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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 Renngearten, 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 Plagiopythyidae 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 are monophyletic, according to current 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’ (http://www.paleotax.de/rudists/intro.htm/Taxonomic 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>
<thead>
<tr>
<th>Abbreviation</th>
<th>Description</th>
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<tr>
<td>am</td>
<td>anterior myophore</td>
</tr>
<tr>
<td>at</td>
<td>anterior tooth</td>
</tr>
<tr>
<td>ct</td>
<td>central tooth</td>
</tr>
<tr>
<td>LV</td>
<td>left valve</td>
</tr>
<tr>
<td>ol</td>
<td>outer shell layer</td>
</tr>
<tr>
<td>pm</td>
<td>posterior myophore</td>
</tr>
<tr>
<td>pt</td>
<td>posterior tooth</td>
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<tr>
<td>RV</td>
<td>right valve</td>
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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 suborders, Requieniida (Section 3.2) and 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 Pehlintsev’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 Capriniae d’Orbigny 1847 (based only on shared possession of pallial canals) and Caprotinidae Gray, 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) (=Trehmannellidae 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 a 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 Trehmannellidae (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.
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 REQUIENIIDINA 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, Dompevirin, 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 prosospiraytate 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 *Requienioida 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 “Réquiénidés” 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 (spiraytate 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.

- **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
- Bayleoida 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:
- Hylasma Paquier, 1898
- Kugleria Bouwman, 1938
- Lovetchenia Masse, 1993
- Matheronia Munier-Chalmas, 1873 (includes Munnieria 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 Requieniida.]

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 generic composition expanded relative to ‘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-eqvalve 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 Requieniida) 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
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 myocardial arc (Figure 6a) with sub-equal, prong-like at and pt that straddle reduced ct ridge* in RV (Figure 6b; or ct secondarily lost in

![Figure 4](image-url)  
**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).

![Figure 5](image-url)  
**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.
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).

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 an gentleman (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 plane-polarised 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.
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 well-substantiated 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 biostreames, 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)
Apolites 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)
Bourbonia Fischer, 1887 (includes Hardaghia Tavani, 1949, fide Pons et al., 1992)
Bystrickya Lupu, 1976 (?)
Chiapassella Müllerried, 1931
Contraspira Mitchell, 2009
Darendeella Karacabey-Oztemür, 1976
Distefanella Parona, 1901
Dubertretia Cox, 1965 (pro Kelleria Milovanović, 1938) (?)
Durania Douvillé, 1908
Eoradiolites Douvillé, 1909
Tekirdagia Özdemir, 2010 (mandatory correction of Tekirdagensis Özdemir, 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 Özdemir, 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 Özdemir (2010), although available and valid, refers mistakenly to Tekirdağ province in the Thrace Basin, west of Istanbul, through confusion of the type locality ‘Tscherkessköi’, as stated by Böhm (1927), with Çerkeş Köyü (Hereke) in the İzmit Bay region southeast of Istanbul (Sacit Özer, pers. comm., Feb., 2012).]
Fossilites Astre, 1957
Fundinia Sladići-Trifunović and Pejović, 1977
Glabrobournonia Morris and Skelton, 1995
Gorjanovicia Polsak, 1967 (see Fenerci-Masse et al., 2011)
Hacobjanella Atabekjan, 1976 (?)
Horechonia 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-Oztemür, 1980 (possibly includes Lattenbergites Lupu, 1987, fide Özer, in prep.)
Lapeirousella Milovanović, 1938 (includes Dechaseuxia Tavani, 1949, fide Pons et al., 1992)
Lapeirousia Bayle, 1878
Laskarevia Milovanović, 1984 (?)
Macgillavryia Rojas, Iturralde-Vinet and Skelton, 1996
Maghrebites Pons et al., 2012
Medeella Parona, 1924
Milovanovicia Polsak, 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
**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 reflected 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 yaegashi* (Yehara); Skelton et al., 2011; 2013; Sano et al., in prep)
- '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).

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**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 yaegashi* (Yehara), LV, 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

**Praepolypeirousia** Wiontzek, 1934

**Praeradiolites** Douvillé, 1902

**Pseudopolyconites** Milovanović, 1935 (includes *Duranddelgata* 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

**Tampa** Stephenson, 1922

**Thyrastylon** Chubb, 1956 (see Mitchell, 2010a)

**Vautrina** Milovanović, 1938
Peter Skelton. Classification of the Rudist Bivalves

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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 to fuel discussion over the phylogenetic classification of hippuritids (e.g., Bilotte, 1992; Steuber, 1999; Simonpiéri 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.
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 pre-occupied 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

**Praebartettia** 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. cornuacumin* (Bromn, 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

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**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 raggawiensis 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 (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 Dechaux 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 adumbral 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).


**Genera:**

- *Dictyoptychus* Douvillé, 1905 (syn. Trechmannella Cox, 1933)
- *Eodictyoptychus* Skelton and El Asa’ad, 1992
- *Semaillia* Morris 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’ dention (sensu Douvillé, 1887), retaining relatively primitive condition of unequal teeth in LV (at significantly larger than pt); LV pm root on posterior valve wall and separated from body cavity by (primitively) large endomyophoral cavity that is limited internally by salient lamina connecting ar 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 paleocommunities; 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
- *Pachytragia* Paquier, 1900 (see Skelton and Masse, 1998)
- *Praecaprina* Paquier, 1905
- *Pseudocaprina* Chartrousse and Masse, 2004
- *Schiosia* Böhm, 1892
- *Sphaerocaprina* 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
- *Guzyella* Alencáster, 1999
- *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)
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. ‘Caprinoida 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 antillocapriniids (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 (umbonal 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 grooves in RV (Figure 14a, b), or secondarily form broad platforms parallel with commissural plane* (Figure 14c, d).

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
- *Roussела* 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:**

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, *Requieniida* 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) to earliest Cretaceous (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 *Hippuritididae*, with the added interest of the polyconid genus *Tepeyacina* 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; Simonpietri 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 *Dictyoptychus*, *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.

**Acknowledgements.** Numerous rudistological and malacological colleagues have helped me in the pursuit both of phylogenetic transparency and of correct taxonomic and nomenclatural practice in the development of this classification over several years. I am especially grateful for helpful comments concerning earlier versions.
of the classification and/or assistance with access to pertinent specimens, literature and images from Javier Aguilar-Pérez, Rüdiger Bieler, Philippe Bouchet, Joe Carter, Stefan Götz, Ahmad Khazaee, Jean-Pierre Masse, Simon Mitchell, Noel Morris, Sacit Özer, Enric Pascual-Cebrian, Jean Philip, Abel Prieur, Shin-ichi Sano, Simon Schneider, Robert Scott, Pietro di Stefano, Jann Thompson, Jon Todd and Thomas Steuber, besides many others too numerous to name here who have also helped in various ways. The final version has benefited from the constructive reviews of Robert Scott and Thomas Steuber, as well as clarifications needed to address the comments of an anonymous reviewer. Notwithstanding the obviously collaborative nature of this enterprise, I must accept the final responsibility for any omissions or errors that remain.

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Peter Skelton. Classification of the Rudist Bivalves


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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 hiripurid 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., Plagiopycthus). The term ‘pseudocanals’ is sometimes used in the literature for those found in the inner shell of certain derived radiolitids (e.g., Colvernia). 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 hiripurids (Figure 9e-h) 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 hiripurids (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).