additional nomenclatural and systematic notes, concerning, for example, junior synonyms, authorship, publication dates, or amended contents (indicated by 'zoological taxon revised herein'), are added after some taxa, in square brackets [thus]. Diagnostic characters are noted for each suprageneric taxon, with key synapomorphies for monophyletic taxa asterisked (*) - though allowance must be made for exceptions due to secondary modification (just as snakes are regarded as 'tetrapods', despite lacking legs). Paraphyletic taxa, by contrast, are necessarily diagnosed by their retained primitive character states. Phylogenetic explanations, additional derived characters found in some constituent genera and palaeoecological or distributional attributes of given taxa are appended under 'Comments'. Doubts over the higher taxonomic assignments of genera that are nevertheless validly established are indicated by a single query mark ('?'). Published taxa that remain of questionable status (e.g., perhaps diagnosed on insufficient evidence, and/or possible candidates for synonymy with other genera) are indicated with double query marks ('??').

Bibliographic references for the majority of taxon authorships cited here are given in Thomas Steuber's (2002) invaluable website resource 'A palaeontological database of RUDIST BIVALVES' (<u>http://www.paleotax.de/rudists/intro.htm/Taxonom</u> ic Database/Publications), so are not repeated here unless pertinent to further discussion.

Ongoing taxonomic descriptions and phylogenetic analyses will undoubtedly require still further revision both to the classification and (especially) to diagnoses before final publication in the revised Bivalvia volumes of the 'Treatise...', and rudist workers are encouraged to submit proposed additions and/or amendments to the scheme for discussion among the rudist working group - copied, please, to the author. It is over forty years since the publication of the first 'Treatise...' classification of rudists (Dechaseaux et al., 1969). Building on the substantial progress that has been made since then, thanks especially to the nine international rudist congresses held from 1988 to 2011, we should now aim to furnish a workable scheme that will still be regarded as a reliable reflection of rudist phylogeny in another four decades.

Abbreviations for morphological features used throughout are listed in **Table 1** (see also **Appendix 1** for a glossary of terms).

Table 1. Abbreviations used for

morphological features of rudists	
am	anterior myophore
at	anterior tooth
ct	central tooth
LV	left valve
ol	outer shell layer
pm	posterior myophore
pt	posterior tooth
RV	right valve

2. RUDIST CLASSIFICATION SINCE DECHASEAUX ET AL., 1969

2.1 Improvement of the phylogenetic basis

The history of work on rudist phylogeny and the defects of the first 'Treatise ... ' classification of rudists (Dechaseaux et al., 1969) in that respect were discussed by Skelton and Smith (2000). The latter authors' cladistic analysis revealed a fundamental phylogenetic dichotomy between rudists attaching by the LV and those attaching by the RV that divides even the paraphyletic Diceratidae Dall, 1895, as conceived by Dechaseaux et al., (1969), confirming Douvillé's (1935) postulate of two evolutionary branches issuing from Epidiceras and Diceras. These two clades are formally established herein as new Requieniidina (Section 3.2) and suborders. Radiolitidina (Section 3.3), respectively. They should not be confused with the 'Dextrodonta' and 'Sinistrodonta' of Pchelintsev (1959), which, as their names indicate, are based instead upon dentition, the first group possessing what Douvillé (1887) had termed 'normal dentition' (two main teeth in the RV and one in the LV) and the second, 'inverse dentition' (two in the LV, and one in the RV). Pchelintsev's (1959) suborders are thus separated at the transition between Diceras and Valletia within the Radiolitidina. Taxonomic division between the consequently paraphyletic Dextrodonta and monophyletic Sinistrodonta is rejected here in favour of the two monophyletic sister groups established below. Also rejected is Mainelli's (1992) attempt to revise Pchelintsev's (1959) suborders in order to reconcile them with Douvillé's (1935) dichotomy by isolating Diceras in a monogeneric suborder, 'Dicerasodonta'. Besides the extreme taxonomic imbalance involved in Mainelli's (1992) tripartite subordinal scheme, and the confusion of derived characters (concerning both dentition and valve of attachment) from different phylogenetic nodes in his diagnoses, the names employed by Mainelli are also unacceptable because they are not taxon-based, contrary to the protocol agreed for the classification of the Bivalvia adopted by Carter et al. (2011).

A comprehensive classification of rudists has also been proposed by Yanin (1990; 1995), in which a large number of new suprageneric taxa were introduced. However, many of the groupings recognized by him are polyphyletic according to the phylogenetic analyses followed here, while the numerous monogeneric subfamilies or even families included are phylogenetically uninformative. Moreover, his two suborders 'Diceratina Yanin, 1989' and 'Hippuritina Newell, 1965', although given taxon-based names, are exactly equivalent to Pchelintsev's (1959) two suborders, already rejected above. Hence, Yanin's (1990; 1995) classification is not considered further here, except in respect of instances of nomenclatural priority.

2.2 The requieniidine clade

Masse (2002) identified a sub-clade within the Early Cretaceous members of the Requieniidae consisting of Requienia, Toucasia and Pseudotoucasia that shared the derived development of relatively pronounced posterior myophores compared with the subdued state of the latter in Matheronia and Lovetchenia. This basic distinction was supported by the cladistic analysis of Scott et al. (2010), who established two subfamilies for the two groupings (including other genera). albeit with some problematical contradictions between branching points in their cladogram, for example in the sequence of [Pseudotoucasia + (Apricardia + (Toucasia + *Requienia*))], and the stratigraphical first appearances of the genera concerned.

2.2 The radiolitidine clade

Skelton (1978) and Skelton and Smith (2000) particularly criticised the polyphyletic composition of the families Caprinidae d'Orbigny 1847 (based only on shared possession of pallial canals) and Caprotinidae Grav. 1848 (likewise for accessory cavities) as conceived by Dechaseaux et al. (1969). Included in the Caprinidae by the latter authors were a number of canaliculate groups the likely independent origins of which had previously been argued by Douvillé (1887, 1888, 1889) and Mac Gillavry (1937). Skelton (1978) addressed this problem in part by distinguishing three such groups from the 'Caprinidae (sensu stricto)' as distinct families (Ichthyosarcolitidae Douvillé, 1887, Antillocaprinidae Mac Gillavry, 1937, and Plagioptychidae Douvillé, 1888), though without supporting cladistic analysis. Subsequently, the 'Dictyoptychidae Skelton' (in Skelton and Benton, 1993) (=Trechmannellidae Cox, 1934; see Section 3.3) were also separated off. The remaining caprinids (sensu stricto) were subsequently resolved by cladistic analysis into two constituent sub-clades, referred to Caprininae d'Orbigny, 1847, and 'Coalcomaninae Coogan, 1973' (= a junior synonym of 'Caprinuloidinae' Damestoy, 1971), by Chartrousse (1998a, b) and Skelton and Masse (1998), confirming a vicariant phylogenetic division previously recognized by Mac Gillavry

(1937). These two subfamilies are elevated herein to family level (as Caprinidae and Caprinuloideidae), within the correspondingly promoted superfamily Caprinoidea d'Orbigny, 1847 (see also Mitchell, this volume, a, for further analysis of the Caprinuloideidae). Also taken into account is a further depletion of the former caprinid constituency following the demonstration by Steuber and Bachmann (2002) that *Neocaprina* and *Caprinula* were probably derived independently from *Sellaea*, a genus closely associated with *Himeraelites*. This last grouping of genera is thus recognized here as a distinct radiolitoid family, Caprinulidae Yanin, 1990.

Further studies of New World canaliculate rudists have since phylogenetically re-connected two of the families separated by Skelton (1978) with the Caprinuloideidae (thus rendering the latter paraphyletic). Following the recognition by Aguilar-Pérez (2008)of а species of Ichthyosarcolites in Mexico, a genus previously regarded as limited to the Old World, Mitchell (this volume, b) has proposed a caprinuloideid ancestry for the Ichthyosarcolitidae. A cladistic study of antillocaprinids by Simon Mitchell (in press) likewise suggests a caprinuloideid ancestry for them. On the other hand, the proposal of a polyconitid ancestry for the Plagioptychidae by Skelton and Smith (2000) has recently received possible support from the discovery of a canaliculate polyconitid in the western Pacific region (Skelton et al., 2013). Such findings suggest that further recovery and study of material from the seamounts and bordering lands of the Pacific may yet fill many more gaps in our current understanding of rudist phylogeny. Among other Late Cretaceous canaliculate taxa, the origin of the Trechmannellidae (syn. Dictyoptychidae) remains obscure, although, by contrast, the attribution of Pseudosabinia Morris and Skelton, 1995, to the Radiolitidae d'Orbigny, 1847, is now well established (Özer, 2010a; Korbar et al., 2010), if not yet that of Sabinia as well, following Philip (1986).

For the polyphyletic Caprotinidae of Dechaseaux et al. (1969), Skelton (1978) adopted a different approach, combining them with the Monopleuridae Munier-Chalmas, 1873 (under the former family name), to create a single broad rootstock for all the more derived clades of uncoiled rudists. However, such large paraphyletic stem groups obscure basal relationships (Smith, 1994), which the cladistic analysis of Skelton and Smith (2000) thus set out to resolve for the rudists. The classification set out below builds on that foundation.



Figure 1. Suprageneric classification of rudists presented in this paper. Exclamation marks (!) denote paraphyletic taxa, considered to include genera ancestral to the taxa shown above them. All other taxa are currently considered to be monophyletic. Sizes of taxon boxes are purely schematic, with no significance regarding relative sizes of taxa.

3. THE CLASSIFICATION

3.1 ORDER HIPPURITIDA Newell, 1965 [Syn. Rudistæ Lamarck, 1819 (Dechaseaux, 1952)]

Diagnosis. Inequivalve shell possessing *ol* of fibrillar prismatic low-Mg calcite microstructure* (primitively thin, ~1 mm); also, aragonitic inner shell (primitively thick) that includes prominent (pachyodont) teeth and myophores.

Comments. This recently redefined order (Bouchet et al., 2010) comprises exclusively the clade of all 'rudists', as currently understood, promoted in rank from their superfamily status 'Hippuritacea Gray, 1848' in Dechaseaux et al. (1969). Other pachyodont taxa previously included in 'Order Hippuritoida Newell, 1965' are placed in a separate order, Megalodontida Starobogatov, 1992, in Carter et al. (2011). As mentioned above (Section 2.1),

rudists are here formally divided into two subordinal sister clades according to (at least initial) attachment to the substrate either by the LV (see Section 3.2), or by the RV (see Section 3.3), respectively. Figure 1 shows a synoptic view of the arrangement of suprageneric taxa recognized within these two suborders.

3.2 SUBORDER REQUIENTIDINA Skelton [new suborder. Name based on root for single constituent superfamily (see below), with sub-ordinal suffix '-idina' (Carter et al., 2011, table 1); note: authorship of newly defined taxa above the 'family group' level is not regulated by the ICZN Code (Ride et al., 1999, Article 1.2.2), hence attribution indicated here (cf., 'Hippuritida Newell, 1965', instead of 'Hippuritida Gray, 1848').]

Diagnosis. Shell attached by LV*; primitive



Figure 2. *Epidiceras sinistrum* (Deshayes), *LV*, partial internal view (Oxfordian, Dompcevrin, Meuse, NE France; Natural History Museum, London, specimen no., LL 31920). Scale bar = 1 cm. See Table 1 for key to abbreviations.



Figure 3. Diagram showing growth geometry of attached LV in (a), epidiceratid, contrasted with that in (b) requieniid. In each, the commissural plane is hatched and the vertical line represents the coiling axis of the valve (modified from Gourrat et al., 2003).

'normal' dentition (*sensu* Douvillé, 1887) retained by all, consisting of two unequal teeth in RV(elongate *pt* considerably larger than *at*) straddling prominent *ct* in *LV*; in addition, one small incipient toothlet situated posterior to ligament in *LV* (**Figure 2**).

Comment. Shell valves were universally limited to proso-spirogyrate growth by the retention of a primitive external parivincular ligament that migrated tangentially in a posterior direction during growth, with continuous anterior splitting and overgrowth of its torn ends by shell increments of *ol* (Skelton, 1978; **Figure 2**).

SUPERFAMILY REQUIENIOIDEA Kutassy, 1934 [correction of 'Requienioidea Douvillé, 1914' (*sic*, = Douvillé, 1915) in Scarlato and Starobogatov (1979; see Boss and Jacobson, 1985); syn. 'Epidiceratoidea Renngarten, 1950' in Yanin, 1990. The family name root for this superfamily was attributed to 'Douvillé (1914)' (*sic*) by Dechaseaux et al., (1969), but it is 'Not available from the vernacular "Réquiéniidés" of Douvillé (1914 [*sic*]: 383). Although Kutassy did not provide a description, reference to Douvillé (who did) makes the name available' (Bouchet et al., 2010, p. 77; see ICZN Article 11.7 in Ride et al. (1999).]

Diagnosis. As for suborder.

• FAMILY EPIDICERATIDAE! Renngarten, 1950 [zoological taxon revised herein]

Diagnosis. Shell sub-equivalve to inequivalve, with coiling axis of each valve oriented at high angle to commissural plane such that the umbones coil outwards away from it (Gourrat et al., 2003; Figure 3a).

Comment. Basal requieniidine group, consisting of three genera. Heterodiceratidae Pchelintsev, 1959, subsumed here.

Genera:

Epidiceras Douvillé, 1935 (including Pchelintsev's (1959) four genera, *Eodiceras* (see Skelton, 1999), *Mesodiceras*, *Paradiceras* and *Megadiceras*, which are all based on arbitrary and subjective sub-division of overlapping myophoral states).

Heterodiceras Munier-Chalmas, in Hébert, 1870 Plesiodiceras Munier-Chalmas, 1882

• FAMILY REQUIENIIDAE Kutassy, 1934 [see note for superfamily concerning authorship.]

Diagnosis. Strongly inequivalve shell, with *LV* coiling axis oriented at low angle to commissural plane such that hooked umbo coils across it* (Gourrat et al., 2003; see **Figure 3b**); *RV* either low-capuloid or operculiform in most genera.

Comment. The spirally extended umbonal growth of the *LV* generated an enlarged basal surface of attachment to, or frictional contact with the substrate on its anterior flank (spirogyrate clinger morphotype of Gili et al., 1995). Gourrat et al. (2003) noted that the small first requieniid, *Hypelasma salevensis* (Favre) could be a paedomorphic derivative of *Plesiodiceras.* Thickening of *ol* (to several mm) is frequent in more derived taxa.

o SUBFAMILY REQUIENIINAE Kutassy, 1934 [*pro* 'Requieniinae Douvillé, 1914 [*sic*, = Douvillé, 1915] new subfamily' (Scott et al., 2010).] **Diagnosis.** 'LV requieniform or toucasiform, tall trochospire translated along the coiling axis; RV flat to convex with little or no coiling translation; the LV myophores are inflated areas on the shell wall or projecting plates; the RV posterior myophore plate is separate from the cardinal platform; RV posterior tooth reduced in size in some genera. Growth rings are suppressed; some genera with radial bands; some with radial striae; some with accessory canals' (Scott et al., 2010).

Genera:

Requienia Matheron, 1842/3 [dated 1842, but complete publication delayed until May 1843 according to 'Notes' on p. 269] *Bayleia* Munier-Chalmas, 1873 *Bayleoidea* Palmer, 1928 (??) *Toucasia* Munier-Chalmas, 1873 *Apricardia* Guéranger, 1853 *Pseudotoucasia* Douvillé, 1911

o SUBFAMILY MATHERONIINAE! Scott et al., 2010

Diagnosis. 'LV matheroniform, low spirogyre translated slightly from the commissure along coiling axis; RV slightly inflated, coiled with little translation along axis; the LV myophores are expanded plates on the valve wall; on the RV the posterior myophore plate extends from the cardinal platform [Masse (2002), however, noted the relatively subdued primitive state of the myophores]; RV posterior tooth a large arcuate ridge' (Scott et al., 2010).

Genera:

Hypelasma Paquier, 1898
Kugleria Bouwman, 1938
Lovetchenia Masse, 1993
Matheronia Munier-Chalmas, 1873 (includes Monnieria Paquier, 1898)
Rutonia Yang et al., 1982

3.3 SUBORDER RADIOLITIDINA Skelton [new suborder, herein; name based on root for senior family group name selected by Bouchet et al., 2010, with sub-ordinal suffix '-idina' (Carter et al., 2011, table 1). See note on authorship for Requieniidina.]

Diagnosis. Shell attached by *RV**

SUPERFAMILY RADIOLITOIDEA! d'Orbigny, 1847 [*pro* 'Radiolitoidea Gray, 1848' (Yanin, 1990); zoological taxon revised herein]

Diagnosis. As for suborder.

Comment. Contains all non-caprinoid radiolitidine rudists, including the basal diceratids; hence

composition expanded relative to generic 'Radiolitoidea Gray, 1848' (sic) in Yanin (1990), which was limited to radiolitids. According to the cladistic analysis of Skelton and Smith (2000), the diceratids form a stem group to all uncoiled rudists and the latter resolve into two distinct clades. (1) the caprinids and caprinuloideids, and (2) the remaining uncoiled taxa, together forming a larger, but less well resolved clade (Figure 1). Inclusion here of the basal diceratids together with the latter clade in the Radiolitoidea, though rendering it paraphyletic (by taking in the presumed ancestors of the caprinoids, as well), is considered more economical than the alternative of creating a separate paraphyletic superfamily just to contain the two diceratid genera.

• FAMILY DICERATIDAE! Dall, 1895 [zoological taxon revised herein]

Diagnosis. Shell sub-equivalve to inequivalve, retaining primitive external parivincular ligament such that prosogyral umbones are directed outwards away from commissural plane (**Figure 4a**; i.e., as in Epidiceratidae, except for attachment by the *RV*).

Comments. Stem group for all uncoiled rudists (Skelton and Smith, 2000), consisting of two genera: (1) Diceras, which retains primitive 'normal' dentition (as in Requieniidina) and pm ledges passing beneath hinge plate in both valves; and (2) Valletia, which has a shortened external ligament* and derived 'inverse' dentition* (sensu Douvillé, 1887; 1896), comprising a single *ct* in the RV (derived from *pt* of 'normal' dentition with loss of former *at*), and two unequal teeth in the LV due to expansion of the post-ligamentary pt, which remains much smaller than the *at* (derived from *ct*) of 'normal' dentition; Douvillé, 1896); also, myophoral ledges attached to hinge plates*. In contrast to Dechaseaux et al., (1969), the family as constituted here excludes those genera attaching by the left valve, which are assigned to the Epidiceratidae (see above).

Genera:

Diceras Lamarck, 1805 (including Macrodiceras Karczewski, 1969)

Valletia Munier-Chalmas, 1873

• FAMILY MONOPLEURIDAE! Munier-Chalmas, 1873

Diagnosis. Ligament invaginated*, yielding uncoiled shell growth (Skelton, 1978; **Figure 4b** herein); low capuloid to operculiform LV^* , with two subequal to equal teeth* (**Figure 5a**) straddling erect *ct* in conical to cylindrical *RV*; myophores extend ventrally from hinge plates, with adductor



Figure 4. Diagram contrasting growth geometries of (a) primitive spirogyrate rudist LV, with external ligament (bold line), and (b) 'uncoiled' rudist RV, with trace of old (torn) invaginated ligament shown by dorsal seam (modified from Skelton, 1978).

insertion surfaces oriented either parallel to commissural plane (**Figure 5a**), or with one or both of the LV myophores projecting down into RV (**Figure 5b, c**) so as to face outwards onto their depressed counterparts there* (Masse and Fenerci-Masse, 2009).

Comment. Some genera have a slightly thickened *ol* (>1 mm, up to several mm). Most were relatively small clingers to elevators (sensu Gili et al., 1995), frequently growing clustered in bouquets.

Genera:

- *Monopleura* Matheron, 1842/3 [dated 1842, but complete publication delayed until May 1843 according to 'Notes' on p. 269]
- Araeopleura Cox, 1965 (pro Stenopleura Počta, 1889) (??)

Arnaudia Fischer, 1887

- Artigesia Freneix and Sornay, 1974 (?)
- *Bicornucopina* Hofmann in Hofmann and Vadász, 1912
- Debrunia Masse and Fenerci-Masse, 2009
- Glossomyophorus Masse, Skelton and Slišković, 1984

Gyropleura Douvillé, 1887 (?)

Mathesia Mainelli, 1996 (ex 'Agriopleura' darderi; see Masse and Fenerci-Masse, 2010)

Petalodontia Počta, 1889

Pseudopetalodontia Masse et al., 2007

Simacia Počta, 1889 (??)

Unnamed new genus, cf., *Glossomyophorus*, from Qishn Formation of Oman (Skelton et al., 2005)

• **FAMILY RADIOLITIDAE d'Orbigny, 1847** [see Manceñido et al., 1993, for date of authorship]

Diagnosis. Ligament invaginated, or secondarily lost in some taxa*; RV cylindrical to conical, and LV operculiform to convex; LV has projecting crescentic myocardinal arc (Figure 6a) with subequal, prong-like *at* and *pt* that straddle reduced *ct* ridge* in RV (Figure 6b; or *ct* secondarily lost in



Figure 5. (a) *Monopleura varians* Matheron, *LV*, internal view (Barremian, Brouzet-les-Alès, Gard, SE France; Université Claude-Bernard, Lyon, specimen no., EM 15681); scale bar = 1 cm. (b, c) *Mathesia darderi* (Astre), computer-generated virtual images from serially ground tomographic sections of *LV* (Lower Albian of Cabo de Ajo headland, NE Spain (Pascual et al., this volume); images courtesy of Enric Pascual-Cebrian), (b) internal view and (c) oblique posterior view. Scale bar for both images = 1 cm. See Table 1 for key to abbreviations.



Figure 6. (a) *Eoradiolites liratus* (Conrad), *LV*, myocardinal arc in dorsal view (Cenomanian, Abeih, Lebanon; Natural History Museum, London, specimen no., L 18683; n.b., specimen mislabelled in Skelton & Smith, 2000). (b) *Radiolites angeiodes* (de Lapeirouse), *RV* in transverse section, adumbonal view, with teeth of *LV* in sockets (Coniacian, Gosau Beds of Brandenberg Basin, Austria; US National Museum of Natural History (USNMNH), Washington DC, specimen no., 259009). (c) *Biradiolites angulosissimus* Toucas, photomicrograph in planepolarised light of *RV ol* in thin radial section, showing cell walls formed from localised ridges of fibrillar prismatic structure (Santonian, Plan d'Aups, Var, SE France; author's collection #154). (d) *Durania cornupastoris* (Des Moulins), broken transverse section of *RV ol* showing celluloprismatic mesostructure (bold arrow) (Turonian, Greenhorn Limestone, from U.S. Geological Survey Mesozoic locality D11226, Otero County, Colorado, USA; USNMNH, specimen no., 442109); (e) *Durania* cf. *apula* (Parona), showing the two finely ribbed radial bands of the *RV* (Maastrichtian, Aruma Formation, Khashm Hajajah, Riyadh, central Saudi Arabia; King Saud University, College of Science, Al Asa'ad & Skelton collection #HN2.2). Scale bars = 1 cm in all figures, except for (c) = 1 mm. See Table 1 for key to abbreviations.

some genera^{*}), and plate-like am and pm apophyses that both face outwards onto inner wall of RV^* ; ol much thickened^{*} (up to many cm), with two distinctly ornamented radial

bands on postero-ventral flank* (Figure 6e); most genera have celluloprismatic mesostructure* in *ol* of at least *RV* (Figure 6c, 6d).

Comments. Of monopleurid ancestry (Masse and Fenerci-Masse, 2010), with strong support for Agriopleura as the basal genus of the radiolitid clade (Skelton and Smith, 2000). For detailed illustration of the characteristic celluloprismatic mesostructure of the *ol* and its mode of growth, see Regidor-Higuera et al. (2007) and Pons and Vicens (2008). Although various subfamilies have previously been proposed for this, the largest rudist family, complete subdivision, with wellsubstantiated phylogenetic support, has yet to be achieved. Moreover, the family includes a number of genera that were established on questionable typological grounds (without regard to natural variability) and which might be considered as candidate junior subjective synonyms of previously established genera. Most radiolitid species grew as clustered elevators (sensu Gili et al., 1995), frequently forming laterally extensive biostromes, though some were clingers, and a few highly modified as crescentic recumbents (e.g., Pseudosabinia).

Genera:

- Radiolites Lamarck, 1801
- Agriopleura Kühn, 1832 (pro Agria, Matheron, 1878)
- Apulites Tavani, 1958 (??)
- Archaeoradiolites Fenerci-Masse, Masse, Arias and Vilas, 2006
- *Biradiolites* d'Orbigny, 1850 (includes *Rajka* Milovanović, 1984, *fide* Pons and Vicens, 1986; and *Synodontites* Pirona, 1869, *fide* Cestari and Sartorio, 1995)
- *Bournonia* Fischer, 1887 (includes *Hardaghia* Tavani, 1949, *fide* Pons et al., 1992)
- *Bystrickya* Lupu, 1976 (??)
- Chiapasella Müllerried, 1931
- *Colveraia* Klinghardt 1921 (possibly includes *Klinghardtites* Lupu, 1971, *Balabania* Karacabey-Öztemür, 1980, *Hatayia* Karacabey-Öztemür and Selçuk, 1981, and *Branislavia* Sladić-Trifunović, 1981, *fide* Özer, in prep.)
- Contraspira Mitchell, 2009
- Darendeella Karacabey-Öztemür, 1976
- Distefanella Parona, 1901
- *Dubertretia* Cox, 1965 (*pro Kelleria* Milovanović, 1938) (??)
- Durania Douvillé, 1908
- *Eoradiolites* Douvillé, 1909
- *Tekirdagia* Özdikmen, 2010 (mandatory correction of *Tekirdagensis* Özdikmen, 2010, to the form of a nominative singular noun (feminine in this instance), in accordance with ICZN Article 11.8 (Ride et al., 1999), '*-ensis*'

being a Latin adjectival suffix meaning 'of' or 'from' a place); ex Favus Laviano and Skelton, 1992, preoccupied by Favus Lanchester, 1900 (crustacean; see Özdikmen, 2010); intended replacement name Favolaviana Skelton and Fenerci-Masse, 2008, unavailable as it is 'not in a published work within the meaning of the Code' according to ICZN Article 9. specifically 9.9 (Ride et al., 1999)). [Unfortunately, the replacement generic name proposed by Özdikmen (2010), although available and valid, refers mistakenly to Tekirdağ province in the Thrace Basin, west of İstanbul, through confusion of the type locality 'Tscherkessköi', as stated by Böhm (1927), with Çerkezköy (Tekirdağ), a confusion previously also made by Laviano and Skelton (1992, figure 3). In fact, however, Böhm's rudist material came from Cerkesli Kövü (Hereke) in the İzmit Bay region southeast of İstanbul (Sacit Özer, pers. comm., Feb., 2012).]

- Fossulites Astre, 1957
- Fundinia Sladić-Trifunović and Pejović, 1977
- Glabrobournonia Morris and Skelton, 1995
- *Gorjanovicia* Polšak, 1967 (see Fenerci-Masse et al., 2011)
- Hacobjanella Atabekjan, 1976 (??)
- Horehronia Andrusov, 1976 (??)
- Jerinella Pejović, 1988 (??)
- Joufia Boehm, 1897 (includes Parasauvagesia Cox, 1960, fide Karacabey, 1969; possibly also Kuehnia Milovanović, 1956; Pseudokuehnia Slišković, 1968; and Miseia Patrulius, 1974, fide Özer, in prep.)
- Katzeria Slišković, 1966
- *Kurtinia* Karacabey-Öztemür, 1980 (possibly includes *Lattenbergites* Lupu, 1987, *fide* Özer, in prep.)
- Lapeirousella Milovanović, 1938 (includes Dechaseauxia Tavani, 1949, fide Pons et al., 1992)
- *Lapeirousia* Bayle, 1878
- Laskarevia Milovanović, 1984 (??)
- *Macgillavryia* Rojas, Iturralde-Vinent and Skelton, 1996
- *Maghrebites* Pons et al., 2012
- *Medeella* Parona, 1924
- Milovanovicia Polšak, 1967
- Monopilarites Philip and Platel, 1998
- Neoradiolites Milovanović, 1935 (??)
- Orestia Lupu, 1972 (??)
- Osculigera Kühn, 1933
- Parabournonia Douvillé, 1927 (??)
- Paronaites Pons et al., 2011
- Paronella Wiontzek, 1934 (??)
- Petkovicia Kühn and Pejović, 1959



Figure 7. (a) Diagrammatic posterior to anterior radial sections of *Horiopleura* (left) and *Polyconites* (right), showing diagnostic myophoral arrangements and thickening of *ol* (black) (modified from Skelton et al., 2010). (b, c) *Praecaprotina yaegashii* (Yehara), *LV*, (b) internal, and (c) ventral views (Upper Aptian part of Miyako Group in Tanohata area, Iwate Prefecture, NE Honshu, Japan; Institute of Geology and Palaeontology, Tohoku University, Sendai, Japan, specimen no., IGPS 35442). Scale bar for (b, c) = 1 cm. See Table 1 for key to abbreviations.

Polsakia Slišković, 1982 (??) *Potosites* Pons et al., 2010

Praelapeirousia Wiontzek, 1934

Praeradiolites Douvillé, 1902

- *Pseudopolyconites* Milovanović, 1935 (includes *Duranddelgaia* Patrulius, 1974, *fide* Pejović and Sladić-Trifunović, 1977)
- *Pseudosabinia* Morris and Skelton, 1995 (see Özer, 2010a)

Radiolitella Douvillé, 1904

Robertella Cossmann, 1903 (1904 in Vokes, 1980, p. 255; pro Mouretia Douvillé, 1903)
Rosellia Pons, 1977
Sauvagesia Choffat, 1886
Sphaerulites Lamarck, 1819
Tampsia Stephenson, 1922
Thyrastylon Chubb, 1956 (see Mitchell, 2010a)
Vautrinia Milovanović, 1938

• FAMILY POLYCONITIDAE! MacGillavry, 1937

Diagnosis. Low-capuloid to operculiform LV; *ol* thickened (> 1mm up to several mm) in RV^* ; subequal teeth in LV (at > pt) straddling robust, erect *ct* in RV; LV pm a reflexed plate attached basally between *pt* and salient lamina that connects *at* to postero-ventral margin, thereby separating off ectomyophoral cavity* (**Figure 7**); LV pm faces down onto ledge-like or depressed pm in RV.

Comment. Mac Gillavry (1937) established the subfamily Polyconitinae in recognition of the close relationship between *Polyconites* and *Horiopleura*. Though omitted from the original '*Treatise...*' classification (Dechaseaux et al., 1969), the phylogenetic grouping was re-affirmed by the analysis of Skelton and Smith (2000), who further identified it as a probable stem grouping for several other rudist taxa including, notably, the Hippuritidae and Plagioptychidae. Polyconitids typically grew as oyster-like facultative clingers to elevators (e.g., Skelton et al., 2010).

Genera:

- *Polyconites* Roulland, 1830 [latinized form also cited by original author, *pace* Vokes, 1980]
- *Douvillelia* Alencaster and Pantoja-Alor, 1998 (?) (*pm* configuration apparently not typically polyconitid)

Horiopleura Douvillé, 1889

Jerjesia Alencáster, 1986 (?) (*pm* configuration apparently not typically polyconitid)

Praecaprotina Yabe and Nagao, 1926

- *Tepeyacia* Palmer, 1928 (see Skelton and Smith, 2000)
- **'Polyconitid new taxon 1'** (probably derived from *Praecaprotina yaegashii* (Yehara); Skelton et al., 2011; 2013; Sano et al., in prep. a)
- **'Polyconitid new taxon 2'** (probably derived from *Praecaprotina kashimae* Masse and Shiba, 2010; Skelton et al., 2013)
- 'Polyconitid new taxon 3' (Skelton et al., 2013)
- **'Polyconitid new taxon 4'** (including *'Horiopleura' juxi* Steuber and *'Caprina' uwajimensis* Shikama and Tanabe; Steuber et al., 2011; Skelton et al., 2013).



Figure 8. (a-c) *Plagioptychus toucasi* Matheron (Santonian, Le Beausset, Var, SE France), internal views of (a) *LV* and (b) *RV* (Université Claude-Bernard, Lyon, specimen nos., EM 15685 and 15686, respectively); (c) antero-posterior radial section of both valves (author's collection). Scale bar for (a-c) = 1 cm. See Table 1 for key to abbreviations.

• FAMILY PLAGIOPTYCHIDAE Douvillé, 1888

Diagnosis. Myocardinal organization essentially similar to Polyconitidae (**Figure 8**), though capuloid LV usually more inflated*, with pallial canals around anterior, ventral and posterior margins* (**Figure 8a**).

Comments. Probably derived from polyconitid ancestor (Skelton and Smith, 2000), for which 'Polyconitid new taxon 1' (see above) is a possible candidate (Sano et al., in prep. a). Growth habits (either gyropleuriform or conical; Steuber, 2004) similar to those of polyconitids.

Genera:

Plagioptychus Matheron, 1842/3 [dated 1842, but complete publication delayed until May 1843 according to 'Notes' on p. 269] (see Steuber, 2004)

Coralliochama White, 1885

Mitrocaprina Böhm, 1895

Paracaprinula Piveteau, 1939 (see Steuber et al., 2009)

• FAMILY HIPPURITIDAE Gray, 1848

Diagnosis. Ligament deeply invaginated on infolding of *ol* (*'arête cardinale'*)*, or secondarily lost in some taxa*; *RV* cylindro-conical, and *LV* operculiform to low-convex; *ol* thickened, with two longitudinally infolded pillars* on posterior flank of *RV* matched by oscules* in *LV* (**Figure 9a, b**); radial canals contained within *ol* of *LV*, opening via pores to exterior* (**Figure 9c-e**) in all genera except *Torreites* and *Praetorreites*, in which they may have been secondarily lost*; prong-like, subequal teeth and *pm* in *LV* project into sockets in *RV* (**Figure 9a, b.**).

Comments. Since the classic monographs by Douvillé (1891-1897) and Toucas (1903-1904), it has been recognized that there is not a simple. consistent match between the distributions among hippuritid species of the different (1) pore types and (2) internal arrangements (concerning the states of the 'arête cardinale', where present, myocardinal elements and the pillars). Hence, there must be some homoplasy of one or other (if not both) of these character sets - a problem that has continued fuel discussion over the phylogenetic to classification of hippuritids (e.g., Bilotte, 1992; Steuber, 1999; Simonpiétri and Philip, 2000). With their LVs committed to their specialized filtering systems of pores and canals (Schumann, 2010), hippuritids grew as obligate elevators, in which role they nevertheless achieved considerable success, forming laterally extensive biostromes (Gili et al., 1995; Schumann, 2000). See Philip and Platel (1994) and Morris and Skelton (1995) for contrasting interpretations of the relationships of Torreites and Praetorreites.

Genera:

Hippurites Lamarck, 1801 (includes *Dorbignya* Woodward, 1862 and other synonyms cited in Dechaseaux et al., 1969; also *Batolites* De



Fig. 9. (a, b) *Hippurites radiosus* Des Moulins, interiors of (a) LV and (b) RV (Campanian, Barbezieux, Charente, SW France; Natural History Museum, London, specimen nos., L 62201 and L 18965, respectively). (c), with magnified detail in (d), *Pseudovaccinites giganteus major* (Toucas), external surface of LV, showing reticulate pores and underlying radial canals (visible in lower part of (c), where porous roofing has collapsed) in *ol* (Santonian, Les Collades de Basturs, southern Central Pyrenees, Spain (author's collection). (e) *Pseudovaccinites galloprovincialis* (Matheron), LV *ol*, photomicrograph (with crossed nicols) of thin section along a canal and its porous roof, showing growth lines (oriented perpendicular to fibrillar prisms) lining base of canal and wrapping upwards around pore walls to meet at dark periostracal insertion lines on top (bold arrow) (Santonian Sant Pere de Vilanoveta Member, Sant Corneli Formation, Riu Carreu, southern Central Pyrenees; author's collection). Scale bars = 1 cm for (a-c) and 1 mm for (d and e). See Table 1 for key to abbreviations.



ectomyophoral cavity

Figure 10. (a, b) *Caprotina striata* d'Orbigny, internal views of (a) LV, and (b) RV (Cenomanian, Le Mans, France; Natural History Museum, London, specimen no., L 96200). Scale bar for (a, b) = 1 cm. See Table 1 for key to abbreviations.

Montfort, 1808 and *Ugarella* Polsak and Slišković, 1987, *fide* Pons et al., 2010).

- *Barrettia* Woodward, 1862 (includes *Pseudobarrettia* Müllerried, 1931)
- *Caribbea* Grubić 2004 ('... the criteria given by Grubić are based on misinterpretations. The genus however is distinct when we look at the sockets': pers. comm., Simon Mitchell, May, 2011)
- *Gloria*' Grubić 2004 [but invalid, with preoccupied name, *fide* Mitchell, 2010c] (??)

Hippuritella Douvillé, 1908

- *Laluzia* Götz and Mitchell, 2009 (*pace* Pons et al., 2010, as '*Laluzia* ... can now be seen to have a different pore system as well as different dentition and is valid', pers. comm., Simon Mitchell, May, 2011)
- Parastroma Douvillé, 1926
- Pironaea Meneghini, 1868
- Praebarrettia Trechmann, 1924
- **Praetorreites** Philip and Platel, 1994 (?)
- *Pseudovaccinites* Sénesse 1946 (see Bilotte, 1992)
- Tetracionites Astre, 1931 (??)
- Torreites Palmer, 1933
- Vaccinites Fischer, 1887 (sensu stricto, after type species with polygonal pores, V. cornuvaccinum (Bronn, 1831); see Steuber, 1999 concerning neotype; also includes Rhedensia Sénesse, 1939, fide Bilotte, 1992; and Tetravaccinites Bilotte, 1981 =teratological form)
- Whitfieldiella Mitchell, 2010b
- Yvaniella Milovanović, 1938

• FAMILY CAPROTINIDAE Gray, 1848 [zoological taxon revised herein]

Diagnosis. Ligament invaginated; shell has externally smooth capuloid to operculiform LV, and spirally twisted conical to cylindrical RV showing distinct ribbing on relatively thin ol; 'inverse' dentition with subequal teeth in LV; spatulate pm in LV extends between pt and lamina connecting at to postero-ventral margin*, and is partly separated from posterior wall by subdivided ectomyophoral cavity* (Figure 10a); LV pm faces in onto up-tilted pm ledge in RV (Figure 10b).

Comment. This family is here provisionally restricted to two closely related genera, because of their currently uncertain phylogenetic position, despite their well understood morphology. Derivation from either a monopleurid (e.g., *Gyropleura*), or a polyconitid (e.g., *Praecaprotina*) seems equally possible at present. As the name Caprotinidae would have priority over either family, it is best 'quarantined' as proposed here for the time-being until this phylogenetic issue can be resolved.

Genera:

Caprotina d'Orbigny, 1842 (*sensu stricto* from type species, *Caprotina striata* d'Orbigny, 1839, by subsequent designation of Douvillé, 1887 (Macé-Bordy, 2007); excludes taxa assigned to genus by Di Stefano, 1889 (see Caprinulidae, below))

Chaperia Munier-Chalmas, 1873



Figure 11. (a-c) *Sellaea* Di-Stefano (from Lower Aptian blocks in slope deposits, Termini Imerese (Palermo), Sicily; Di-Stefano Collection, Museo geologico G.G. Gemmellaro, Palermo): (a) articulated shell of *S. zitteli* Di-Stefano (specimen no., 203), type species of genus; (b) *S. ciofaloi* Di Stefano, *LV*, transverse section, adumbonal view (specimen no., 209); (c) *S. zitteli*, *RV*, transverse section in adumbonal view (no. unknown). (d) *Neocaprina raghawiensis* Steuber & Bachmann, *LV*, drawing of transverse section in adumbonal view (copy of Steuber & Bachmann, 2002, fig. 5B, labelled herein; Upper Albian Halal Formation, Gebel Raghawi, northern Sinai, Egypt. (e, f) drawings of transverse sections (adumbonal views) of *Caprinula sharpei* Choffat, (e) *LV*, and (f) *RV* (copies of Douvillé, 1888, Pl. 23, figs. 5a, b, re-labelled; Cenomanian, Alcantara, Portugal. Scale bars for (a-d) = 1 cm; no scales originally indicated for (e, f). See Table 1 for key to abbreviations.

• FAMILY CAPRINULIDAE Yanin, 1990 [zoological taxon revised herein]

Diagnosis. Ligament invaginated; uncoiled shell with capuloid LV and twisted and/or curved cylindro-conical RV (**Figure 11a**); myocardinal apparatus analogous to Caprinidae (see below), but differing in that LV teeth are sub-equal*, and buttress-like $LV pm^*$ projects strongly into broad ectomyophoral cavity in RV, where it faces inwards onto a pm ledge, or erect ridge* (**Figure 11b, c**). Pallial canals* present in some genera (**Figure 11d-f**).

Comments. Pallial canals are present in *Neocaprina* and *Caprinula*, which were previously placed in Caprinidae (e.g., in Dechaseaux et al., 1969), but were probably derived from *Sellaea*, *fide* Steuber and Bachmann (2002). The origin of the family remains uncertain, though polyconitid ancestry (with a secondary reduction in ol

thickness) is a possibility.

Genera:

- Himeraelites di Stefano, 1889 (possibly includes Parapachytraga Yanin, 1986 (??); Skelton and Masse, 1998)
 Sellaea di Stefano, 1889
 'Caprotina', sensu di Stefano, 1889
- Neocaprina Pleničar, 1961
- Caprinula d'Orbigny, 1847

• FAMILY TRECHMANNELLIDAE Cox, 1934 [family name retained in place of Dictyoptychidae Skelton, in Skelton and Benton, 1993, despite genus *Trechmannella* Cox, 1933, being a junior synonym of *Dictyoptychus* Douvillé, 1905, according to ICZN article 40.1, *fide* Bouchet et al., 2010]

Diagnosis. RV ol thickened; ligament absent*; inner shell canaliculate throughout in both valves*; *pt* dorso-ventrally flattened*, flanking body cavity



Figure 12. Dictyoptychus morgani Douvillé (labelled 'Trechmannella persica Cox', = junior synonym; Maastrichtian, Bard-i-Nizami Hill, Pul-i-Kerah, Bakhtiari Country, Iran): (a, b) RV, transverse sections in adumbonal view, (a) close to commissure and (b) about 2 cm further down same specimen (Natural History Museum, London (NHML), specimen no. L 58424); (c, d) ventral-dorsal sections of another, articulated shell from same locality, (c) passing through posterior tooth and (d) about 1 cm more posteriorly, passing through posterior myophore (NHML, specimen no. L 58422). Scale bar for (a-d) = 1 cm. See Table 1 for key to abbreviations.

and separated from dorsal margin by accessory cavity* (Figure 12a, b); LV pm adjacent to body cavity, projecting down, and facing outwards, into recess or socket in posterior wall of RV^* (Figure 12a-d).

Comments. Endemic to the Afro-Arabian plate (Özer, 2010b). Origins unclear, though Morris and Skelton (1995) discuss similarities with *Praetorreites*.

Genera:

DictyoptychusDouvillé,1905(syn.TrechmannellaCox,1933)EodictyoptychusSkelton and El Asa'ad,1992SemailiaMorris and Skelton,1995 (?)

SUPERFAMILY CAPRINOIDEA d'Orbigny, 1847 [*pro* 'Caprinoidea Orbigny, 1850' (Yanin, 1990); zoological taxon revised herein]

Diagnosis. Ligament invaginated*, or secondarily lost in some taxa*: uncoiled shell has capuloid (sometimes extended*) LV and twisted and/or curved cylindro-conical RV; 'inverse' dentition (sensu Douvillé, 1887), retaining relatively primitive condition of unequal teeth in LV (at significantly larger than pt); LV pm rooted on posterior valve wall and separated from body cavity by (primitively) large endomyophoral cavity that is limited internally by salient lamina connecting at to postero-ventral margin* (though secondarily reduced or lost* in some derived taxa); also, pallial canals* present in inner shell of one or both valves in all but a few primitive genera; ol primitively thin (~1 mm) or secondarily thinned even further (< 0.5 mm)*.

Comment. For detailed phylogenetic analyses in recent years, see Chartrousse (1998a); Skelton and Masse (1998); Skelton and Smith (2000); Aguilar-Pérez (2008); and Mitchell (this volume, a, b), from among a voluminous literature on caprinoid taxa. Many caprinoids showed opportunistic variation between elevator and recumbent morphotypes, depending in ambient conditions of sedimentation, though a number of more derived genera, usually of remarkably large size, became obligate recumbents, dominating mobile bioclastic banks along the margins of carbonate platforms, in some cases associated with coral-algal paleocommunites; caprinoids also formed localised banks on the interior shelf (Scott, 1990; Gili et al., 1995; Hughes, 2004).

• **FAMILY CAPRINIDAE d'Orbigny, 1847** [see Manceñido et al., 1993, for date of authorship]

Diagnosis. RV pm a robust vertical plate* attached to salient lamina connecting ct to postero-ventral margin, and separated from posterior valve wall by a narrow ectomyophoral cavity*; RV pm projects into endomyophoral cavity of LV, where it faces outward onto inner face of LV pm (Figure 13a-d); canals absent or sparse in RV, except in Offneria.

Genera:

Caprina d'Orbigny [C.M. ('père'), not A.D.], 1822 (probably includes Kipia Harris and Hodson, 1922 (??), representing incomplete internal mould)
Offneria Paquier, 1905
Orthoptychus Futterer, 1892
Pachytraga Paquier, 1900 (see Skelton and Masse, 1998)
Praecaprina Paquier, 1905
Pseudocaprina Chartrousse and Masse, 2004
Schiosia Böhm, 1892
Sphaerucaprina Gemmellaro, 1865

• FAMILY CAPRINULOIDEIDAE! Damestoy, 1971 [syn. Coalcomaninae Coogan, 1973; see Bouchet et al., 2010]

Diagnosis. LV pm projects into endomyophoral cavity in RV, where it faces outwards onto inner surface of RV posterior wall* (Chartrousse, 1998b; **Figure 13e-g**); pallial canals present in nearly all genera, in both valves* (**Figure 13f, g**).

Comment. Largely limited to Caribbean-Pacific. Important taxonomic revisions have been published in recent years by Chartrousse (1998a), Scott (2002), Aguilar-Pérez (2008) and Mitchell (this volume, a; also containing additional proposals for new subfamilies). Moreover, *'Immanitas* and a number of other forms lack an external ligamental groove even in the Albian, [showing] transition towards *Antillocaprina*' (pers. comm., Simon Mitchell, May, 2011), emphasizing the recently recognized paraphyletic constitution of the family.

Genera:

Caprinuloidea Palmer 1928 Amphitriscoelus Harris and Hodson, 1922 Coalcomana Harris and Hodson, 1922 Conchemipora Chartrousse and Masse, 1998 Guzzyella Alencáster, 1999 Huetamia Alencáster and Pantoja-Alor, 1998 Immanitas Palmer, 1928 (see Aguilar-Pérez, 2008; Sano et al., 2013 (this volume) Jalpania Alencáster and Aguilar-Pérez, 1996 Kimbleia Coogan, 1973 Mexicaprina Coogan, 1973 Muellerriedia Alencáster, 1999 Neokimbleia Mitchell, 2013a (this volume)



Figure 13. Myophoral organisation in (a-d) Caprinidae, contrasted with (e-g) Caprinuloideidae. (a) Diagrammatic antero-posterior radial section of generalized articulated caprinid shell (modified from Chartrousse, 1998b). (b-d) *Pachytraga paradoxa* (Pictet & Campiche) (Lower Aptian, Rustrel, Vaucluse, SE France; Natural History Museum, London, specimen no., PI MB 129): internal views of (b) LV, and (c) RV, and (d) posterior view of whole shell, showing erect pm wall in RV facing outwards onto LV pm. (e) Diagrammatic antero-posterior radial section of generalized articulated caprinuloideid shell (modified from Chartrousse, 1998b). (f, g) *Amphitriscoelus waringi* Harris & Hodson (Lower Aptian, Plum Road, Trinidad; Paleontological Research Institution, Ithaca, NY, USA, paralectotype, specimen no. 1539; see Chartrousse, 1998a): transverse sections of (f) both valves, cut obliquely across commissure, and (g) RV, with teeth and pm of LV; both views inverted to facilitate direct comparison with (b and c). Scale bars for (b-d) and (f, g) = 1 cm. See Table 1 for key to abbreviations; additional abbreviations, *ec* ectomyophoral cavity, *en* endomyophoral cavity.

New genus from Japan, apparently a relatively derived sister taxon to *Conchemipora* (Skelton et al., in press; Sano et al., in prep. b) *Oedomyophorus* Skelton, 2004 *Pantojaloria* Alencáster and Pantoja-Alor, 1996 *Planocaprina* Palmer, 1928 *Retha* Cox, 1965 [*pro Ethra* Matheron, 1878] (see Skelton and Masse, 1998) *Texicaprina* Coogan, 1973 *Youngicaprina* Mitchell, this volume, a

• FAMILY ICHTHYOSARCOLITIDAE Douvillé, 1887

Diagnosis. 'Caprinoidea lacking an external ligamental groove, bearing an anterior tooth and a ... [supplementary posterior*] toothlet ...in the left valve that fit into slots in the right valve, and with wall-like myophores in the left valve that are rotated to attach directly to the inside wall of the body cavity in the right valve[*]' (Mitchell, this volume, b) – i.e., in pseudo-radiolitiform fashion;

also, *ol* greatly thinned* and inner shell layer of both valves invaded by fine capillary-like pallial canals*.

Comment. Recently recognized as of caprinuloideid ancestry (Mitchell, 2013b [this volume]), involving range extension from the New World to the Old World.

Genera:

Ichthyosarcolites Desmarest, 1817 [1812?, *fide* Vokes, 1980] (includes '*Mexicaprina*' *alata* (Filkorn, 2002), *fide* Aguilar-Pérez (2008)). *Curtocaprina* Mitchell, 2013b (this volume).

• FAMILY ANTILLOCAPRINIDAE Mac Gillavry, 1937

Diagnosis. Ligament deeply internalized or absent*, with no external trace of infolding; *ol* much reduced to thin skin*, and capillary-like pallial canals present throughout thick inner shell in both valves* (**Figure 14a-d**); *ct* socket pinched ventrally, such



Figure 14. (a-e) acid-etched silicified antillocaprinids (Maastrichtian, El Rayo Formation, 125 m-high hill east of Quebrada Jicara, 4.75 km S-SW of Sabana Grande, Barrio Lajas Arriba, Municipio de Lajas, Puerto Rico; N.F. Sohl Collection, US National Museum of Natural History; see Sohl, 1998, for locality details): (a, b) *Parasarcolites monotubularis* Mitchell and Gunter (specimen no., NS 74), partial LV (umbo and part of rim missing), (a) adumbonal view, (b) oblique ventral view, showing teeth, projecting blade-like myophores, and supplementary toothlets (bold arrows) on ventral and posterior margins; (c-e) *Antillocaprina suboccidentalis* Chubb, (c, e) LV (specimen no. NS 78), internal and external views, (d) RV (specimen no., NS 77), internal view, showing flat myophoral platforms. (f) The iconic Caribbean rudist, *Titanosarcolites giganteus* (Whitfield) from the Maastrichtian of Bruce Hall, Great River, Marchmont Inlier, Jamaica, articulated specimen arranged as in life position (Department of Geography and Geology Museum, The University of the West Indies, Mona Campus, Kingston, Jamaica). Scale bars for (a-e) = 1 cm; scales for (f) = some members of the organisation committee for the 9th International Congress on Rudists, held at UWI in 2011 (l. to r.), Gavin Gunter, Sherene James and Simon Mitchell.

that pt is adjacent to body cavity*; LV myophores either project into groves in RV (Figure 14a, b), or secondarily form broad platforms parallel with commissural plane* (Figure 14c, d). *Comments.* Caribbean endemics, probably of caprinuloideid ancestry (pers. comm., Simon Mitchell, May, 2011; in press, including proposals of ten new genera). Includes the largest-shelled

rudist genus known, the distinctive recumbent form *Titanosarcolites* (**Figure 14f**).

Genera:

Antillocaprina Trechmann, 1924 Antillosarcolites Chubb, 1967 Parantillosarcolites Mitchell, 2010b Parasarcolites Mitchell and Gunter, 2006 Titanosarcolites Trechmann, 1924

3.4. Incertae sedis

• FAMILY (AND/OR STATUS AS RUDIST) UNCERTAIN

Genera:

Anodontopleura Felix, 1891 Baryconites Palmer, 1928 Cryptaulia Počta, 1889 Dessia Pamouktchiev, 1983 Lithocalamus Lupher and Packard, 1930 Palus Palmer, 1928 Rousselia Douvillé, 1898

Sabinia Parona, 1908 (assigned to Radiolitidae by Philip, 1986, or possibly a plagioptychid, according to Morris and Skelton, 1995; but derivation from the radiolitid *Pseudosabinia* through suppression of celluloprismatic structure in *ol* of *RV* is a possibility that needs further testing).

NON-RUDIST:

Genera:

Somalites Pamouktchiev, 1983 (scleractinian coral, fide Löser, 1999)

4. CONCLUDING DISCUSSION AND REMAINING PROBLEMS

The cladistic analysis of Skelton and Smith (2000) succeeded in its main aim of determining the most basal nodes in the rudist clade, thereby supporting the establishment herein of the two new suborders, Requieniidina and Radiolitidina, as well as the revised definition of the three superfamilies. Requienioidea, Radiolitoidea and Caprinoidea (Figure 1). Nevertheless, the taxonomy of primitive radiolitidine rudists of latest Jurassic (Kimmeridgian) earliest Cretaceous to (Valanginian) age, currently assigned to Valletia and Monopleura, requires revision - incorporating new material from Japan (Sano et al., 2008; Kakizaki et al., 2011; Sano & Skelton, 2011) - and their relationships with later uncoiled forms need to be investigated. In particular, the evolution of ligamentary invagination in such forms should be documented in detail in order to address the question of whether the monopleurids and

caprinoids indeed shared a single uncoiled common ancestor, or whether, perhaps, they evolved from different species currently assigned to *Valletia*.

The monophyly of some long-recognized families was also confirmed by Skelton and Smith (2000), most notably the largest rudist family. Radiolitidae, as well as the Hippuritidae, with the added interest of the polyconitid genus Tepevacia emerging as sister group to the latter. However, evolutionary relationships within these two families remain unresolved probably because of relatively frequent convergent and iterative evolution of characters within different lineages. Further detailed studies are therefore needed, especially of modes of cell development in the outer shell layer of radiolitids (e.g., Fenerci-Masse et al., 2006; Pons and Vicens, 2008) and of pore and canal morphogenesis in hippuritids (e.g., Schumann, 2010), as well as their patterns of shell growth (e.g., Vicens, 1992; Steuber, 1999; Simonpiétri and Philip, 2000), before division into phylogenetically valid subfamilies can be achieved.

The phylogenetic position of a number of relatively derived taxa, especially those devoid of primitive character states that might link them unambiguously with more primitive taxa, has long been problematical. The three highly specialized, large canaliculate taxa Dictvoptychus, Antillocaprina and Ichthyosarcolites, for example, ended up implausibly placed as stem groups to the radiolitids in the cladogram of Skelton and Smith (2000). Fortunately, the subsequent recognition of intermediate forms has shown the two families containing the last two genera to have been derived from the caprinuloideids (Aguilar-Pérez, 2008; Mitchell, 2013b (this volume), and in press), as reflected in the family classification given herein; but the origin of *Dictyoptychus* remains unresolved.

Other issues that need to be addressed include the phylogenetic position of the Caprotinidae (with possible family-level nomenclatural implications, as noted above), as well as that of the Caprinulidae, besides investigation of a number of potential candidates for synonymy among rudist genera, not to mention species. On the other hand, much still remains to be done in terms of primary description on the rudists that dwelt in and around the margins of the Pacific (Skelton et al., 2013), with further possible implications for rudist phylogeny and classification.

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APPENDIX 1 GLOSSARY OF TERMS USED IN THE DESCRIPTION OF RUDIST MORPHOLOGY

- **Abapical/abumbonal.** Orientational term applied to a transverse section of a valve meaning viewed as if looking towards the commissural end of the valve from its apical, or umbonal end. When a *RV* is viewed thus, with its dorsal margin at the top, anterior is to the right and posterior to the left, and the converse is so for a *LV*.
- Accessory cavity. Discrete cavity that opens into the interior of a rudist valve, other than a tooth socket, and which is more or less separate from the main body cavity. An accessory cavity that lies on the outer side of a myophore (thereby separating it from the valve wall) is termed an ectomyophoral cavity (e.g., Figure 7), while one that is situated directly to the inside of a myophore, and is separated from the body cavity by a lamina, is termed an endomyophoral cavity (Figure 13).
- Adapical/adumbonal. Orientational term applied to a transverse section of a valve meaning viewed as if looking towards the apex, or umbo of the valve from its commissural end (equivalent to looking 'into' an isolated valve). When a RV is viewed thus, with its dorsal margin at the top, anterior is to the left and posterior to the right (e.g., Figure 11c), and the converse is so for a LV (e.g., Figure 11b).

Anterior myophore (am). See myophore.

Anterior tooth (at). See dentition.

Arête cardinale. See ligament.

- **Capuloid.** Used in reference to the shape of an upper valve: cap-shaped with the umbo usually projecting obtusely in the style of a Phrygian (or French 'Liberty') cap (**Figure 11a**).
- **Celluloprismatic** mesostructure. Distinctive modification of the ol in the RV and, in some, also the LV of most (but not all) radiolitids consisting of repeatedly stacked layers of tiny (usually of millimetric, to submillimetric width) hollow cells

(Figure 6d). In each cell layer the bounding vertical walls of the cells were built up from a continuous basal surface by localised enhancement of incremental shell growth, and abruptly capped off by the floor of the succeeding cell layer, on which the cell growth process was repeated (Regidor-Higuera et al., 2007; Figure 6c herein).

Central tooth (ct). See dentition.

Dentition. The arrangement of the interlocking hinge teeth and sockets, forming part of the aragonitic inner shell in rudists, with two prominent, knobby, 'pachyodont' teeth (anterior, *at*, and posterior, *pt*) in one valve, situated on either side of one (central, *ct*) tooth in the other. Primitive 'normal' dentition consists of two teeth in the *RV* and one, plus an incipient posterior toothlet, in the *LV* (**Figure 2**), while derived 'inverse' dentition comprises two *LV* teeth and one *RV* tooth (**Figure 5**; Douvillé, 1887; 1896). The central tooth is reduced or even lost in some highly derived inverse forms, while others possess supplementary toothlets (e.g., some antillocaprinids; **Figure 14a, b**).

Ectomyophoral cavity. See accessory cavity.

Endomyophoral cavity. See accessory cavity.

Left valve (LV). See shell.

Ligament. Primitively, rudist shell valves were connected by a functional external dorsal ligament of modified 'parivincular' type (i.e., of C-shaped cross section, with an extensional outer lamellar layer inserting along a flat, track-like bourrelet, and a compressive inner fibrous layer attached to the outer face of a thickened nymph; Figure 2). In the majority of rudists attaching by the *RV*, however, the ligament was secondarily invaginated (Figures 6b, 10b; see also Skelton, 1978; 1979), so becoming ineffective, and was eventually lost in some more derived forms. In some taxa, most notably in radiolitids and hippuritids, it became drawn inwards at the tip of an acute infolding of the *ol* (e.g., Figures 6a, b and 9a, b), sometimes referred to in the literature as the '*arête cardinale*'.

- Myophore. Projection on the inside of the shell supporting the insertion of an adductor muscle (e.g., Figures 2, 5, 6a, 7, among others). All rudists possessed myophores as part of the aragonitic inner shell, displaying a taxonomically useful variety of forms, and in some cases tilted in such a way as to yield neighbouring accessory cavities (e.g., Figures 7a, 13). Commonly used abbreviations are *am* for anterior myophore, and *pm* for posterior myophore.
- **Myocardinal apparatus.** The combined dentition and myophores, which in most rudist taxa are closely associated in each valve (e.g., **Figure 6a**). The configuration of the myocardinal apparatus is of fundamental importance in the higher level taxonomy of rudists.
- **Oscules.** External openings in the hippuritid *LV* formed by infolding of the valve margin above the heads of the pillars (**Figure 9a, b**). Similar structures are present also in the *LV* of a few derived radiolitids (e.g., *Osculigera*; see Vogel, 1970).

Outer shell layer (ol). See shell.

Pallial canals. Elongate, blind-ending canals penetrating the shell from the inner surface of one (usually the upper), or both valves, which in life housed papillae projecting from the outer surface of the mantle (Vogel, 1978). In many taxa their openings are limited to the periphery of the inner (aragonitic) shell, where they usually show a radially oriented, narrow tear-, to flame-like ('pyriform'; Figure 8a), or sub-rectangular cross-sectional shape (Figure 11d), but in more derived taxa canals of polygonal or rounded cross-sectional shape may invade the inner parts of the valve, as well, eventually even including the teeth and/or myophores in some (Figure 14a-d). They vary considerably in size and shape between different taxa and may contain tabulae (e.g., Offneria), or not (e.g., Plagioptychus). The term 'pseudocanals' is sometimes used in the literature for those found in the inner shell of certain derived radiolitids (e.g., Colveraia). Although the latter evolved independently from the canals seen in caprinids, for example (i.e., they are not homologous with the latter), they are nevertheless basically analogous in terms of mode of formation. Use of the term 'pseudocanal' dates from when virtually all canaliculate rudists other than the radiolitid examples were systematically treated as if they were related (as 'caprinids' sensu lato; e.g., in Dechaseaux et al., 1969). But with the explicit recognition that canals evolved independently in several different clades (as reflected in the classification herein), the distinction between canals and 'pseudocanals' has become meaningless, rendering the latter term redundant. Exceptionally, in a few radiolitids (e.g., Joufia), radiating canals also evolved in the calcitic ol of the LV. Vogel (1978) discussed a variety of possible (and not mutually exclusive) functions for pallial canals, from weight reduction and economic provision of rigidity to the shell as

well as inhibition of penetration by boring organisms, to the enhancement of respiration and/or suspension-feeding on the expanded mantle surface. Indeed, given the variety of form and distribution of canals among different groups of rudists, it is likely that their functions were correspondingly diverse. However, the pore and canal system in the *ol* of the LV in hippuritids (**Figure 9c-e**) is fundamentally distinct from the internally closed pallial canals, as they retain links with the outside via the open pores, through which they probably conducted suspension feeding currents (Schumann, 2010).

Parivincular ligament. See ligament.

Pillars. A pair of radial infoldings of the *ol* on the posterior flank of the *RV* in hippuritids (**Figure 9b**).

Posterior myophore (pm). See myophore.

Posterior tooth (pt). See dentition.

Proso-spirogyrate growth. See spirogyrate growth.

- **Radial.** Term applied to any feature (e.g., ribs, costae or pallial canals), or plane of section (e.g., **Figure 7a**), with an umbo-to-commissure orientation.
- **Radial bands.** A pair of radially oriented, discretely demarcated bands on the posterior flank of the attached valve, present in certain rudist taxa (most notably the radiolitids, in which their morphology is of taxonomic importance; **Figure 6e**).

Right valve (RV). See shell.

- Shell. Rudist bivalves are inequivalve, with one valve either the left valve (LV) or the right valve (RV), according to taxon – attached at least initially to some hard surface, and the other remaining free. All have an outer shell layer (ol), of variable thickness, consisting of fibrillar low-Mg calcite (e.g., Figure 9e), and an originally aragonitic (though rarely preserved thus; Figure 6b) inner shell, which includes the teeth and myophores. Primitively, the ol is relatively thin (~1 mm), but secondary thickening is a diagnostic character for certain taxa.
- Spirogyrate growth. Spiral valve growth in the style of a ram's horn, due to continuous tangential displacement of successive shell growth increments, causing the umbones to twist around as they are built out from the commissural margin (Figure 4a). Forward-spiralling umbonal growth is termed prosogyrate (Figure 2), and backward-spiralling, opisthogyrate.
- **Transverse section.** Section cutting across a rudist valve more or less parallel with the commissural plane (hence perpendicular to a radial section).
- **Uncoiled growth.** Tubular (conical to cylindrical) valve growth (**Figure 4b**) permitted by removal of the constraint of continuous tangential displacement of successive shell growth increments associated with invagination of the ligament in rudists (in contrast to spirogyrate growth).

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Rudist classification: nomenclatural correction of 'Suborder Radiolitidina Skelton, 2013' to 'Suborder Hippuritidina Newell, 1965'

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ABSTRACT. Following the protocol for taxon names above the family-group adopted for the revision of the Bivalvia volumes of the 'Treatise on Invertebrate Paleontology', 'Suborder Radiolitidina Skelton, 2013' is hereby replaced by 'Suborder Hippuritidina Newell, 1965'.

Key words: Bivalvia, Rudists, Order Hippuritida, Suborder Requieniidina, Suborder, nomenclature correction.

In the classification of rudist bivalves proposed by the author (Skelton, 2013, this volume) for use in the revised Bivalvia volumes of the 'Treatise Invertebrate Paleontology'. on currently in preparation, two new sister-group monophyletic suborders were erected within the Order Hippuritida Newell, 1965 (rudists), and named Requieniidina and Radiolitidina. The familial roots for these names were based on the oldest validly established families within each suborder, namely Requieniidae Kutassy, 1934, and Radiolitidae d'Orbigny, 1847, as determined by Bouchet et al. (2010). However, the Bivalvia 'Treatise' Coodinator, Joe Carter, has since drawn the author's attention to the protocol adopted for the volumes (Carter et al., 2011, p.

2), whereby 'Separate priority for names above and within the family-group is preferred because it allows for the retention of a number of widely used but otherwise lesser priority names above the family-group, such as Order Hippuritida'. Although taxon names above the family-group are not regulated by the ICZN Code (Ride et al., 1999), it is clearly desirable to maintain consistent practice for such names in the Bivalvia 'Treatise'. Accordingly, 'Suborder Radiolitidina Skelton, 2013' is hereby replaced by the name 'Suborder Hippuritidina Newell, 1965', in keeping with the priority of the established Order Hippuritida Newell, 1965. The name 'Requieniidina Skelton, 2013' is unaffected, however, so remains unchanged.

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