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## ***Pachyrisma grande* Morris & Lycett, 1850: redescription and assessment of its potential role as an ancestor to the Hippuritida**

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### Abstract

*Pachyrisma grande* Morris & Lycett, 1850, the type species of the genus *Pachyrisma*, from the Bathonian (Middle Jurassic) of western England is redescribed, a new lectotype is designated, and rich photographic illustration is provided. The validity of the family Pachyrismatidae is substantiated. The phylogenetic relationships of *Pachyrisma grande* are discussed. Based on reinterpretation of several shell characters and newly discovered features of ornamentation and hinge dentition, an origin in the Cardioidea rather than the Megalodontidae is suggested for *Pachyrisma grande*. These characters also support the species as the closest known ancestor of the Hippuritida, implying a potential origin of the Hippuritida in the Cardioidea. A phylogenetic analysis of *Pachyrisma grande* and presumed related taxa is needed to put the suggested evolutionary relationships to test.

**Key words:** Bivalvia, Megalodontidae, Cardioidea, Jurassic, Triassic, phylogeny, taxonomy.

### Zusammenfassung

*Pachyrisma grande* Morris & Lycett, 1850, die Typusart der Gattung *Pachyrisma* aus dem Bathonium (Mitteljura) von West-England wird beschrieben, ein neuer Lectotyp wird festgelegt, und die Art wird ausführlich fotografisch dokumentiert. Die Gültigkeit der Familie Pachyrismatidae wird bestätigt. Die phylogenetischen Beziehungen von *Pachyrisma grande* werden diskutiert. Basierend auf einer Neuinterpretation einiger Schalenmerkmale und mehrerer neu entdeckter Eigenheiten der Ornamentierung und des Schlosses wird für *Pachyrisma grande* eine Abstammung von den Cardioidea, nicht von den Megalodontidae, vorgeschlagen. Diese Merkmale sprechen auch für die Annahme, dass es sich bei *Pachyrisma grande* um den letzten bekannten Vorläufer der Hippuritida handelt. Folglich stammen die Hippuritida möglicherweise von den Cardioidea ab. Eine phylogenetische Analyse von *Pachyrisma grande* und mutmaßlich nahe verwandten Taxa ist notwendig, um die vorgeschlagenen Verwandtschaftsverhältnisse zu überprüfen.

**Schlüsselwörter:** Bivalvia, Megalodontidae, Cardioidea, Jura, Trias, Phylogenie, Taxonomie

## 1. Introduction

The family Pachyrismatidae was first established in a revised classification scheme for the Bivalvia by Scarlato & Starobogatov (1979), but never further documented. As a result, its content beyond the nominal genus *Pachyrisma* Morris & Lycett, 1850 remains ambiguous. While at first sight this might simply be considered an issue of classification, there is a wider phylogenetic implication to this topic, since the genus *Pachyrisma* and several supposedly closely related taxa have been suggested to form the phylogenetic link between two important and highly diversified groups of Mesozoic Bivalvia, i.e. the Triassic Megalodontoidea and the Late Jurassic to terminal

Cretaceous Hippuritida (e.g. Skelton & Smith 2000).

Similarities of *Pachyrisma grande* with *Megalodon* were noted already by Morris & Lycett (1850, 1853), who established the family Megalodontidae Morris & Lycett, 1853 [albeit originally misspelled as ‘Megalodontidae’; see Opinion 1829 (1996)] and included *Pachyrisma* therein. Later on, the peculiar morphology of *Pachyrisma* attracted the attention of Georg Boehm, who started to analyse its evolutionary relationships. However, his research focused on several other species collected in Poland, Germany and northern Italy rather than on the type species *Pachyrisma grande* (e.g. Boehm 1882b, 1884, 1891, 1892). He agreed with Morris & Lycett (1850, 1853) that *Pachyrisma* descended from Devonian megalodontids, and pro-



**Figure 1:** Overview map of the area southeast of Stroud, Gloucestershire, United Kingdom. Locations where *Pachyrisma grande* has been found are indicated. Base map modified from British Ordnance Survey sources.

posed that it had given rise to a group of cardiids, possibly to *Fragum* or *Serripes* (Boehm 1891: p. 54). Furthermore, he considered another Triassic 'megalodontid', *Megalodon triqueter* var. *pumilus* Gümbel, 1862, which he placed in his new genus *Protodicerias* Boehm, 1891, as the progenitor of *Dicerias* Lamarck, 1805, and thus the Hippuritida (Boehm 1891: p. 54). Dechaseaux (1940) agreed on the origin of *Pachyrisma* in megalodontids, but did not further elaborate on its descendants; apparently, she did not have a specimen of *Pachyrisma grande* for study. Cox & LaRocque (1969) continued to include *Pachyrisma* in the Megalodontidae without discussing its phylogenetic relationships. The sketchy drawings of the hinge of *Pachyrisma* by Végh-Neubrandt (1982: p. 122) do not suggest a deep understanding of its true morphology. He basically confirmed Boehm's (1891) concept, but added a number of Triassic megalodontids to the two clades terminating in *Pachyrisma* and *Dicerias* (Végh-Neubrandt 1982: p. 134). To summarise, for nearly 150 years the relationships of *Pachyrisma* were discussed based on drawings, without proper restudy of the type species *Pachyrisma grande*.

However, as will be shown below, the illustrations of the hinge region of *Pachyrisma grande* by Morris & Lycett (1850, 1853) were misleading, likely due to the limited preservation of the respective specimens. Boehm (1882b) had produced a more accurate drawing, but his specimen of *Pachyrisma grande* was rather fragmentary. The incorrect drawings published by Morris & Lycett (1853) were reproduced in several textbooks as well as in the bivalve volumes of the *Treatise on Invertebrate Paleontology* (Cox & LaRocque 1969), which established the misunderstanding of the morphology of this species as well as an incorrect interpretation of its phylogenetic context. Skelton & Smith (2000) were the first to go back to the type material of *Pachyrisma grande*, and included the species in their phylogenetic analysis to infer the potential ancestry of 'megalodontids' to the Hippuritida. However, their analysis was focused on the Hippuritida, and *Pachyrisma* was treated only cursorily.

The validity and content of the family Pachyrismatidae Scarlato & Starobogatov, 1979 as well as its relationships can only be established based on

restudy of type or topotypic material. Six Jurassic genera that were thought to be closely related form the basis for discussion on the composition of the Pachyrismatidae (Tab. 1; see also MolluscaBase 2015). For the present study, type specimens and/or topotypic material of *Pachyrisma grande* Morris & Lycett, 1850, *Pachyrisma beaumonti* Zejszner, 1862 and *Bucardites chamaeformis* von Schlotheim, 1820 was assessed, and various additional material was studied. *Pachyrisma grande* is redescribed, errors in previous descriptions are specified and corrected, and newly discovered characters are presented. The validity of the family Pachyrismatidae and its potential phylogenetic relationships are briefly discussed, and the necessity of further phylogenetic analysis is highlighted.

## 2. Material and methods

All specimens of *Pachyrisma grande* come from a relatively small area in the county of Gloucestershire in southwestern England (Fig. 1). 'In the vicinity of Minchinhampton and Chalford' is given as the type locality by Morris & Lycett (1850). Two of the originals of Morris & Lycett (1853) were collected at Bussage (GB3D Type Fossils 2016). Further material in the Sedgwick Museum, Cambridge, UK, comes from Minchinhampton, Bisley and 'near Stroud'.

As indicated by Woodward (1894) and Arkell (1933), *Pachyrisma grande* was found in Bussage and at Cowcombe Hill, in rocks that are now assigned to the White Limestone Formation, presumably belonging to the Ardley Member sensu Palmer (1979) and Sumbler (1984); thus, the species is mid Bathonian in age. The shells probably occur in a single bed or a few successive beds, over no more than half a metre of stratigraphic thickness (Morris & Lycett 1853; Arkell 1933).

Due to the lack of present-day outcrop, we were unable to find the respective bed(s) and fossils during a short survey undertaken in Gloucestershire in spring 2015. Instead the present study is based on museum material only. Approximately 30 specimens of *Pachyrisma grande* were studied, but only a few of them are sufficiently preserved to provide insight into hinge morphology. Well preserved specimens of several supposedly related species were studied for comparison. All specimens with the exception of those in Figure 11 were coated with ammonium chloride for the photographs.

### 2.1. Material of *Pachyrisma grande* studied

Naturhistorisches Museum Wien (NHMW): left valve (NHMW 1869/0010/0400), syntype of Morris & Lycett (1850), paralectotype designated herein; several additional specimens.

Bayerische Staatssammlung für Paläontologie und Geologie, Munich (SNSB-BSPG): right valve,

original of Boehm (1882b) (SNSB-BSPG AS I 1973).

British Geological Survey (BGS): articulated specimen (BGS GSM 9799) and left valve (BGS GSM 9800), originals of Morris & Lycett (1853) [= lectotype and syntype sensu Cox & Arkell (1948)]; photographs downloaded from GB3D Type Fossils (2016).

Sedgwick Museum, University of Cambridge (SMC): one left valve (J24220), three right valves (J24213, J24214, J24224); several additional specimens.

Natural History Museum London (NHM): right valve (NHM 49964), syntype of Morris & Lycett (1850), original of Morris & Lycett (1853) and Skelton & Smith (2000), new lectotype proposed herein; several additional specimens.

### 2.2. Additional material studied

Geologische Bundesanstalt, Wien (GBA): *Pachyrismegalon chamaeformis* (von Schlotheim, 1820); originals of Tausch von Gloeckelsturn (1890).

Muséum national d'histoire naturelle, Paris (MNHN): numerous specimens of *Diceras* and *Epidiceras*.

Museu Geológico, Lisbon (GML): type material of *Protocardia gigantea* Schneider, Fürsich & Werner, 2010.

## 3. Systematic palaeontology

Family Pachyrismatidae Scarlato & Starobogatov, 1979

Genus *Pachyrisma* Morris & Lycett, 1850  
[synonym: *Pachyerisma* Bayan, 1874; unjustified emendation]

Type species: *Pachyrisma grande* Morris & Lycett, 1850, by monotypy.

Remark: In a preliminary account, Lycett (1848) had assigned *Pachyrisma grande* to '*Cardilla*', a misspelling of the extant genus *Cardilia* Deshayes, but without establishing it as a new species. The validity of the genus *Pachyrisma* and its type species was thus never questioned. Bayan (1874) emended the spelling of *Pachyrisma* to *Pachyerisma*, which constitutes an incorrect subsequent spelling, and is thus an unjustified emendation.

*Pachyrisma grande* Morris & Lycett, 1850  
Figs 2–9

\*v 1850 *Pachyrisma grande*. – Morris & Lycett: pp. 401–402, unnumbered text-fig.

1853 *Pachyrisma grande*, Lycett. – Morris & Lycett: pp. 79–80, pl. 8, figs 1–5.

Description: Shell up to several millimetres thick and heavy; large, likely up to 150 mm in height, as indicated by proportions of large fragmentary specimens. Shell equivalve; shell higher than long, outline suboval, with a distinct, blunt, almost rectangular posterior-ventral corner. Anterior shell margin gently incurved directly below umbo. Shell strongly



coiled; umbo strongly prosogyrate. Sharp posterior bend separating shell flank and area, which meet at a sharp angle. Upper, oldest third of area almost flat, with a shallow median sulcus (Fig. 7B, C). Anterior and posterior parts of area starting to bend to enclose a blunt angle approximately at and below hinge plate (Fig. 7B). Shell almost rhombic in dorsal view (Fig. 7B). Shell flank and area ornamented with distinct, slightly irregular growth lines (Figs 7A, 8B, D). Area additionally ornamented with ten or more radial costellae, at least in its anterior part (Figs 6, 7C).

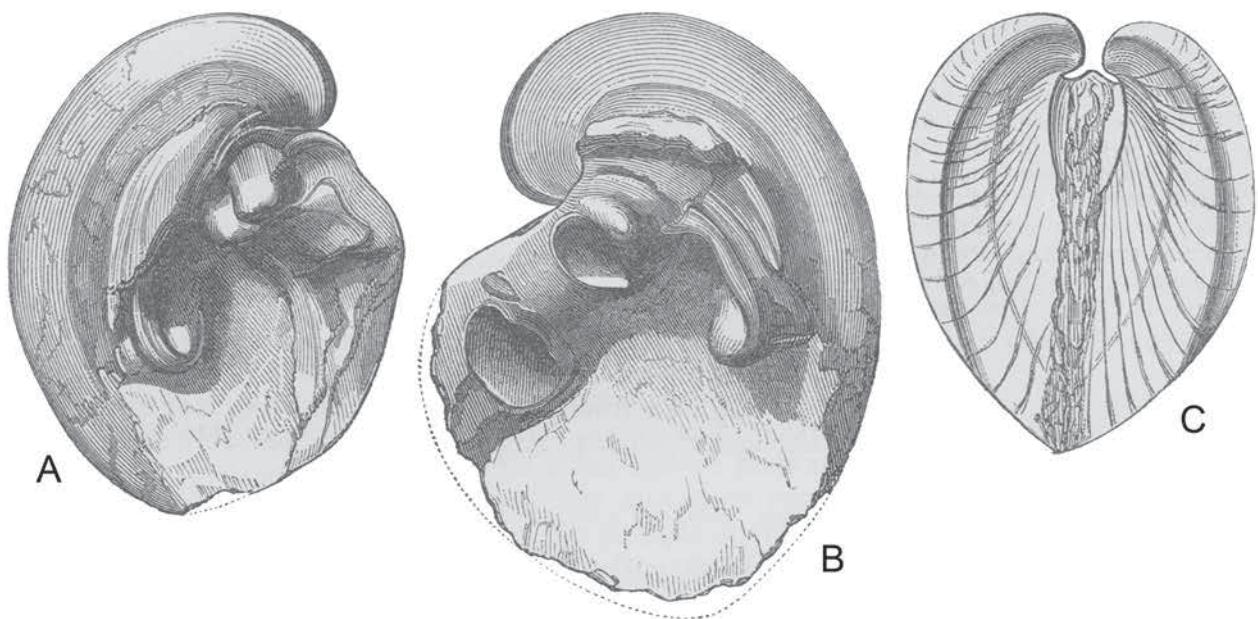
Hinge plate massive, very high. Nymph moderately long (approximately half of length of hinge plate), arcuate, very prominent, blade-like; sharply truncated, almost straight at posterior end. Hinge of right valve (Figs. 6, 7, 8C) with prominent, elongate, almost blade-like, arcuate posterior cardinal tooth 3b, its top end almost fusing with anterior end of nymph. Anterior cardinal tooth 3a weak, fusing with shallow ventral rim of deep tooth socket 2'. Anterior lateral tooth AI small but distinct, blunt, positioned directly above anterior adductor muscle scar; flanked by shallow tooth socket AI' at its anterior side. Posterior lateral tooth PI a faint elongate swelling, indistinct in larger specimens (Fig. 9); flanked by shallow, elongate tooth socket PII' at its posterior side. Hinge of left valve (Figs. 4, 5, 8F) with single, prominent, peg-shaped, central cardinal tooth 2, flanked by relatively deep sockets 3a' and 3b'; sockets connected at dorsal side of tooth, forming an arcuate trench. Anterior lateral tooth AI small but distinct, blunt, positioned directly above anterior adductor muscle scar; tooth socket AI' not distinct. Posterior part of hinge plate not preserved.

Anterior adductor muscle scar large, deeply sunken (Figs 7C, 8C, F). Posterior adductor muscle scar indistinct, positioned on elongate, channel-shaped posterior myophore below hinge plate (Fig. 5). Pallial line consisting of a 'dotted line' of small distinct attachment scars (Fig. 7C). Additional row of wider-spaced mantle attachment scars possibly present; only two scars visible in one specimen (Fig. 7C).

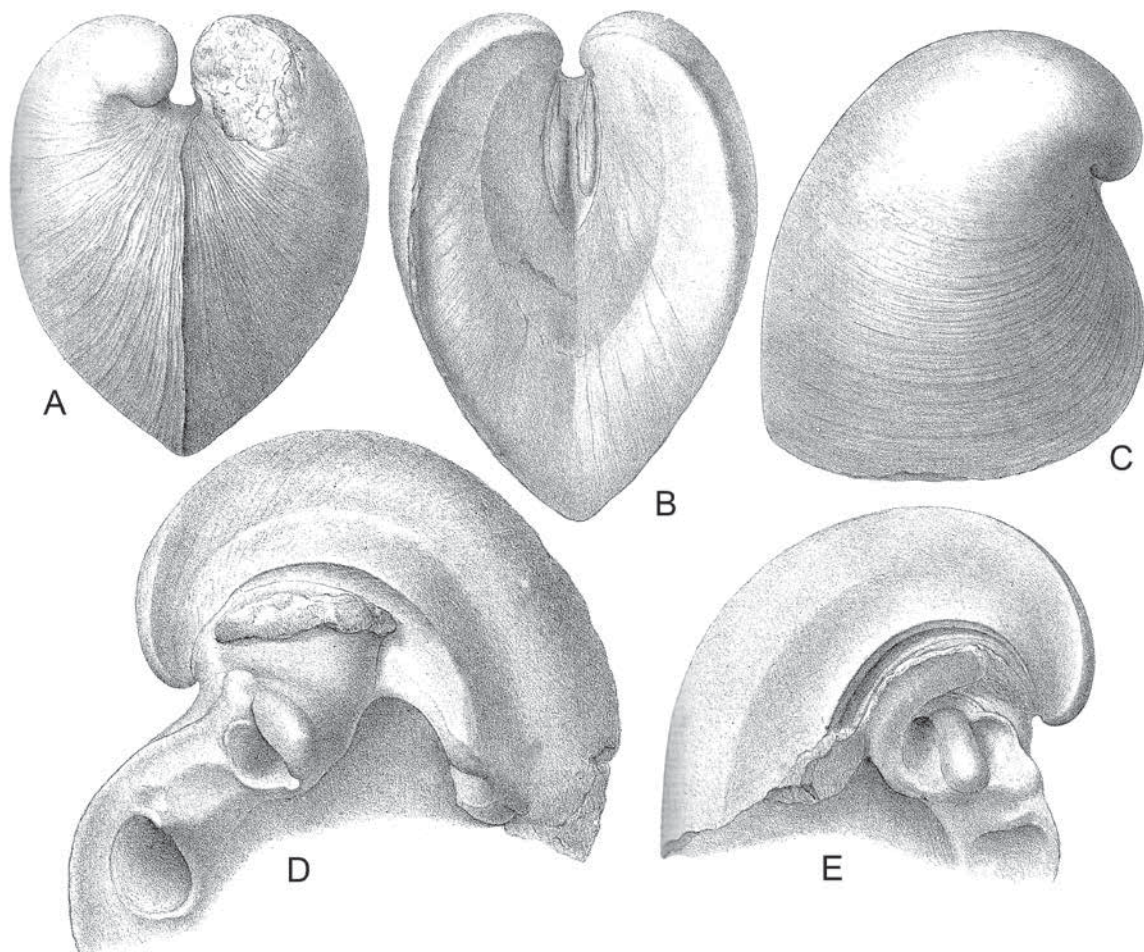
## 4. Discussion

### 4.1. Syntypes and lectotype

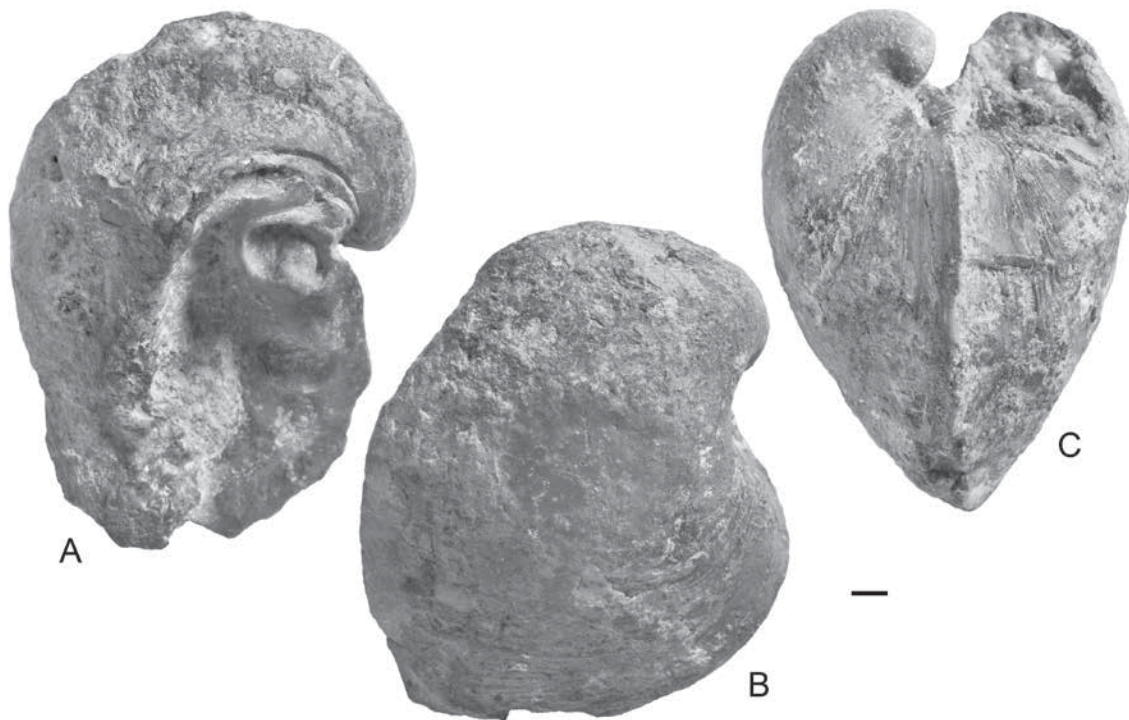
*Pachyrisma grande* was established by Morris & Lycett (1850: p. 401). A diagnosis in Latin and a short description in English were provided and three specimens of *Pachyrisma grande* were illustrated as woodcuts in an unnumbered text-figure: a left valve, a right valve (both shown from inside) and a specimen with contiguous valves (posterior-dorsal view; Fig. 2). No holotype was designated, so these three specimens are syntypes. In the bivalve volume of their monograph on the 'Mollusca from the Great Oolite', Morris & Lycett (1853) provided additional description and greatly improved drawings of *Pachyrisma grande*. Again, three specimens were illustrated, a left valve (pl. 8, fig. 3), a right valve (pl. 8, fig. 4) (both shown from inside), and a specimen with contiguous valves, (anterior, posterior-dorsal and right-lateral views) (pl. 8, figs 1, 2, 5; Fig. 3). Only the right valve was figured both in 1850 and 1853 and is a syntype of *Pachyrisma grande*; the other two specimens were not illustrated in 1850, and are



**Figure 2:** Rearranged unnumbered text-figure of Morris & Lycett (1850), showing drawings of the syntypes of *Pachyrisma grande*. A. Left valve from inside; paralectotype designated herein; NHMW 1869/0010/0400. B. Right valve from inside; new lectotype designated herein; NHM 49964. C. Articulated specimen from back.

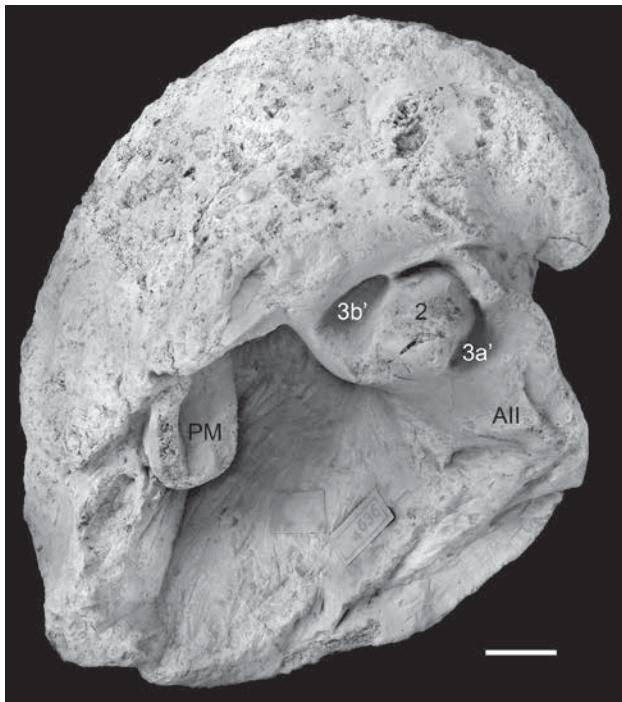


**Figure 3:** Rearranged plate of Morris & Lycett (1853), showing drawings of *Pachyrisma grande*. A–C. Double-valved specimen from front (A), back (B) and right side (C); BGS GSM 9799. D. Right valve from inside; syntype; lectotype designated herein; NHM 49964. E. Left valve from inside; BGS GSM 9800.



**Figure 4:** Originals of *Pachyrisma grande* figured by Morris & Lycett (1853). A. Left valve from inside; Bussage, Gloucestershire, UK; BGS GSM 9800. B, C. Double-valved specimen from right side (B) and front (C); Bussage, Gloucestershire, UK; BGS GSM 9799. Photographs downloaded from GB3D Type Fossils (2016). Scale bar approximately 10 mm.

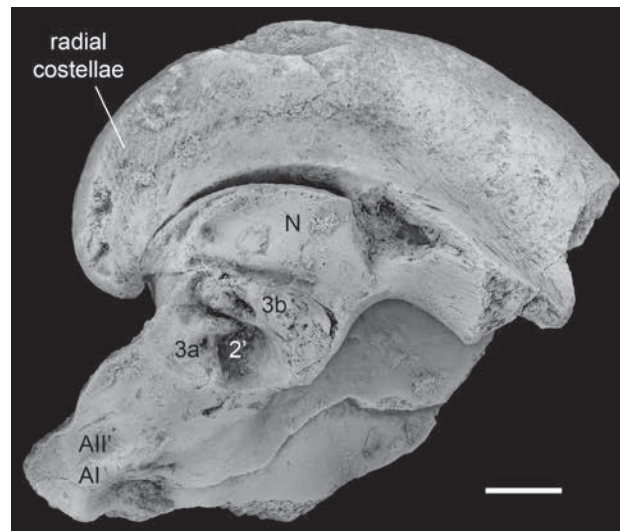




**Figure 5:** Left valve of *Pachyrisma grande* from inside; syntype of Morris & Lycett (1850), paralectotype designated herein; NHMW 1869/0010/0400. Abbreviations used in Figures 5–11: AA = anterior adductor muscle scar. AI, All = anterior lateral teeth of right valve. All, All' = anterior lateral tooth of left valve and corresponding socket. AM = anterior myophore. N = nymph. PI = posterior lateral tooth of right valve. PlI' = corresponding socket of posterior lateral tooth in left valve. PL = pallial line. PM = posterior myophore. 2, 2' = central cardinal tooth of left valve and corresponding socket. 3a, 3a' = anterior cardinal tooth of right valve and corresponding socket. 3b, 3b' = posterior cardinal tooth of right valve and corresponding socket. Scale bar = 10 mm.

thus not types. The articulated specimen illustrated in 1850 (Fig. 2C) is clearly broken posteriorly where the valves join. In the articulated specimen illustrated in 1853 the posterior shell portion is complete (Fig. 3B). The left valve illustrated in 1850 has the posterior myophore preserved (Fig. 2A), while it is broken in the left valve illustrated in 1853 (Fig. 3E).

When Cox & Arkell (1948) revised the taxonomy of Morris & Lycett (1853), the articulated specimen figured in 1853, held by the British Geological Survey (GB3D Type Fossils 2016), was designated as the lectotype of *Pachyrisma grande* (see revised plate captions of Cox & Arkell 1948). However, since this specimen is not a syntype (see above), the designation is invalid, and a new lectotype has to be designated from the three syntypes figured by Morris & Lycett (1850). One of these syntypes, the right valve, is stored at the British Museum of Natural History in London (NHM 49964; figured by Skelton & Smith 2000: p. 99, fig. 1a). Since it was figured in both the original article and the monograph (Morris & Lycett 1850, 1853), it is designated as the new lectotype herein. A second syntype, the left valve, was recently discovered at the Naturhistorisches Museum Wien (Fig. 5), and is designated as a paralectotype herein. The whereabouts of the third syntype are unknown.

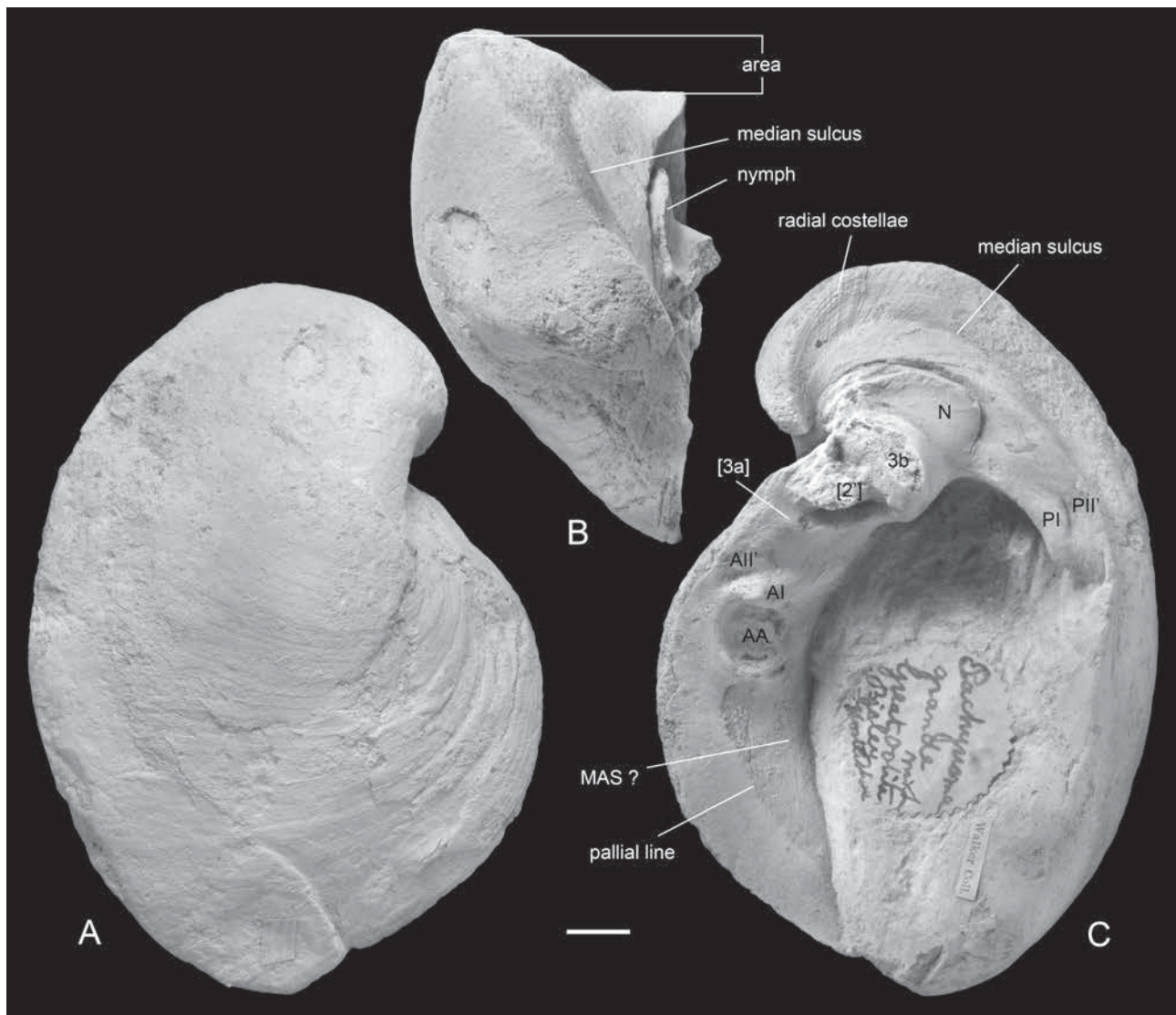


**Figure 6:** Right valve of *Pachyrisma grande* from inside. Original of Boehm (1882b); Minchinhampton, Gloucestershire, UK; SNSB-BSPG AS I 1973. For abbreviations see Figure 5. Scale bar = 10 mm.

#### 4.2. Shell shape, shell structure and ornamentation

*Pachyrisma grande* generally resembles several Late Triassic Megalodontoidea, in particular of the genera *Neomegalodon* or *Triadomegalodon*, with respect to shell shape (see Hoernes 1880: pls 2–7 and Végh-Neubrandt 1982 for illustrations). Common features are the coiled, strongly opisthogyrate shell, the pronounced posterior bend, where the shell flank and area join at sharp angles, the almost rectangular posterior-ventral corner and the gentle incurvature of the anterior shell margin just below the umbo. However, *Pachyrisma* lacks the pronounced lunula seen in all species of the aforementioned megalodontids. Shell shapes similar to *Pachyrisma* – without a lunula – occur in *Protodicerias* Boehm, 1891 from the Pliensbachian of northern Italy, *Pachymegalodus timorensis* Krumbeck, 1923 from the Pliensbachian of Timor (Indonesia) and *Pachyrisma bayani* Gemmelaro, 1876 from the Lower Tithonian of Sicily (Italy).

As already reported by Hautmann (2006), the shells of *Pachyrisma grande* generally consist entirely of sparry calcite, suggesting recrystallisation of a formerly aragonitic shell. Often, this results in a somewhat granular, rough shell surface, obstructing details of ornamentation. Of all the specimens studied, a single superbly preserved right valve has distinct radial ornament of ten or more costellae on the area, at least during early growth (Fig. 7C). A second specimen may show at least traces of it (Fig. 6). Similar ornament occurs in *Pachyrisma beaumonti* Zeisner, 1862 (Fig. 10B), *Cardium septiferum* Buvignier, 1843 and in several other cardiids, e.g. in *Protocardia* (Fig. 10D). Radial ornamentation is also common in Hippuritida, including the basal Dice-ratidae and Epidiceratidae, where it is confined to the thin outer calcitic shell layer, and commonly not



**Figure 7:** Right valve of *Pachyrisma grande* from outside (A), top (B) and inside (C); Bisley, Gloucestershire, UK; SMC J24213. Important shell characters are indicated. Squared brackets indicate hinge characters not properly featured. For abbreviations see Figure 5. Scale bar = 10 mm.

preserved in recrystallised shells (own observations and personal communication P. Skelton, 2015; Fig. 11). This outer calcitic shell layer is regarded as an important apomorphy of the Hippuritida by Skelton & Smith (2000). Whether the radial ornament in *Pachyrisma grande* is also confined to an outer calcitic shell layer would need to be tested, however, by sectioning a less beautifully preserved specimen than that shown in Fig. 7.

#### 4.3. Nymph and dentition

The erroneous illustration of the nymph was one of the main issues in the drawings provided by Morris & Lycett (1850, 1853; Figs 2A, B, 3D, E) and Boehm (1882b). As can be seen in the respective photographs, the nymph was not properly preserved or simply not freed from the matrix in the specimens studied by these scholars (Figs 4A, 5), or seemingly broken due to adjacent shell breakage (Fig. 6).

As can be inferred from Figures 7C, 8F and 9, the nymph is arcuate, moderately long, very prominent, and has a sharply truncated almost straight posterior end. It thus indicates the presence of a well-developed parivincular external ligament. Its anterior end and the anterior-dorsal end of the main hinge tooth 3b emerge at roughly the same position from the hinge plate and seem almost fused. A similarly shaped nymph occurs in *Cardium septiferum* Buvignier, 1843, *Pachyrisma beaumonti* Zejssner, 1962 (Fig. 10A), *P. royeri* Bayan, 1874 and *P. tombecki* Bayan, 1874, but also in *Pterocardia* Bayan, 1874. Moreover, basal rudists, i.e. Diceratidae and Epidiceratidae, have similarly arcuate nymphs, albeit without the sharp posterior truncation (Fig. 11).

The woodcuts and drawings of the hinge teeth provided by Morris & Lycett (1850, 1853) are partly erroneous and misleading. As correctly stated in the original description, the left valve has a single cardinal tooth 2. Two cardinal teeth are present in the





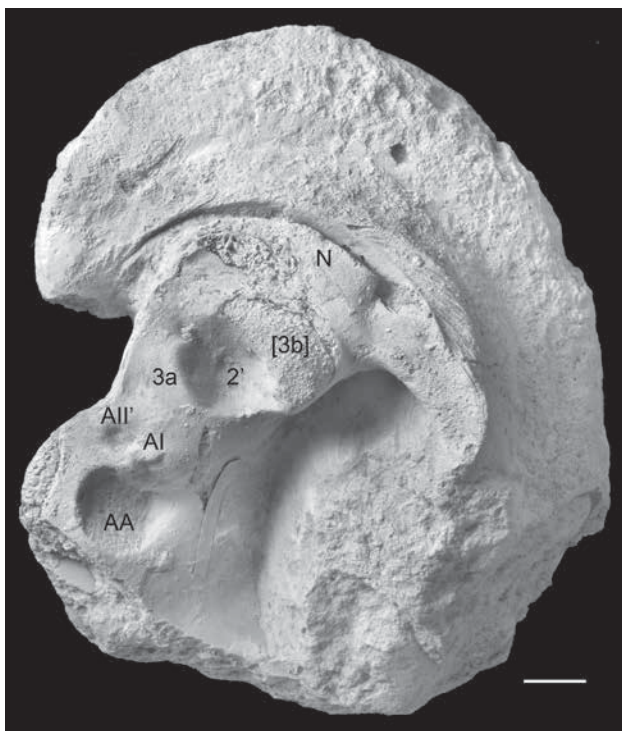
**Figure 8:** *Pachyrisma grande*. A–C. Right valve; near Stroud, Gloucestershire, UK; SMC J24224. A. Oblique view from front. B. View from front. C. Inside view. D–F. Left valve; Minchinhampton, Gloucestershire, UK; SMC J24220. D. View from front. E. Oblique view from front. F. Inside view. For abbreviations see Figure 5. Scale bar = 10 mm.

right valve, the anterior of them (3a) relatively small but distinct (accessory tooth of Morris & Lycett 1850, 1853), the posterior one (3b) prominent. Moreover, a weak anterior lateral tooth is present in both valves (Al, All), not only in the right one, as stated by Morris & Lycett (1850, 1853). The presence of a posterior lateral tooth (PI) is a newly discovered character, and is best seen in the ontogenetically relatively young specimen of Figure 7C. In the much larger, older specimen in Figure 8F, the posterior lateral tooth is much reduced; it is absent in the specimen in Figure 9. Adequately preserved left valves are unavailable, and the presence of a posterior lateral PII could not

be established, but seems likely, based on the shallow socket behind PI in the right valve of Figure 7C. The presence of weak lateral teeth at least in young specimens suggests that these are a plesiomorphic character, and became progressively reduced in *Pachyrisma grande*. However, several stratigraphically much younger species that have been assigned to *Pachyrisma*, e.g. *Pachyrisma beaumonti* Zejszner, 1962 (Fig. 10A), *P. royeri* Bayan, 1874 and *P. tombecki* Bayan, 1874 show strongly expressed anterior and posterior cardinals.

In Oxfordian basal Hippuritida assigned to *Diceras* Lamarck, 1805 or *Epidiceras* Douvill , 1935, the





**Figure 9:** Right valve of *Pachyrisma grande* from inside; Minchinhampton, Gloucestershire, UK; SMC J24214. Note that the posterior cardinal tooth 3b is broken and was restored. For abbreviations see Figure 5. Scale bar = 10 mm.

hinge is similarly structured as in *Pachyrisma grande* (Skelton & Smith 2000; Fig. 11). A distinct anterior cardinal tooth 3a and a prominent posterior cardinal tooth 3b in the right valve, both arcuate in cross section, enclose a prominent arcuate central cardinal tooth 2 in the left valve; lateral teeth are absent (Fig. 11).

#### 4.4. Pallial line, mantle attachment scars and muscle attachment.

These features are only preserved in the near-immaculate specimen of Figure 7, where the anterior part of the inner shell surface is free from matrix. The pallial line is distinct and entire, with a continuous series of more deeply engraved attachment scars, giving the impression of a dotted line. A second row of more widely spaced, small mantle attachment scars is possibly present at approximately 10 mm distance from the pallial line, where at least two small scars seem to occur. Similar scars, both along the pallial line and in a second, more widely spaced row, occur in *Pachyrisma beaumonti* Zejszner, 1862 (Fig. 10A). A peculiar feature of *Pachyrisma grande* is the presence of a posterior myophore, or myophoral ledge. Similar myophoral ledges exist in *Cardium septiferum* Buvignier, 1843, *Pachyrisma beaumonti* Zejszner, 1862 (Fig. 10A), *P. royeri* Bayan, 1874 and *P. tombecki* Bayan, 1874, but also in *Diceras* and *Epidiceras* (Fig. 11).

#### 4.5. Palaeoecology

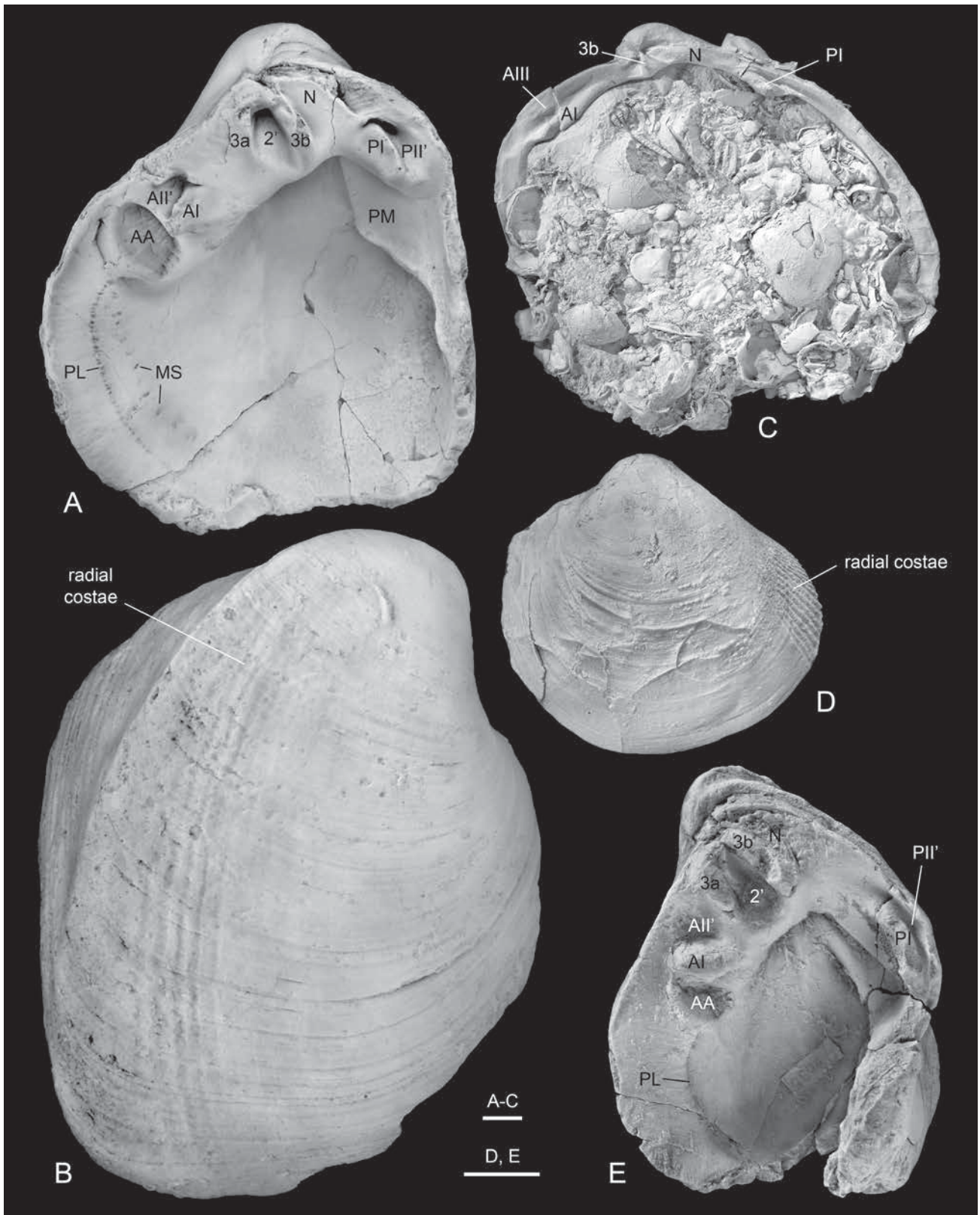
Morris & Lycett (1850: p. 399) describe the fossil assemblage with *Pachyrisma grande* as follows: “*Pachyrisma* occurs in a vertical thickness of only half a yard; ... the shells are clustered together in great numbers, the valves being both separated and in apposition; and it is worthy of notice that they constituted almost the sole testaceous animals within the narrow limits of their habitat; no other bivalve is found there, and the univalves consist only of a few casts of two species of our new genus *Purpuroidea* and two of *Natica*.” In other words, the shells occur in high abundance and form a dense, almost monospecific shell bank, accompanied only by a few gastropods (Lycett 1848; Morris & Lycett 1850, 1853; Woodward 1894). Judging from its shell shape, *Pachyrisma grande* was an epibenthic recliner, resting on the sediment on its broad posterior side. This position would have been very stable, since the centre of gravity of the shell, and certainly also of the living animal, is positioned in its dorso-posterior part. Furthermore, this position would have permitted respiration and food intake along the anterior-ventral margins of the shell when opened, opposite to the ligament and perpendicular to an axis intersecting both adductor muscles. A life position with the anterior shell face half submerged in the sediment, as suggested for certain megalodontids by Zapfe (1957), is anatomically impossible. Likely, *Pachyrisma grande* settled in lagoonal habitats with a relatively low sedimentation rate, since fairly stable conditions over several years are a prerequisite for the growth of shells of that size.

The formation of large, dense, virtually monospecific shell clusters is a trait shared with Diceratidae and Epidiceratidae (and numerous more derived Hippuritidae), which often formed extensive, paucispecific bio-constructions largely devoid of cementing epibionts and dwellers (personal observation; work in progress).

#### 4.6. Phylogenetic implications

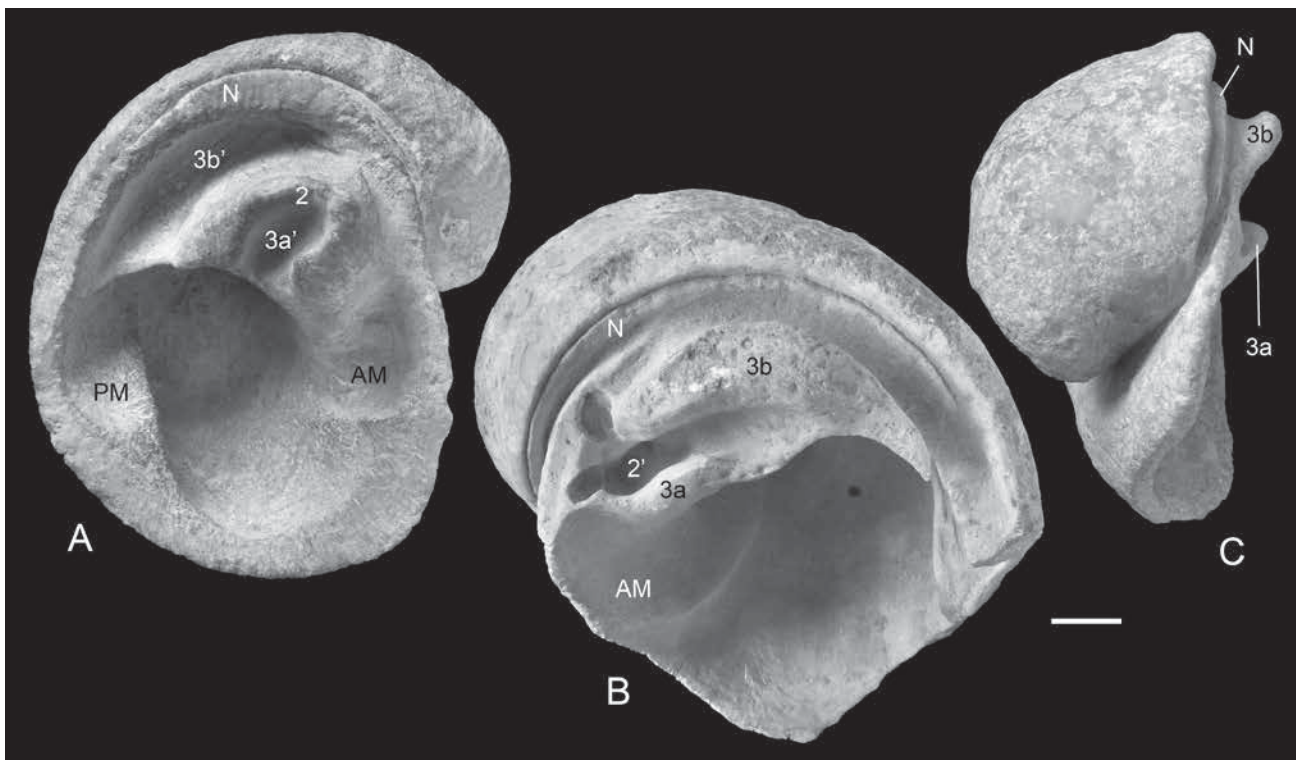
##### 4.6.1. Origins

The origin of *Pachyrisma grande* is enigmatic. Most Triassic Megalodontidae are insufficiently known, due to the lack of shell preservation, or the lack of exposed hinges, and the author has not had the opportunity to study sufficiently well-preserved material. Two features, however, seem to be consistent in Megalodontidae, but significantly different from *Pachyrisma grande*. Megalodontidae generally seem to lack the distinct and well defined nymph seen in *Pachyrisma*, while they generally possess a distinct lunule, which is absent in *Pachyrisma*. Moreover, no radial ornament has been reported in megalodontids. With *Protocardia* Beyrich, 1845, which is well known from Late Triassic to Late Cretaceous strata, *Pachyrisma grande* shares a single set of la-



**Figure 10:** Cardioida. A, B. *Pachyrisabella beaumonti* (Zejszner, 1862); Tithonian; Inwald, Poland. A. Right valve, from inside; original of Boehm (1883: pl. 61, fig. 4); SNSB-BSPG AS III 792. B. Right valve, from outside; original of Boehm (1883: pl. 61, figs 1, 2); SNSB-BSPG AS III 793. C, D. *Protocardia gigantea* Schneider, Fürsich & Werner, 2010; Kimmeridgian-Tithonian transition; Santa Cruz, Portugal. C. Right valve, from inside; paratype 1 of Schneider et al. (2010: fig. 6C, E); GML 25931. D. Left valve, from outside; paratype 3 of Schneider et al. (2010: fig. 6C, E); GML 25933. E. *Pachymegalodon chamaeformis* (von Schlotheim, 1820); right valve; Pliensbachian; Podpeč, Slovenia; original of Tausch von Gloeckelsturn (1890); GBA 1862/2/5/2. Scale bars = 10 mm.





**Figure 11:** Basal Hippuritida. Outer calcitic shell layer not preserved. A. *Dicerca* sp., left valve; Oxfordian; Coulanges-sur-Yonne, France; MNHN 1886-34. B. *Epidiceras* sp., right valve; Oxfordian; Mercy-sur-Yonne, France; MNHN 1908-36. C. *Epidiceras* sp., right valve; Oxfordian; Coulanges-sur-Yonne, France; MNHN 1896-29. Scale bar = 10 mm.

teral teeth in both valves; usually an additional anterior lateral tooth All is present in *Protocardia*, but may be almost reduced (Fig. 10C). Both taxa lack a lunule and possess posterior radial ornament (Fig. 10D). Several Jurassic Fimbriinae, e.g. *Sphaeriola* Stoliczka, 1871 or *Cerkesia* Monari, 2003, have a hinge similar to *Protocardia* consisting of AI, All, Alll (may be reduced), 2, 3a (small), 3b, 4b (very weak), PI and PII. Additionally, they have partial radial ornament. However, Fimbriinae generally have a narrow but distinct lunule (Monari 2003). Taking these observations into account, *Pachyrisma grande* is much more likely a Mesozoic offshoot of the Cardioidea than the Megalodontidae (or Fimbriinae).

#### 4.6.2. Family status

*Pachyrisma grande* shares several features with other species assigned to *Pachyrisma* or the supposedly closely related genera *Pachymegalodon* Gumbel, 1862 and *Pachyrismella* Cox, 1964. These are a high, posteriorly truncated nymph (shared, e.g. with *Pachymegalodon chamaeformis* (von Schlotheim, 1820) (Fig. 10E), *Pachyrismella septifera* (Buvignier, 1843), *Pachyrisma beaumonti* Zejszner, 1962 (Fig. 10 A, B), *P. royeri* Bayan, 1874, *P. tombecki* Bayan, 1874); posterior radial ornamentation (shared with *Pachyrismella septifera* and *Pachyrisma beaumonti*; Fig. 10B); posterior myophore (shared with *Pachyrismella septifera*, *Pachyrisma beaumonti*, *P. royeri*,

*P. tombecki*; Fig. 10A); dotted pallial line and additional row of mantle attachment scars (shared with *Pachyrisma beaumonti*; Fig. 10A); and general arrangement of the dentition. However, *Pachyrisma grande* differs from all these species in its general shape. While *Pachyrisma grande* is strongly prosogyrate with a sharp posterior bend, thus 'megalodontid' in shape, all other taxa mentioned in this paragraph are moderately prosogyrate and of general cardioid shape (Fig. 10A, B, E). Moreover, the lateral hinge teeth, which are faint and almost reduced in *Pachyrisma grande*, are prominent in all the other species (Fig. 10A, E), and these include forms distinctly older and younger than *P. grande*. This suggests that *Pachymegalodon chamaeformis*, *Pachyrismella septifera*, *Pachyrisma beaumonti*, *P. royeri*, *P. tombecki* and probably several other species form a clade separate from *Pachyrisma grande*. As already stated by Morris (1978: p. 267) these species are seen as a separate group within Cardioidea, and tentative assignment to the Pterocardiidae will be proposed in the preliminary classification for the updated bivalve volumes of the Treatise on Invertebrate Paleontology (work in progress). *Pachyrisma beaumonti*, *P. royeri* and *P. tombecki* are removed from *Pachyrisma* Morris & Lycett, 1853 and assigned to *Pachyrismella* Cox, 1964.

Shell shape and presumably dentition of *Pachyrisma grande* seem to be similar to the insufficiently known genus *Protodiceras* Boehm, 1891. The type

**Table 1.** Genera discussed in the context of *Pachyrisma*, their type species, age and country of origin.

| Genus                                   | Type species   | Age, country of origin  |
|---|--|-------------------------|
| <i>Pachyrisma</i> Morris & Lycett, 1850 | <i>Pachyrisma grande</i> Morris & Lycett, 1850 [monotypy]              | Bathonian, England      |
| <i>Pachymegalodon</i> Gümbel, 1862      | <i>Bucardites chamaeformis</i> von Schlotheim, 1820 [monotypy]         | Pliensbachian, Slovenia |
| <i>Durga</i> Boehm, 1884                | <i>Durga nicolisi</i> Boehm, 1884 [OD]                                 | Pliensbachian, Italy    |
| <i>Protodicerias</i> Boehm, 1891        | <i>Megalodon triqueter</i> var. <i>pumilus</i> Gümbel, 1862 [monotypy] | Pliensbachian, Italy    |
| <i>Pachyrismella</i> Cox, 1964          | <i>Cardium septiferum</i> Buvignier, 1843 [OD]                         | Oxfordian, France       |
| <i>Juramegalodus</i> Sirna, 1974        | <i>Juramegalodus viallii</i> Sirna, 1974 [monotypy]                    | Tithonian, Italy        |

of *Protodicerias pumilum* (Gümbel, 1862) is lost, and only a dubious specimen figured by Tausch von Gloeckelsturn (1890) was available for study at the Geologische Bundesanstalt Wien. Moreover, *Pachymegalodus timorensis* Krumbek, 1923 from the Pliensbachian of Timor (Indonesia) and *Pachyrisma bayani* Gemmellaro, 1876 from the Lower Tithonian of Sicily (Italy) are highly similar to *P. grande* in shape, and probably also dentition. The type material of both species is available from the collections of the Goldfuß-Museum (Bonn, Germany) and the Museo di paleontologia e geologia 'Gaetano Giorgio Gemmellaro' (Palermo, Italy), respectively (courtesy Georg Heumann, Bonn and Carolina D'Arpa, Palermo) and will be studied for further phylogenetic analysis. In summary, *Pachyrisma grande* is regarded as sufficiently distinct from Megalodontidae, Pterocardiidae and Protocardiinae to justify the preservation of a separate family Pachyrismatidae, which may include the genera *Pachyrisma* Morris & Lycett, 1853 and *Protodicerias* Boehm, 1891, and potentially ranges over most of the Jurassic.

#### 4.6.3. Are Hippuritida derived from *Pachyrisma*?

The Hippuritida make their first appearance in the Oxfordian, and *Dicerias* and *Epidicerias* are among their earliest representatives. *Pachyrisma grande* is Bathonian in age, and thus roughly five million years older. *Pachyrisma grande* has only been reported from western England. Oxfordian Hippuritida are known, e.g., from northern France (e.g. Skelton 1999) and northern Germany (Schneider 2015), and thus at distances of roughly 500–1000 km from western England. From a spatial and temporal perspective, it is thus not implausible that *Pachyrisma grande* and the Hippuritida are closely related. *Pachyrisma grande*, as well as basal Hippuritida, lived in stable lagoonal settings and were gregarious with regard to their own kind, but not surrounded by much additional life.

With regard to morphology, strongly coiled, opisthogyrate shells, arcuate nymphs that carried a parivincular external ligament, a distinct cardinal tooth 3a and prominent teeth 2 and 3b are common to

*Pachyrisma*, *Dicerias* and *Epidicerias*. Lateral hinge teeth are absent in basal rudists, and strongly reduced in adult *Pachyrisma*. Moreover, these taxa share areas of external radial ornament; however, it is not clear whether it is expressed by a calcitic outer shell layer in *Pachyrisma*. A posterior myophore is present in *Pachyrisma*, while *Dicerias* and *Epidicerias* have both anterior and posterior myophoral ledges; however, the anterior ledge is often less well expressed, and may have evolved from the slightly raised rim of the anterior adductor muscle scar in *Pachyrisma*. In summary, these characters strongly support a close phylogenetic relationship of *Pachyrisma* and the Hippuritida.

## 5. Conclusions

*Pachyrisma grande* Morris & Lycett, 1850 is redescribed based on type and additional material. Radial external ornament on the area, the shape and position of the nymph, the presence of a posterior lateral tooth PI and a 'dotted' pallial line are documented for the first time.

The family Pachyrismatidae Scarlato & Starobogatov, 1979 is revised to contain non-lunulate bivalves of megalodontid general shape, but with a cardioid hinge, where lateral teeth are, or are in the process of becoming reduced. This may indicate that the Pachyrismatidae are derived from a *Protocardia*-like ancestor rather than from the Megalodontidae. The family is thought to comprise only *Pachyrisma* Morris & Lycett, 1850 and *Protodicerias* Boehm, 1891.

*Pachyrisma grande* is regarded as the closest known ancestor of the Hippuritida, based on similarities with respect to shell shape, nymphs, hinge dentition, ornamentation, muscular attachment and lifestyle. If Pachyrismatidae are derived from early cardioids, this would also imply that the Hippuritida are rooted in the Cardioidea.

All taxa discussed in the present study and several additional species need to be subjected to phylogenetic analysis in order to test the evolutionary scenario proposed herein.



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