

Paleontological Contributions

Number 8

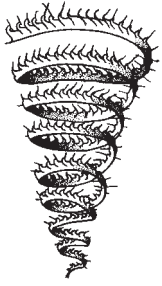
Comprehensive database on Induan (Lower Triassic) to
Sinemurian (Lower Jurassic) marine bivalve genera and their
paleobiogeographic record

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COMPREHENSIVE DATABASE ON INDIAN (LOWER TRIASSIC) TO SINEMURIAN (LOWER JURASSIC) MARINE BIVALVE GENERA AND THEIR PALEOBIOGEOGRAPHIC RECORD

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ABSTRACT

Marine bivalve genera that were described or mentioned for Triassic and Lower Jurassic deposits worldwide are reviewed in terms of their validity, stratigraphic range, paleogeographic distribution, paleoautecology, and shell mineralogy. Data were originally compiled at species level and are arranged systematically. A brief discussion for each genus includes synonymy, taxonomic status, and included subgenera, as well as current uncertainties about their validity and range. The distribution of each genus is also shown on paleogeographic maps. Type species and first and last appearances of each genus are also mentioned. We recognize as valid 281 genera and their included subgenera, and we further discuss 148 genera (arranged alphabetically) that were mentioned for the study interval but are not included for different reasons. The purpose of this paper is to provide an updated critical assessment of all available basic information for each genus, in order to obtain a sound database to study the generic paleodiversity of marine bivalves in the time interval from the Induan (Early Triassic) to the Sinemurian (Early Jurassic). This was a critical time for bivalve evolution and diversification, which began with the recovery from the Permian–Triassic extinction and ended with the recovery from the Triassic–Jurassic extinction.

Keywords: Bivalvia, paleoecology, paleogeography, Triassic, Early Jurassic

INTRODUCTION

In order to study the generic paleodiversity of marine bivalves in the time interval from Induan (Early Triassic) to Sinemurian (Early Jurassic) (In-Sin), which begins with the recovery from the Permian–Triassic extinction and ends with the recovery from the Triassic–Jurassic extinction, a significant critical review of each genus was badly needed. The purpose of this paper is not merely to offer such a compendium of data extracted from the published literature, but to provide an updated critical assessment of all available information for each genus as well.

This paper is thus a review of all marine bivalve genera that were described for Triassic and Lower Jurassic deposits worldwide, in terms of their validity, stratigraphic range, paleogeographic distribution, paleoautecology, and shell mineralogy. We include marine bivalves only, and thus the families Pachycardiidae, Unionidae, and Neomiodontidae are not considered. Data were compiled at species level, with the purpose being to contrast the assignment of each species to the genera. Only published monographs and papers that include images and descriptions of the taxa were considered. This paper is a revised version of part of a Ph.D. thesis (Ros, 2009).

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Methodology

We based our study mostly on bibliographic data, but the different records attributed to each genus were revised, checked, and critically updated as far as possible from systematic, stratigraphic, and geographic points of view.

First, we looked for all genera described in our study interval. The *Treatise on Invertebrate Paleontology* (Cox & others, 1969; Stenzel, 1971) was taken as reference for the period previous to 1965, accepting in most cases the proposed synonyms, although in some genera, subsequent literature that changed the *Treatise* views was also taken into account. However, we frequently used literature prior to the *Treatise* to try to elucidate some pending questions. For the time span between 1965 and the present, an exhaustive literature search was performed. To carry out this task, we referred to *Zoological Record* from 1965 to 2005 and other sources (Diener, 1923; Kutassy, 1931; Neave, 1939; Cox & others, 1969; Sepkoski, 2002; and several electronic sources, such as Paleobiology Database [PBDB] and *Nomenclator Zoologicus*).

Then we compiled all references into a bibliography about these genera and reviewed it. Since the amount of literature and data discussed here is quite large, we first proceeded to develop a bibliographic database that allowed us to handle them rapidly and effectively. This database was made using the computer program FileMaker Pro 8.5. The selection of this program was based on the simplicity of its construction, handling, and relation of information. The introduction of the species with author and year in the database is very important, instead of compiling the genera directly, since it allows us to control the different scope given to them over time. For example, the species *decidens* Bittner, 1899, was described in the genus *Pseudomonotis*, assigned later to *Streblochondria* and *Claraia*, in the end to be assigned by Newell and Boyd (1995) to *Crittendenia* and also as type species of *Claraia* (*Bittnericlaraia*) by Gavrilova (1996). If we had not introduced the species in the database, it would have been impossible to continue the history of this species, and we would have had the occurrence of the same species in four different genera.

Through a careful revision of the literature, we eliminated all genera that, for one reason or other, should not be considered, including those with only doubtful occurrence in our study interval. These are treated in the section Genera not Included (see p. 156), listed alphabetically, with a brief explanation of the reason for their exclusion. Specifically, we do not include: (1) genera convincingly placed in synonymy; (2) subgenera for which we did not find any publication elevating them to genus level; (3) genera with no solid presence during the temporal study range, although they could have been mentioned for the study range; and (4) generic homonyms. Finally, there are some taxa that were listed in the *Compendium of Fossil Marine Genera* published by Sepkoski (2002), but which were not included in this analysis because they are regarded as subgenera.

Taxonomic data were reviewed as far as possible in order to assign all species to genera. We compared the generic diagnosis with the species descriptions and figures offered in the literature, and, in some instances, we consulted different specialists. We are aware that, even considering these meticulous analyses, it is impossible to eliminate all mistakes, and taxonomic decisions are always subjective, so the opinion of different authors is frequently indicated in the genus

discussion. For the assignment of genera to different families, we followed Cox and others (1969) for genera described earlier than the *Treatise*, but more recent bibliographies that proposed changes in assignation are discussed and listed for each case. For genera described after 1965, we follow critically the assignment published in the literature. The survey includes only papers published before 2011.

Data Organization

Stratigraphic Ranges.—We follow the stratigraphic chart of Gradstein and Ogg (2004), using their stage names, except for the Permian, which is subdivided into three epochs: Cisuralian, Guadalupian, and Lopingian, here listed as early, middle, and late Permian, respectively.

For the equivalence between the different charts used in the reviewed bibliography, we used the conversion tables provided by the Paleobiology Database (<http://www.paleodb.org/>) and GeoWhen Database (<http://www.stratigraphy.org/geowhen/index.html>).

We had some problems distinguishing between Rhaetian and Norian in papers older than the redefinition of Rhaetian by Dagys and Dagys (1994). At least the Kössen Formation in Austria and the Gabbs Formation in the United States can be regarded as Rhaetian in age (Dagys & Dagys, 1994; Hallam, 2002).

We used H. J. Campbell and Raine (in Cooper, 2004) and H. J. Campbell, Raine, and Wilson (in Cooper, 2004) for the correlation of New Zealand stages with the Global Geochronological Scale.

For each genus, we indicate the entire stratigraphic range observed after reviewing the literature, and the two records we regard as the first and last appearances. Stratigraphic ranges are compared with those in Cox and others (1969), which is the most recent published review with a thorough taxonomic revision and stratigraphic data. In most cases, those ranges are changed with the new information here considered. We also compared our data with Sepkoski's (2002) compilation.

It should be pointed out that the stratigraphic ranges offered are observed, i.e., the first and last occurrences of a taxon are the limits of its stratigraphic range, which is only an approximation to the real range, and therefore also to the moment of origination and extinction. The effects of sampling, stratigraphic hiatuses, transgressions and regressions, Signor-Lipps effect, and other factors may greatly influence or distort the actual ranges (Holland, 1995). We must also bear in mind that the distribution of fossil bivalves is particularly dependent on facies.

Paleogeographic distribution.—For each genus, we provide the paleogeographic distribution during the time interval considered in this review. For those genera present in the Paleozoic, the paleogeographic distribution during the late Permian is also given. This section is not intended as a paleobiogeographic study, although the domains considered were established both in a paleogeographic and a paleobiogeographic sense (Westermann, 2000). We merely review the distribution of each genus and represent it on paleogeographic maps. Consequently, the term domain as used here has no paleobiogeographic implication.

The distribution of each genus in space and time is shown in three maps, for Permian–Triassic, Middle Triassic, and Triassic–Jurassic intervals. These representations sketch the position of continents at the three time moments selected, but they are not strictly faithful to all recent knowledge in every detail. The maps are based on and

adapted from various sources. The first map was compiled mainly following Ziegler, Hulver, and Rowley (1997) and Christopher Scotese's maps available on his website Paleomap Project (<http://www.scotese.com>); the following two maps were based on Golonka and Ford (2000) and Golonka (2004, 2007). We introduced some changes, especially in the configuration of Cimmerian block, Lhasa block, and southern part of the Tethys following Dèzes (1999), Nicoll (2002), J. Yin and Grant-Mackie (2005), and J. Yin and McRoberts (2006).

The paleogeographic distribution for each genus was recorded by using contemporary country names, which were then grouped into the following paleogeographic informal domains: Tethys, Circumpacific, Boreal, and Austral. As here understood, the Tethys domain covers the entire length of the Tethys Sea during the time interval here considered, without differentiating between Neotethys and Paleotethys. The Boreal domain includes mainly the northern part of Russia, Greenland, northern Canada, and Alaska. The Austral domain comprises the southern part of South America (part of Argentina and Chile), New Zealand, New Guinea, and Antarctica. Finally, the Circumpacific domain covers the Paleopacific, being limited to the north and south by the Boreal and Austral domains, respectively. For the location of countries in the different domains, we mostly follow Nakazawa (1991), Dercourt, Ricou, and Vrielynck (1993), Metcalfe (1998, 1999), Gaetani and others (2000a, 2000b, 2000c), Acharyya (2000), Stampfli and others (2001), Stampfli and Borel (2002, 2004), Chumakov and Zharkov (2003), and Klets (2005), in addition to those cited above for construction of the maps. Every genus, even those with localized occurrences, was referred to one or more of these domains.

Although we indicate the distribution of each genus only during the time interval considered in this review, in some cases, we also discuss their paleogeographic range before or after this interval, if we find this relevant for any reason. The distribution of each genus is listed according to the domains just mentioned, and each indicates the countries in which the genus was found with the relevant bibliographic data sources. If a distribution for a genus in the literature is uncertain, we use a question mark (?) herein for that record. We occasionally discuss data included in papers with no illustrations of the specimens, but these records were not taken into account for the distribution of genera. These are mostly related to Russia and China, especially to some pre-1980 literature that we could not see for this study.

Paleoautecology.—The modes of life of the genera included are assigned according to the original bibliographic source, and, when this was not possible, they were inferred by functional morphology or analogy with related Recent species. The categories recognized here are based mainly on S. M. Stanley (1968, 1969, 1970, 1972), Kauffman (1969), Bambach (1977, 1983), Bambach, Bush, and Erwin (2007), and others. We are aware that there are many exceptions to the general guidelines given for the recognition of modes of life, so they will necessarily be tentative and always referred to adult specimens (the different modes of life that a bivalve can display along its ontogeny were not taken into account). Sometimes it was not possible to assign a unique mode of life to one genus, because the included species may differ in this aspect. When there was not enough information about the genus morphology or about the

environment in which it is recorded, we refer to the predominant mode of life within the family.

The following aspects were taken into account for establishing the different modes of life: life position in relation to water column and substrate, trophic group, mobility, and fixation. The mode of life assigned to each genus is coded by letters, as follows:

Position on the water column: benthic [B] or pseudoplanktonic [Ps].

Trophic group: suspensivorous [S] and detritivorous [D]. Carnivorous bivalves are mostly beyond our study interval, because septibranchs appeared in the Jurassic (later than Sinemurian). In addition, we indicate possible photosymbiotic [Ph] and chemosymbiotic [Ch] relationships with microorganisms.

Life position in relation to the substrate: epifaunal [E], shallow infaunal [Is], deep infaunal [Id] or semi-infaunal [Se].

Mobility: sedentary [Sed], facultative mobile [FaM], slow mobile [SM], and fast mobile [FM]. Regarding mobility, SM and FM are categories only considered for burrower bivalves, while FaM refers to swimmer and pseudoplanktonic bivalves.

Fixation: we consider if they lived attached to the substrate or unattached [Un]; attached bivalves can be byssate (endobysate [Endo] or epibysate [Epi]) or cemented [C].

Several modes of life are then defined by the intersection of the categories just mentioned: shallow burrower in soft substrate [Sb], deep burrower [Db], borer [Bo], byssate [By], cemented [C], recliner [R], swimmer [Sw], nestler [N].

Mineralogy.—Shell mineralogy data provided here are taken mostly from J. D. Taylor, Kennedy, and Hall (1969, 1973), Carter (1990a, 1990b, 1990c), Carter, Lawrence, and Sanders (1990), and Carter, Barrera, and Tevesz (1998). In specific cases, we used other sources that are indicated in the discussion of each genus.

Mineralogy of shell layers is given for each genus, when this information is available; alternatively, we assign the predominant mineralogy for the family. Three types of mineralogy are considered: aragonitic, when all shell layers are fully formed by aragonite; bimineralic: when at least one of the shell layers is calcitic and the others aragonitic; and calcitic, when all shell layers are formed by calcite.

INCLUDED GENERA

The systematic arrangement used here follows Amler (1999), Amler, Fischer, and Rogalla (2000), and Bouchet and Rocroi (2010) with some modifications. Those are the most complete general Bivalve mollusk classifications that include fossil families introduced after the *Treatise on Invertebrate Paleontology*. The changes introduced here are: Lipodonta is recognized as a subclass following Cope (1995) and including the Solemyoidea; family Pichleriidae is included with the Limopsoidea; superfamilies Dimyoidea and Plicatuloidea are included within the Ostreida rather than the Pectinida; the name Terquemiidae Cox, 1964, is replaced by Prospodyliidae Pchelincev, 1960 (Hautmann 2001a), the classification of the superfamily Kalenteroidea Marwick, 1953, has been emended, according to Z. Fang and Morris (1997) and Damborenea (2004).

The genera included in this review are listed in systematic order below (Table 1). Each of them is then briefly discussed separately, with indication of type species, possible synonym names, and details of stratigraphic and paleogeographic distribution, mode of life, and shell structure.

Table 1. Summary of various data for included genera, arranged in the order in which they are discussed herein. Abbreviations: (1) Stratigraphic range: *O*, Ordovician; *Tr*, Tremadocian; *Dev*, Devonian; *Llan*, Llanvirnian; *Fam*, Famennian; *Car*, Carboniferous; *Miss*, Mississippian; *Vis*, Visean; *Penn*, Pennsylvanian; *Pe*, Permian; *Sak*, Sakmarian; *Art*, Artinskian; *Guad*, Guadalupian; *Wuch*, Wuchiapingian; *Chang*, Changhsingian; *Tr*, Triassic; *In*, Induan; *Ol*, Olenekian; *Ani*, Anisian; *Lad*, Ladinian; *Car*, Carnian; *Nor*, Norian; *Rha*, Rhaetian; *J*, Jurassic; *Hett*, Hettangian; *Sin*, Sinemurian; *Plie*, Pliensbachian; *Toa*, Toarcian; *Aal*, Aalenian; *Baj*, Bajocian; *Call*, Callovian; *Oxf*, Oxfordian; *Kim*, Kimmeridgian; *Tit*, Tithonian; *Cret*, Cretaceous; *Berr*, Berriasian; *Val*, Valanginian; *Haut*, Hauterivian; *Apt*, Aptian; *Alb*, Albian; *Cen*, Cenomanian; *Tur*, Turonian; *Cam*, Campanian; *Maa*, Maastrichtian; *P*, Paleocene; *Dan*, Danian; *L.*, Lower; *M.*, Middle; *U.*, Upper; (2) Paleoautoecology: *B*, benthic, *P*, pseudoplanktonic, *D*, detritivorous, *S*, suspensivorous, *Ph*, photo-symbiotic; *Ch*, chemo-symbiotic, *E*, epifaunal, *Is*, shallow infaunal, *Id*, deep infaunal, *SI*, semi-infaunal, *FM*, fast mobile, *SM*, slow mobile, *FaM*, facultative mobile, *Sed*, sedentary, *Un*, unattached, *Endo*, endobyssate, *Epi*, epibyssate, *C*, cemented, *Sb*, burrower in soft substrate, *Db*, deep burrower, *Bo*, borer, *By*, byssate, *R*, recliner, *Su*, swimmer, *N*, nestler.

Genus	Stratigraphic range	Paleogeographic distribution	Paleoautoecology	Mineralogy
<i>Palaeonucula</i>	M. Tr (l. Ani)–L. Cret (Apt)	Tethys, Circumpacific, and Boreal	B, D, Is, FM; Sb	Aragonitic
<i>Trigonucula</i>	U. Tr (Car–u. Rha)	Tethys and Circumpacific	B, D, Is, FM; Sb	Aragonitic
<i>Nuculoma</i>	U. Tr (Rha)–L. Cret (Val)	Tethys and Circumpacific	B, D, Is, FM; Sb	Aragonitic
<i>Nuculana</i>	M. Tr (Ani)–Recent	Cosmopolitan	B, D, Is, FM; Sb	Aragonitic
<i>Phestia</i>	M. O (l. Llan)–U. Tr (Car)	Tethys, Circumpacific and Boreal	B, D, Is, FM; Sb	Aragonitic
<i>Veteranella</i>	L. Pe (Art)–U. Tr (Nor)	Tethys	B, D, Is, FM; Sb	Aragonitic
<i>Eleganuculana</i>	U. Tr (Nor)	E Tethys	B, D, Is, FM; Sb	Aragonitic
<i>Xiaoschuiculana</i>	U. Tr	Tethys and Circumpacific	B, D, Is, FM; Sb	Aragonitic
<i>Phaenodesmia</i>	M. Tr (Ani)–U. Tr (Rha)	Tethys and Circumpacific	B, D, Is, FM; Sb	Aragonitic
<i>Prosoleptus</i>	M. Tr (Ani)–U. Tr (Car)	Tethys and Boreal?	B, D, Is, FM; Sb	Aragonitic
<i>Palaeoneilo</i>	L. O (Tre)–L. J (Toa)	Cosmopolitan	B, D, Is, FM; Sb	Aragonitic
<i>Lapteviella</i>	M. Tr (Ani)	Boreal	B, D, Is, FM; Sb	Aragonitic
<i>Dianucula</i>	U. Tr (Nor)	E Tethys	B, D, Is, FM; Sb	Aragonitic
<i>Ningliconcha</i>	U. Tr (Nor)	E Tethys	B, D, Is, FM; Sb	Aragonitic
<i>Yongshengia</i>	U. Tr (Nor)	E Tethys	B, D, Is, FM; Sb	Aragonitic
<i>Rollieria</i>	L. J (Hett)–L. Cret	Tethys and Circumpacific	B, D, Is, FM; Sb	Aragonitic
<i>Ryderia</i>	U. Tr (Rha)–L. J (Toa)	Tethys and Circumpacific	B, D, Is, FM; Sb	Aragonitic
<i>Dacryomya</i>	U. Tr (Nor)–U. J (Kim)	Tethys, Circumpacific and Boreal	B, D, Is, FM; Sb	Aragonitic
<i>Mesoneilo</i>	U. Tr (Nor–Rha)	Tethys and Boreal?	B, D, Is, FM; Sb	Aragonitic
<i>Nucinella</i>	L. J (Hett)–Recent	E Tethys	B, D/Ch, Is, FM; Sb	Aragonitic
<i>Solemya</i>	U. Car (u. Penn)–Recent	Tethys and Circumpacific	B, Id, S/Ch, FM; Db	Aragonitic
<i>Modiolus</i>	U. Dev (Fam)–Recent	Cosmopolitan	B, Se, S, Endo, Sed; By	Bimineralic
<i>Promytilus</i>	Car (Miss)–L. Tr (In)	Boreal	B, E, S, Epi, Sed; By	Bimineralic
<i>Inoperma</i>	U. Tr (Rha)–U. Cret (Maa)	Tethys and Austral?	B, Se, S, Endo, Sed; Bo?	Bimineralic
<i>Falcimytilus</i>	U. Tr (Car)–U. J (Tit)	Tethys, Circumpacific and Boreal	B, E, S, Epi, Sed; By	Bimineralic?
<i>Lycetia</i>	L. J (Sin)–U. Cret (Maa)	Austral	B, E, S, Epi, Sed; By	Aragonitic
<i>Lithophaga</i>	U. Tr (Nor)–Recent	Tethys	B, I, S, By, Sed; Bo	Bimineralic
<i>Mysidiella</i>	U. Tr (Car–Rha)	Tethys and Circumpacific	B, E, S, Epi, Sed; By	Bimineralic
<i>Botulopsis</i>	M. Tr (Lad)–U. Tr (Car)	W Tethys	B, E, S, Epi, Sed; By	Bimineralic
<i>Promysidiella</i>	M. Tr (l. Ani)–U. Tr (l. Nor)	Tethys, Circumpacific and Boreal?	B, E, S, Epi, Sed; By	Bimineralic
<i>Protopsis</i>	M. Tr (Ani)–U. Tr (Car)	Tethys	B, E, S, Epi, Sed; By	Bimineralic ?
<i>Joannina</i>	L. Tr (In)?–U. Tr (Car)	Tethys	B, Se, S, Endo, Sed; By	Bimineralic ?
<i>Leidapocncha</i>	M. Tr (Ani)	E Tethys	B, Se, S, Endo, Sed; By	Bimineralic ?
<i>Waijiaonella</i>	M. Tr (Ani)	E Tethys	B, Se, S, Endo, Sed; By	Bimineralic ?
<i>Qingyaniola</i>	M. Tr (Ani)	E Tethys	B, Se, S, Endo, Sed; By	Bimineralic ?
<i>Macrodontella</i>	M. Tr (Ani)	Tethys	B, E/Se, S, Epi/Endo, Sed; By	Aragonitic
<i>Catella</i>	U. Tr (Car)–L. P (Dan)	E Tethys	B, Se, S, Endo, Sed; By	Aragonitic
<i>Parallelodon</i>	M. Dev–U. Cret	Cosmopolitan	B, E, S, Epi, Sed; By	Aragonitic
<i>Grammatodon</i>	L. Pe (Art)–U. Cret (Maa)	Cosmopolitan	B, E, S, Epi, Sed; By	Aragonitic
<i>Bapristodia</i>	U. Tr (Nor)	E Tethys	B, E, S, Epi, Sed; By	Aragonitic
<i>Cucullaea</i>	L. J (Hett)–Recent	Circumpacific	B, Is/Se, S, SM; Sb	Aragonitic
<i>Eophyllobryoidella</i>	M. Tr (u. Ani)	E Tethys	B, E, S, Epi, Sed; By	Aragonitic
<i>Hoferia</i>	U. Tr (Car)	Tethys	B, Is, S, Endo, SM; Sb	Aragonitic
<i>Pichleria</i>	U. Tr (Car)	Tethys	B, Is/Se, S, Sed; ?	Aragonitic
<i>Elegantarca</i>	M. Tr (Ani)–U. Tr (Car)	Tethys	B, Se, S, Endo, Sed; By	Aragonitic
<i>Myalina</i>	Car (l. Miss)–U. Pe, ?L. Tr?	Circumpacific	B, E, S, Epi, Sed; By	Bimineralic
<i>Myalinella</i>	Car (Vis)–L. Tr (u. Ol)	Tethys, Circumpacific and Boreal	B, Se, S, Endo, Sed; By	Bimineralic
<i>Promyalina</i>	U. Pe (u. Chang)–L. Tr (u. Ol)	Tethys, Circumpacific and Boreal	B, Se, S, Endo, Sed; By	Bimineralic
<i>Aviculomyalina</i>	M. Tr (Ani)	W Tethys	B, E, S, Epi, Sed; By	Bimineralic
<i>Parainoceramus</i>	L. J (Hett)–U. J (Tit)	Tethys, Circumpacific and Boreal	B, E, S, Epi, Sed; By	Bimineralic
<i>Pseudomytiloides</i>	L. J (Hett)–M. J (Aal)	Tethys	B/Ps, E, S, Epi, Sed/FaM; By	Bimineralic
<i>Arctomytiloides</i>	L. J (Sin–Toa?)	Boreal and Circumpacific	B, E, S, Epi, Sed; By	Bimineralic
<i>Pteria</i>	L. Tr (Ol)–Recent	Tethys, Circumpacific and Boreal	B, E, S, Epi, Sed; By	Bimineralic
<i>Arcavicula</i>	L. Tr (l. Ol)–U. Tr (Rha?)	Tethys and Circumpacific	B, E, S, Epi, Sed; By	Bimineralic
<i>Rhaetavicula</i>	U. Tr (Rha)	Tethys and Circumpacific	B, E, S, Epi/Un, Sed; By/R	Bimineralic
<i>Stefania</i>	M. Tr (u. Lad)–U. Tr (Car)	W Tethys	B, E, S, Epi, Sed; By	Bimineralic
<i>Bakevellia</i>	U. Pe–U. Cret	Cosmopolitan	B, Se, S, Endo, Sed; By	Bimineralic
<i>Gervillella</i>	L. J (Hett)–U. Cret (?)	W Tethys, Circumpacific and Austral	B, Se, S, Endo, Sed; By	Bimineralic
<i>Gervillia</i>	M. Tr (Lad)–U. Cret (Maa)	Tethys and Circumpacific	B/Ps, Se/E, S, Endo/Epi, Sed; By	Bimineralic
<i>Hoernesia</i>	L. Tr (Ol)–U. Tr (Rha)	Tethys and Boreal	B, Se, S, Endo, Sed; By	Bimineralic
<i>Langsonella</i>	M. Tr (Ani)–U. Tr (Car)	E Tethys	B, Se, S, Endo, Sed; By	Bimineralic
<i>Cuneigervillia</i>	L. J (Hett)–L. Cret (?)	W Tethys	B, Se, S, Endo, Sed; By	Bimineralic
<i>Gervillaria</i>	M. Tr (Ani)–U. Cret (Tur)	Tethys, Circumpacific and Austral	B, Se, S, Endo, Sed; By	Bimineralic
<i>Gervillancea</i>	U. Tr (Car–Nor)	S Tethys	B, Se, S, Endo, Sed; By	Bimineralic

Table 1 (continued). See facing page for heading.

Genus	Stratigraphic range	Paleogeographic distribution	Paleoautoecology	Mineralogy
<i>Songdaella</i>	U. Tr (Nor)	E Tethys	B, E, S, Epi, Sed; By	Bimineralic
<i>Aguilerella</i>	U. Tr (Rha)—L. Cret (Haut)	E Tethys and Circumpacific	B, E, S, Epi, Sed; By	Bimineralic
<i>Towapertia</i>	L. Pe (Sak)—L. Tr (In)	Tethys and Circumpacific?	B, E, S, Epi, Sed; By	Bimineralic
<i>Virgellia</i>	U. Tr (Car)—U. J (Kim)	S Tethys	B, Se, S, Endo, Sed; By	Bimineralic
<i>Gervilleioperna</i>	L. J (Sin)—M. J (Aal)	Circumpacific	B, Se, S, Endo, R, Sed; By	Aragonitic
<i>Cassianella</i>	Pe?, M. Tr (Ani)—U. Tr (Rha)	Cosmopolitan	B, E, S, Un, Sed; R	Aragonitic
<i>Burckhardtia</i>	U. Tr (Car)	Circumpacific	B, E, S, Un, Sed; R	Aragonitic
<i>Hoernesiella</i>	U. Tr (Car)	W Tethys	B, E, S, Un, Sed; R	Aragonitic
<i>Lilangina</i>	M. Tr (Ani) - U. Tr (Car)	E Tethys	B, E, S, Un, Sed; R	Aragonitic
<i>Reubenia</i>	U. Tr (Car)	W Tethys	B, E, S, Un, Sed; R	Aragonitic
<i>Septihoernesia</i>	M. Tr (Lad)—U. Tr (Car)	Tethys and Circumpacific	B, E, S, Un, Sed; R	Aragonitic
<i>Datta</i>	U. Tr (Rha)	S Tethys	B, E, S, ?, ?	Bimineralic
<i>Isognomon</i>	U. Tr (Car)—Recent	Tethys	B, Se, S, Endo, Sed; By	Bimineralic
<i>Leproconcha</i>	M. Tr	W Tethys	B, E, S, ?, ?	Unknown
<i>Waagenoperna</i>	L. Pe (Sak)—U. Tr (u. Nor)	Tethys and Circumpacific	B, Se, S, Endo, Sed; By	Bimineralic
<i>Bositra</i>	L. Tr (l. Ol)—M. J (l. Oxf)	Tethys, Circumpacific and Boreal	B, E, S, Un, Sed; R	Bimineralic
<i>Amonotis</i>	U. Tr (Car)	Tethys	B, E, S, Epi, Sed; By	Bimineralic
<i>Veldidenella</i>	M. Tr (u. Ani)—u. Lad	W Tethys	B, E, S, Epi, Sed; By	Bimineralic
<i>Caenodiotis</i>	L. J (Sin—Plie)	W Tethys	B, E, S, Epi, Sed; By	Bimineralic
<i>Steinmannia</i>	L. J (u. Sin—l. Toa)	Boreal	B, E, S, Un, Sed; R	Bimineralic
<i>Ellesmerella</i>	L. Tr (u. Ol)	Boreal	B, E, S, Un, Sed; R	Bimineralic
<i>Pinna</i>	L. Tr (?)—Recent	Tethys, Circumpacific and Austral	B, Se, S, Endo, Sed; By	Bimineralic
<i>Atrina</i>	M. Tr (Ani)—Recent	Tethys and Circumpacific	B, Se, S, Endo, Sed; By	Bimineralic
<i>Palaeolima</i>	U. Dev (Fam?)—U. Tr (Nor)	Tethys and Circumpacific	B, E, S, Epi, Sed; By	Bimineralic
<i>Aviculolima</i>	M. Tr (Ani)	W Tethys	B, E, S, Epi, Sed; By	Bimineralic
<i>Badiotella</i>	M. Tr (Lad)—U. Tr (Car)	Tethys	B, E, S, Epi/Un, Sed; By/R	Bimineralic
<i>Limatula</i>	M. Tr (Lad) - Recent	Tethys, Circumpacific and Austral	B, E, S, Epi, FaM; By/Sw	Bimineralic
<i>Limea</i>	M. Tr (Ani)—Recent	Cosmopolitan	B, E, S, Epi, Sed; By	Bimineralic
<i>Mysidioptera</i>	L. Tr (Ol)—U. Tr (Rha)	Cosmopolitan	B, E, S, Epi, Sed; By	Bimineralic
<i>Plagiostoma</i>	M. Tr (Ani)—U. Cret (Maa)	Cosmopolitan	B, E, S, Epi, Sed; By	Bimineralic
<i>Serania</i>	U. Tr (Nor - Rha)	E Tethys	B, E, S, Epi, Sed; By	Bimineralic
<i>Tirolidia</i>	M. Tr (Lad)—U. Tr (Car)	W Tethys	B, E, S, Epi, Sed; By	Bimineralic
<i>Antiquilima</i>	M. Tr (Lad)—L. Cret (Apt)	Cosmopolitan	B, E, S, Epi, Sed; By	Bimineralic
<i>Ctenostreon</i>	U. Tr (u. Rha)—L. Cret (Val?)	Tethys, Circumpacific and Austral	B, E, S, Epi, Sed; By	Bimineralic
<i>Gryphaea</i>	U. Tr (Car)—U. Cret (Cam)	Cosmopolitan	B, E, S, Un, Sed; R	Bimineralic?
<i>Umbrostrea</i>	M. Tr (Ani)—U. Tr (Rha)	Tethys	B, E, S, C, Sed; C	Bimineralic
<i>Actinostreon</i>	U. Tr (Rha)—U. Cret (Maa)	Tethys, Circumpacific and Austral	B, E, S, C, Sed; C	Calcitic
<i>Liotrea</i>	U. Tr (Car)—U. Cret (Cen)	Cosmopolitan	B/Ps, E, S, C, Sed/FaM; C	Calcitic?
<i>Atreta</i>	U. Tr (Car)—U. Cret (Maa)	Tethys	B, E, S, C, Sed; C	Bimineralic
<i>Protostrea</i>	M. Tr (Ani)	E Tethys	B, E, S, C, Sed; C	Bimineralic
<i>Harpax</i>	U. Tr (Nor)—L. J (Toa)	Austral and Boreal, Tethys?	B, E, S, C, Sed; C	Bimineralic
<i>Eoplicatula</i>	U. Tr (Car—Rha)	Tethys	B, E, S, C, Sed; C	Bimineralic
<i>Pseudoplacunopsis</i>	M. Tr (Ani)—U. Tr (Rha)	Tethys and Circumpacific	B, E, S, C, Sed; C	Bimineralic
<i>Claraia</i>	U. Pe (Wuch)—L. Tr (m. Ol)	Cosmopolitan	B/Ps, E, S, Epi, Se/FM	Bimineralic
<i>Eumorphotis</i>	L. Tr (In—Ol)	Tethys and Circumpacific	B, E, S, Epi, Sed; By	Bimineralic
<i>Ornithopecten</i>	M. Tr (Ani)—U. Tr (Car)	Tethys	B, E, S, Epi, Sed; By	Bimineralic
<i>Oxytheria</i>	U. Tr (Car)	W Tethys	B, E, S, Epi, Sed; By	Bimineralic
<i>Antijanira</i>	M. Tr (Ani)—U. Tr (Car)	W Tethys	B, E, S, Epi, Sed; By	Bimineralic
<i>Amphijanira</i>	M. Tr (Ani)—U. Tr (Car)	W Tethys	B, E, S, Epi, Sed; By	Bimineralic
<i>Primabinnites</i>	U. Tr (Nor—Rha)	Tethys	B, E, S, Epi, Sed; By	Bimineralic
<i>Neomorphotis</i>	M. Tr (Ani)	Tethys	B, E, S, Epi, Sed; By	Bimineralic
<i>Crittendenia</i>	L. Tr	Tethys and Circumpacific	B/Ps, E, S, Epi, Sed/FaM; By	Bimineralic
<i>Streblopteria</i>	Car (Miss)—M. Tr (Ani)	Boreal	B, E, S, Epi, Sed; By	Bimineralic
<i>Leptochondria</i>	M. Pe (Quad)—U. Tr (Nor)	Tethys and Circumpacific	B, E, S, Epi, Sed; By	Bimineralic
<i>Bittneria</i>	U. Tr (Car)	W Tethys	B, E, S, Epi, Sed; By	Bimineralic?
<i>Hokouia</i>	U. Tr (u. Car—Nor)	Austral	B, E, S, Epi, Sed; By	Bimineralic
<i>Sichuania</i>	U. Tr (Nor)	E Tethys	B, E, S, Epi, Sed; By	Bimineralic?
<i>Marwickiella</i>	M. Tr (Ani)	Austral	B, E, S, Epi, Sed; By	Bimineralic
<i>Anningella</i>	L. J (Hett - Sin)	W Tethys	B, E, S, Epi, Sed; By	Bimineralic
<i>Monotis</i>	U. Tr (Nor—l. Rha)	Cosmopolitan	B/Ps, E, S, Epi, Sed/FaM; By	Calcitic?
<i>Otapiria</i>	L. Tr (Ol)—U. J (Kim)	Cosmopolitan	B, E, S, Epi, Sed; By	Calcitic?
<i>Oxytoma</i>	L. Tr?, M. Tr (Lad)—U. Cret (Maa)	Cosmopolitan	B/Ps, E, S, Epi, Sed/FaM; By	Calcitic
<i>Avicularca</i>	M. Tr (Lad)—U. Tr (Car)	W Tethys	B, E, S, Epi, Sed; By	Unknown
<i>Meleagrinnella</i>	U. Tr (Nor)—L. Cret (Alb)	Tethys, Circumpacific and Boreal	B/Ps, E, S, Epi, Sed/FaM; By	Bimineralic
<i>Jianchuania</i>	U. Tr (Rha?)	E Tethys	B, E, S, Epi, Sed; By	Bimineralic
<i>Palmoxytoma</i>	L. J (Hett—Plie)	Cosmopolitan	B, E, S, Epi, Sed; By	Calcitic
<i>Asoella</i>	M. Tr (Ani)—L. J (Plie)	Tethys, Circumpacific and Austral	B, E, S, Epi/Un, Sed; By/R	Calcitic?
<i>Eitalia</i>	M. Tr (Ani)	Austral	B, E, S, Epi, Sed; By	Calcitic?
<i>Terquemia</i>	L. J (Sin)—U. J?	Tethys	B, E, S, C, Sed; C	Bimineralic
<i>Newaagia</i>	M. Tr (Ani)—U. Tr (Rha)	E Tethys and Boreal	B, E, S, C, Sed; C	Bimineralic
<i>Persia</i>	U. Tr (Nor)—L. J (l. Hett)	Tethys	B, E, S, C, Sed; C	Bimineralic
<i>Pegmavalvula</i>	L. Pe (Art)—L. Tr (Ol)	Circumpacific	B, E, S, C, Sed; C	Bimineralic

Table 1 (continued). See p. 4 for heading.

Genus	Stratigraphic range	Paleogeographic distribution	Paleoautoecology	Mineralogy
<i>Pergamidia</i>	U. Tr (Nor)	Tethys	B, E, S, Epi, Sed; By	Bimineralic
<i>Krumbeckiella</i>	U. Tr (Car-u. Rha)	Tethys	B, E, S, Epi, Sed; By	Bimineralic
<i>Manticula</i>	U. Tr (Car? - Nor), L. Cret (Berr)	Austral	B, E, S, Epi, Sed; By	Bimineralic
<i>Semuridia</i>	L. J (Sin)	W Tethys	B, E, S, Epi, Sed; By	Bimineralic
<i>Parapergamidia</i>	U. Tr (u. Car?-l. Nor)	E Tethys	B, E, S, Epi, Sed; By	Bimineralic
<i>Oretia</i>	U. Tr (l. Nor)	Austral	B, E, S, Epi, Sed; By	Unknown
<i>Halobia</i>	U. Tr (l. Car-m. Nor)	Cosmopolitan	B/Ps, E, S/Ch, Epi/Un, Sed/FaM; By/R	Bimineralic
<i>Daonella</i>	M. Tr (Ani-Lad)	Cosmopolitan	B/Ps, E, S/Ch, Epi/Un, Sed/FaM; By/R	Bimineralic
<i>Enteropleura</i>	M. Tr (m. Ani)	Tethys and Circumpacific	B/Ps, E, S/Ch, Epi/Un, Sed/FaM; By/R	Bimineralic
<i>Aparimella</i>	M. Tr (u. Ani)-U. Tr (l. Car)	E Tethys, Austral and Boreal	B/Ps, E, S/Ch, Epi/Un, Sed/FaM; By/R	Bimineralic
<i>Kolymonectes</i>	U. Tr (Nor?)-L. J (l. Toa)	Circumpacific, Austral and Boreal	B, E, S, Un, FaM; R/Sw	Bimineralic
<i>Parvamussium</i>	M. Tr (Ani)-Recent	Tethys, Circumpacific and Boreal	B, E, S, Un, FaM; R/Sw	Bimineralic
<i>Chlamys</i>	M. Tr (Ani)-Recent	Cosmopolitan	B, E, S, Epi/Un, FaM; By/R/Sw	Bimineralic
<i>Weyla</i>	L. J (Hett-Toa)	Circumpacific and Austral	B, Se, S, Un, Sed; R	Bimineralic
<i>Indopecten</i>	U. Tr (Nor-Rha)	Tethys	B, E, S, Epi/Un, FaM; By/R/Sw	Aragonitic
<i>Camptonectes</i>	M. Tr (Ani)-U. Cret (Maa)	Cosmopolitan	B, E, S, Epi, FaM; By/Sw	Bimineralic
<i>Crenamussium</i>	U. Tr (Car-Nor)	Tethys and Circumpacific	B, E, S, Epi, Sed; By	Bimineralic
<i>Avichlamys</i>	L. Tr (Ol)	E Tethys	B, E, S, Epi, Sed; By	Bimineralic
<i>Pseudopecten</i>	L. J (Hett)-M. J (Baj)	W Tethys	B, E, S, Un, FaM; R/Sw	Bimineralic
<i>Agerchlamys</i>	U. Tr (Car)-L. J (Toa)	Circumpacific, Austral and Boreal	B, E, S, Epi, Sed; By	Bimineralic
<i>Canadonectites</i>	L. J (Sin-Plie)	Circumpacific	B, E, S, Epi, Se; By	Bimineralic
<i>Eopecten</i>	U. Tr (Car)-L. Cret (Alb)	Tethys, Circumpacific and Austral	B, E, S, Epi/C, Sed; By/C	Bimineralic
<i>Janopecten</i>	M. Tr (Ani)-U. Tr (l. Car)	Boreal	B, E, S, Epi, FaM; By/Sw?	Bimineralic
<i>Ochotochlamys</i>	U. Tr (Nor) - L. J (Toa)	Boreal	B, E, S, Epi, Sed; By	Bimineralic
<i>Tosapecten</i>	U. Tr (Car-Rha)	Circumpacific and Boreal	B, E, S, Epi, Sed; By	Bimineralic
<i>Nevadapecten</i>	M. Tr (u. Lad)	Circumpacific	B, E, S, Epi, Sed; By	Bimineralic
<i>Loxochlamys</i>	M. Tr (Lad)-U. Tr (Car)	Circumpacific	B, E, S, Epi, Sed; By	Bimineralic
<i>Pleuronectites</i>	M. Tr (Ani)-U. Tr (Car)	Tethys and Circumpacific	B, E, S, Epi, Sed; By	Bimineralic
<i>Periclararia</i>	L. Tr (u. Ol) - M. Tr (l. Ani)	E Tethys	B, E, S, Epi, Sed; By	Bimineralic
<i>Radulonectites</i>	L. J (Hett - Plie)	E Tethys	B, E, S, Epi, Sed; By	Bimineralic
<i>Entolium</i>	L. Tr-U. Cret (Maa)	Cosmopolitan	B, E, S, Un, FaM/Sed; R/Sw	Bimineralic
<i>Scythentolium</i>	L. Tr	Tethys	B, E, S, Epi, Sed; By	Bimineralic
<i>Filopecten</i>	U. Tr (Car-Rha)	Tethys and Boreal	B, E, S, Epi, Sed; By	Bimineralic
<i>Posidonotis</i>	L. J (Sin-Toa)	Circumpacific	B, E, S, Un, Sed; R	Bimineralic
<i>Entolioides</i>	L. Tr-U. Tr (Car)	Tethys and Circumpacific	B, E, S, Epi, FaM; By/Sw	Bimineralic
<i>Permophorus</i>	Car (Miss)-L. Tr (Ol)	Circumpacific	B, Is, S, Endo/Un, Sed/SM; By/Sb	Aragonitic
<i>Curionia</i>	L. Tr (?)-U. Tr (Rha)	Tethys	B, Is/Se, S, Endo/Un, Sed/SM; By/Sb	Aragonitic
<i>Triaphorus</i>	U. Tr (Car-Nor)	Circumpacific, Austral and Boreal	B, Is/Se, S, SM; Sb	Aragonitic
<i>Somareoides</i>	U. Tr (Car)	S Tethys	B, Se, S, Endo/Un, Sed/SM; Sb	Aragonitic
<i>Kalentera</i>	U. Tr (Nor)-L. J (Toa)	Circumpacific and Austral	B, Se/Is, S, SM; Sb	Aragonitic
<i>Ouamoia</i>	U. Tr (Nor - Rha)	Austral	B, Is, S, Endo/Un, Sed/SM; By/Sb	Aragonitic
<i>Weixiella</i>	U. Tr (Nor - Rha)	Tethys	B, Is, S, Endo/Un, Sed/SM; By/Sb	Aragonitic
<i>Myoconcha</i>	U. Tr (Rha)-U. Cret (Maa)	Tethys and Austral	B, Se, S, Endo, Sed; By	Aragonitic
<i>Pseudomyoconcha</i>	M. Tr (Lad)-U. Tr (Rha)	Tethys, Circumpacific and Boreal	B, Se, S, Endo, Sed; By	Aragonitic
<i>Healeyia</i>	U. Tr (Nor-Rha)	Tethys	B, Se, S, Endo, Sed; By	Aragonitic
<i>Hippopodium</i>	U. Tr (Rha?)-U. J (Tit)	W Tethys and Boreal	B, Se, S, Endo, Sed; By	Aragonitic
<i>Trigonia</i>	M. Tr (Ani)-U. Cret (Cen)	Tethys, Circumpacific and Austral	B, Is, S, FM; Sb	Aragonitic
<i>Praegonia</i>	M. Tr (Lad)	Austral	B, Is, S, FM; Sb	Aragonitic
<i>Prorotrigonia</i>	U. Tr (Nor)	Tethys	B, Is, S, FM; Sb	Aragonitic
<i>Prosogyrotigonia</i>	U. Tr (Nor)-L. J (Sin)	Tethys and Circumpacific	B, Is, S, FM; Sb	Aragonitic
<i>Geratrigonia</i>	L. J (Hett-Toa)	Circumpacific	B, Is, S, FM; Sb	Aragonitic
<i>Vaugonia</i>	L. J (Hett)-U. J (Oxf)	Circumpacific	B, Is, S, FM; Sb	Aragonitic
<i>Kyushutrigonia</i>	U. Tr (Car-Nor)	Circumpacific	B, Is, S, FM; Sb	Aragonitic
<i>Acanomyophoria</i>	U. Tr (Car)	E Tethys	B, Is, S, FM; Sb	Aragonitic
<i>Jaworskiella</i>	L. J (Hett-Plie)	Circumpacific and Austral	B, Is, S, FM; Sb	Aragonitic
<i>Guineana</i>	U. Tr (Car-Nor)	Austral	B, Is, S, FM; Sb	Aragonitic
<i>Frenquelliella</i>	U. Tr (Car)-M. J (Baj)	Circumpacific y Austral	B, Is, S, FM; Sb	Aragonitic
<i>Costatoria</i>	U. Pe-U. Tr (Rha)	Tethys, Circumpacific and Austral	B, Is, S, SM; Sb	Aragonitic
<i>Myophoria</i>	M. Tr (Ani)-U. Tr (Rha)	Tethys	B, Is, S, FM; Sb	Aragonitic
<i>Neoschizodus</i>	M. Pe (Guad)-U. Tr (Rha)	Cosmopolitan	B, Is, S, FM; Sb	Aragonitic
<i>Agonisca</i>	M. Tr (Lad)	Austral	B, Is, S, FM; Sb	Aragonitic
<i>Gruenewaldia</i>	U. Tr (Car - Rha)	Tethys and Circumpacific	B, Is, S, FM; Sb	Aragonitic
<i>Elegantinia</i>	L. Tr (Ol)-U. Tr (Rha)	Tethys and Circumpacific	B, Is, S, FM; Sb	Aragonitic
<i>Caledogonia</i>	U. Tr (u. Car-l. Nor)	Austral	B, Is, S, FM; Sb	Aragonitic
<i>Atalantia</i>	U. Tr (l. Car)	W Tethys	B, Is, S, FM; Sb	Aragonitic
<i>Liotrigonia</i>	L. J (Hett?-Plie)	Tethys and Circumpacific	B, Is, S, FM; Sb	Aragonitic
<i>Erugonia</i>	U. Tr (Nor)	Circumpacific	B, Is, S, FM; Sb	Aragonitic
<i>Guizhoumyophoria</i>	M. Tr (Ani)	E Tethys	B, Is, S, FM; Sb	Aragonitic
<i>Minetrigonia</i>	U. Tr (Car-Rha)	Circumpacific, Austral and Boreal	B, Is, S, FM; Sb	Aragonitic
<i>Myophorigonia</i>	U. Tr (Car-Rha)	Circumpacific	B, Is, S, FM; Sb	Aragonitic
<i>Perugonia</i>	U. Tr (Car?-Rha?)	Circumpacific	B, Is, S, FM; Sb	Aragonitic
<i>Maoritrigonia</i>	U. Tr (Car-Rha)	Circumpacific and Austral	B, Is, S, FM; Sb	Aragonitic

Table 1 (continued). See p. 4 for heading.

Genus	Stratigraphic range	Paleogeographic distribution	Paleoautoecology	Mineralogy
<i>Groeberella</i>	L. J (Sin)–M. J (Baj)	Circumpacific and Austral	B, Is, S, FM; Sb	Aragonitic
<i>Antiquicorbula</i>	U. Tr (Nor–Rha)	Tethys	B, Is, S, SM; Sb	Aragonitic
<i>Pseudosaxicava</i>	L. J (Hett)–U. J (Tit)	E Tethys	B, E, S, Epi, Sed; By/N	Aragonitic
<i>Conchodon</i>	U. Tr (u. Nor? - Rha)	W Tethys	B, E/Se, S, Un, Sed; R	Aragonitic
<i>Pachyrisma</i>	L. J (Sin)–U. J (Tit)	Tethys	B, E/Se, S, Un, Sed; R	Aragonitic
<i>Paramegalodus</i>	U. Tr (Nor)	Tethys and Circumpacific	B, E/Se, S, Un, Sed; R	Aragonitic
<i>Pomaringina</i>	U. Tr (Car)	E Tethys	B, E/Se, S, Un, Sed; R	Aragonitic
<i>Ampezzania</i>	U. Tr (Nor)	W Tethys	B, E/Se, S, Un, Sed; R	Aragonitic
<i>Triadomegalodon</i>	U. Tr (Car–Rha)	Tethys, Circumpacific?	B, Se, S/Ph, Un, Sed; R	Aragonitic
<i>Quemocuomegalodon</i>	U. Tr (Nor)	E Tethys	B, E/Se, S, Un, Sed; R	Aragonitic
<i>Neomegalodon</i>	U. Tr (Car - Rha)	Tethys and Boreal	B, E/Se, S, Un, Sed; R	Aragonitic
<i>Rhaetomegalodon</i>	U. Tr (Nor–Rha)	W Tethys	B, E/Se, S, Un, Sed; R	Aragonitic
<i>Dicerocardium</i>	U. Tr (u. Car–Rha)	Tethys and Circumpacific	B, E/Se, S/Ph, Un, Sed; R	Aragonitic
<i>Cornucardia</i>	U. Tr (Car)	Tethys	B, E/Se, S, Un, Sed; R	Aragonitic
<i>Physocardia</i>	M. Tr (Ani)–U. Tr (Car)	W Tethys	B, E/Se, S, Un, Sed; R	Aragonitic
<i>Carinocardia</i>	U. Tr (l. Car)	W Tethys	B, E/Se, S, Un, Sed; R	Aragonitic
<i>Laubeia</i>	U. Tr (Car)	W Tethys	B, E/Se, S, Un, Sed; R	Aragonitic
<i>Wallowaconcha</i>	U. Tr (Nor)	Tethys and Circumpacific	B, E/Se, S/Ch/Ph, Un, Sed; R	Aragonitic
<i>Sinbadiella</i>	L. Tr (Ol)	Circumpacific	B, Is, S/Ch?, SM; Sb	Aragonitic
<i>Luciniola</i>	U. Tr (Rha)–L. J (Plie)	Tethys and Circumpacific	B, Is, S/Ch?, SM; Sb	Aragonitic
<i>Storbodon</i>	M. Tr (Lad)	W Tethys	Unknown	Unknown
<i>Schafhaeutlia</i>	M. Tr (Ani)–U. Tr (Rha)	Tethys, Circumpacific and Boreal	B, Is, S, SM; Sb	Aragonitic
<i>Sphaeriola</i>	L. J (Sin)–M. J (Call)	Tethys, Circumpacific and Austral	B, Is, S/Ch, SM; Sb	Aragonitic
<i>Tutcheria</i>	U. Tr (Car)–M. J (Aal)	Tethys, Circumpacific and Austral	B, Is, S, SM; Sb	Aragonitic
<i>Palaeocardita</i>	U. Tr (Car–Rha)	Tethys, Circumpacific and Austral	B, Is, S, Endo/Un, Sed/SM; By/Sb	Aragonitic
<i>Septocardia</i>	U. Tr (Car–Rha)	Tethys, Circumpacific and Austral	B, Is, S, Endo/Un, Sed/SM; By/Sb	Aragonitic
<i>Schizocardita</i>	U. Tr (Nor)	Circumpacific	B, Is/Se, S, SM; Sb	Aragonitic
<i>Coelopsis</i>	M. Tr (Lad)–L. Cret (?)	Tethys	B, E, S, Epi, Sed; By	Aragonitic
<i>Astarte</i>	M. Tr (Ani)–Recent	Tethys, Circumpacific and Austral?	B, Is, S, SM; Sb	Aragonitic
<i>Coelastarte</i>	L. J (Hett)–U. Cret (Tur)	Circumpacific	B, Is, S, SM; Sb	Aragonitic
<i>Astartopsis</i>	L. J (Sin), U. J (Oxf)	E Tethys	B, Is, S, SM; Sb	Aragonitic
<i>Nicaniella</i>	L. J (Hett)–Pa	E Tethys	B, Is, S, SM; Sb	Aragonitic
<i>Radiastarte</i>	U. Tr (Car)	E Tethys	B, Is, S, SM; Sb	Aragonitic
<i>Neocrassina</i>	L. J (Hett)–L. Cret (Berr)	Circumpacific	B, Is, S, SM; Sb	Aragonitic
<i>Praeconia</i>	U. Tr (Nor)–U. J (Tit)	Tethys and Circumpacific	B, Is, S, SM; Sb	Aragonitic
<i>Opis</i>	U. Tr (Nor)–U. Cret (Maa)	E Tethys	B, E, S, Un, Sed; R	Aragonitic
<i>Cardinia</i>	U. Tr (Car)–L. J (Toa)	Cosmopolitan	B, Is, S, SM; Sb	Aragonitic
<i>Balantioselena</i>	M. Tr (Lad)	Austral	B, Is, S, SM; Sb	Aragonitic
<i>Isopristes</i>	U. Tr (Nor)	Circumpacific	B, Is, S, SM; Sb	Aragonitic
<i>Minepharus</i>	U. Tr (Car)	Circumpacific	B, Se, S, Endo, Sed; By	Aragonitic
<i>Tonastarte</i>	U. Tr (Rha)–L. J (Toa)	Tethys and Austral	B, Is, S, MS; Sb	Aragonitic
<i>Pseudastarte</i>	L. J (Hett)–Sin	Tethys	B, Is, S, SM; Sb	Aragonitic
<i>Myophoricardium</i>	U. Tr (Car–Rha)	Tethys	B, Is, S, SM; Sb	Aragonitic
<i>Myophoriopsis</i>	M. Tr (Ani)–U. Tr (Rha)	Tethys and Circumpacific	B, Is, S, FM; Sb	Aragonitic
<i>Pseudocorbula</i>	M. Tr (Ani)–U. Tr (Rha)	Tethys	B, Is, S, FM; Sb	Aragonitic
<i>Protocardia</i>	U. Tr (Nor)–U. Cret (Maa)	Tethys and Circumpacific	B, Is, S, SM; Sb	Aragonitic
<i>Tulongocardium</i>	U. Tr (Nor–Rha)	Tethys	B, Is, S, SM; Sb	Aragonitic
<i>Integricardium</i>	L. J (Hett)–P (Dan)	Circumpacific	B, Is, S, MS; Sb	Aragonitic
<i>Rhaetidia</i>	M. Tr (Lad)–U. Tr (Nor)	W Tethys	B, Is, S?, SM; Sb	Aragonitic
<i>Tancredia</i>	L. J (Sin)–P (Dan)	Tethys	B, Id, S, FM; Db	Aragonitic
<i>Sakawanella</i>	U. Tr (Car)	Circumpacific	B, Id, S, SM; Db	Aragonitic
<i>Isocyprina</i>	U. Tr (Rha)–L. Cret (Apt)	Tethys	B, Is, S, FM; Sb	Aragonitic
<i>Pseudotrapezium</i>	L. J (Hett)–U. J (Oxf)	Tethys	B, Is, S, FM; Sb	Aragonitic
<i>Langvophorus</i>	U. Tr (Nor–Rha)	E Tethys	Unknown	Aragonitic
<i>Pholadomya</i>	U. Tr (Rha)–Recent	Tethys, Circumpacific and Austral	B, Id, S, SM; Db	Aragonitic
<i>Anomalopleuroides</i>	U. Tr (Car)	W Tethys	B, Id?, S, SM; Db?	Aragonitic
<i>Cortinia</i>	U. Tr (Car)	W Tethys	B, Is?, S, SM; Sb?	Aragonitic
<i>Goniomya</i>	L. J (Hett)–U. Cret (Maa)	Circumpacific	B, Id, S, SM; Db	Aragonitic
<i>Homomya</i>	M. Tr (Ani)–L. Cret (Val)	Tethys and Circumpacific	B, Id, S, SM; Db	Aragonitic
<i>Pachymya</i>	M. Tr (Ani)–U. Cret (Tur)	Tethys and Circumpacific	B, Id, S, SM; Db	Aragonitic
<i>Dianomya</i>	M. Tr (Ani)	E Tethys	B, Id, S, SM; Db	Aragonitic
<i>Osteomya</i>	L. J (Sin)–M. J (Call)	Circumpacific	B, Id, S, SM; Db	Aragonitic
<i>Pleuromya</i>	L. Tr (Ol)–L. Cret (Val)	Tethys, Circumpacific and Austral	B, Id, S, SM; Db	Aragonitic
<i>Burmesia</i>	U. Tr (Car)–L. J (Hett)	E Tethys and Circumpacific	B, Id, S, SM; Db	Aragonitic
<i>Prolaria</i>	U. Tr (Nor–Rha)	E Tethys	B, Id, S, SM; Db	Aragonitic
<i>Pseudoburmesia</i>	U. Tr (Car)	Tethys	B, Id, S, SM; Db	Aragonitic
<i>Pteromya</i>	U. Tr (Rha)–L. J (Hett)	W Tethys	B, Is, S, SM; Sb	Aragonitic
<i>Ochotomya</i>	U. Tr (Nor - Rha)	Austral and Boreal	B, Is, S, SM; Sb	Aragonitic
<i>Gresslya</i>	L. J (Hett) - U. J (Tit)	E Tethys and Circumpacific	B, Id, S, SM; Db	Aragonitic
<i>Thracia</i>	U. Tr (Nor) - Recent	Tethys and Circumpacific	B, Id, S, SM; Db	Aragonitic
<i>Cercomya</i>	U. Tr (Car)–U. Cret (Maa)	Tethys	B, Id, S, SM; Db	Aragonitic
<i>Tulongella</i>	M. Tr (Ani) - U. Tr (Rha)	E Tethys	B, Id, S, SM; Db	Aragonitic
<i>Orthomya</i>	U. Tr (Car)	E Tethys	B, Id, S, SM; Db	Aragonitic

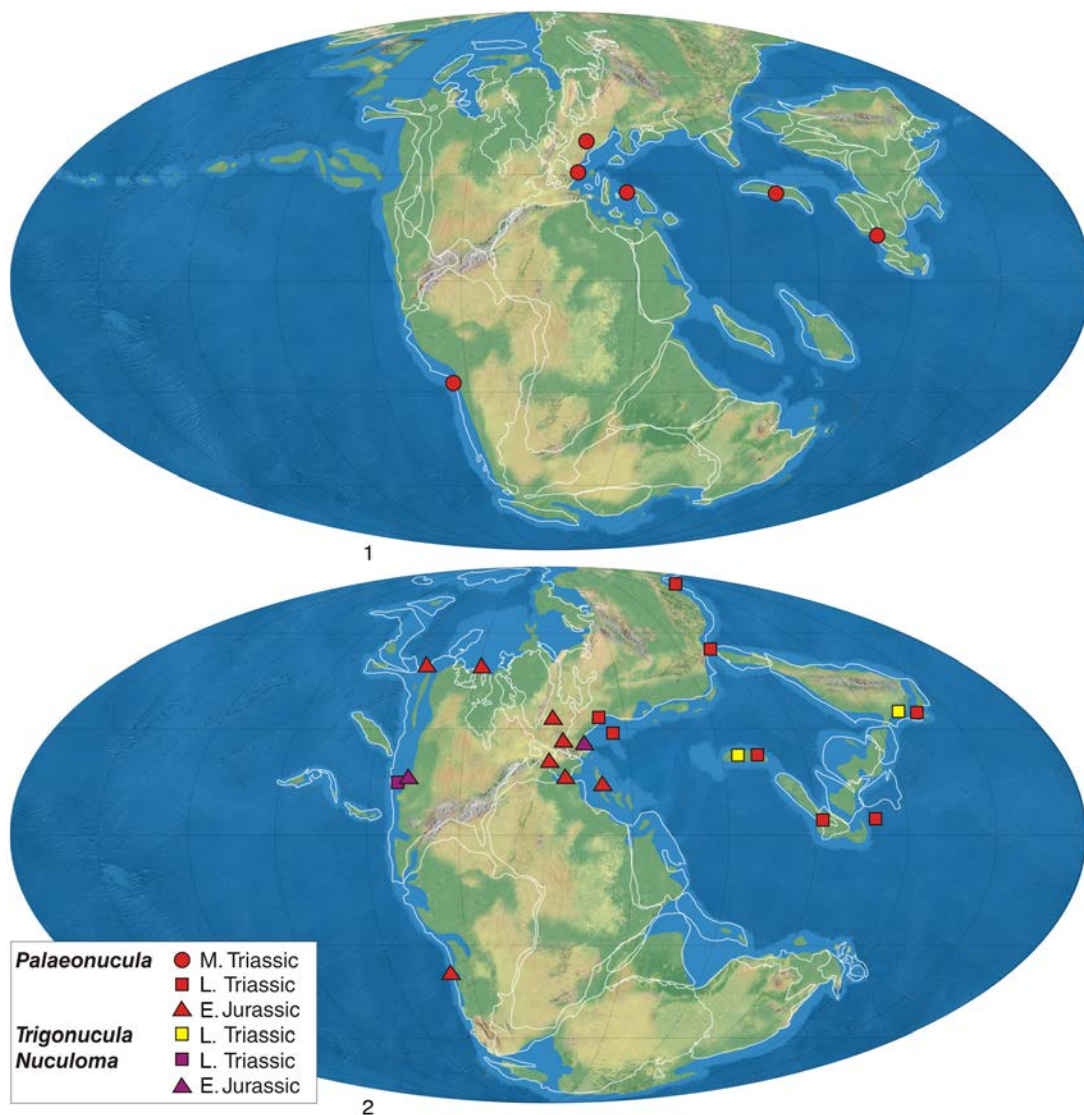


Figure 1. Paleogeographical distribution of Nuculidae (*Palaeonucula*, *Trigonucula*, *Nuculoma*). 1, Middle Triassic; 2, Late Triassic–Early Jurassic.

Superfamily NUCULOIDEA Gray, 1824

Family NUCULIDAE Gray, 1824

Genus PALAEONUCULA Quenstedt, 1930, p. 110

Type species.—*Nucula hammeri* DeFrance, 1825b, p. 217.

Remarks.—*Palaeonucula* was regarded as subgenus of *Nuculoma*, *Nucula*, and *Nuculopsis* (see Hodges, 2000, p. 13) and even as a synonym of the last (Nakazawa & Newell, 1968); it is here regarded as a valid genus, following Carter (1990a) and Hodges (2000).

Stratigraphic range.—Middle Triassic (lower Anisian)–Lower Cretaceous (Aptian) (Komatsu, Chen, & others, 2004; Gang, 2001). The stratigraphic range was here extended, both with respect to the Triassic–Jurassic range in Cox and others (1969), and also to Sepkoski (2002), who assigned a Triassic (Ladinian)–Jurassic (Tithonian) age. The oldest records we accept are Anisian (Tamura & others, 1975; Wen & others, 1976; Komatsu, Chen, & others, 2004). Although Bailey (1978) mentioned the species *Palaeonucula strigilata* from the Mississippian of Arkansas, this will not be taken into account because

the source is an abstract in a conference proceedings volume, and we did not find any reference where the author figured or described the species. The genus was widely mentioned throughout the interval Middle to Late Jurassic (Pugaczewska, 1986; Sha & Fürsich, 1994; Holzapfel, 1998; Harries & Little, 1999; Gahr, 2002; Delvene, 2003; J. Yin & Grant-Mackie, 2005).

Paleogeographic distribution.—Tethys, Circumpacific, and Boreal (Fig. 1).

Tethys domain: Middle Triassic: northern Vietnam (Komatsu, Huyen, & Huu, 2010); Anisian of China (Wen & others, 1976; Komatsu, Chen, & others, 2004), Spain (Márquez-Aliaga, 1985), Malaysia (Tamura & others, 1975); Ladinian of Germany (Ürlich, 1992), Spain (Márquez-Aliaga, 1985; Niemeyer, 2002), Malaysia (Tamura & others, 1975); Late Triassic: of China (Gou, 1993); Carnian of China (Wen & others, 1976), Italy (Fürsich & Wendt, 1977), Malaysia (Tamura & others, 1975); Norian of China (Lu, 1981), Iran (Repin, 2001; Hautmann, 2001b); Rhaetian of Iran

(Hautmann, 2001b), Hungary (Vörös, 1981); Early Jurassic: Hettangian–Sinemurian of England (Liu, 1995; Hodges, 2000); Sinemurian of Turkey (M. A. Conti & Monari, 1991); Sinemurian of southwestern France, Spain, & Portugal (Liu, 1995).

Circumpacific domain: Middle Triassic: Anisian of Chile (Barthel, 1958); Late Triassic: Carnian of Japan (Hayami, 1975); Early Jurassic: Hettangian–Sinemurian of Chile (Aberhan, 1994a; Damborenea, 1996a); Sinemurian of Canada (Aberhan, 1998a).

Boreal domain: Late Triassic: northeastern Siberia (Yakutia Region) (Kurushin, 1987); Triassic–Jurassic: northeastern Asia (Kurushin, 1990).

Paleoautoecology.—B, D, Is, FM; Sb. Holocene nuculids dig into the surface layers of the sediment and remain very close to its surface. They actively use the foot to dig and move around and use the palp proboscis to feed on detritus (Reid, 1998). A similar mode of life is suggested for *Palaeonucula*. Its external form would facilitate a fairly quick movement through the sediment. Pallial sinus is not observed, and thus it probably did not have siphons. Living nuculids are commonly found in shallow waters and fine-grained sandy sediments, and this is consistent with the associated lithology of fossil species (Hodges, 2000). All previous authors considered *Palaeonucula* as an infaunal, mobile, and shallow burrowing detritivorous bivalve (see e.g., Pugaczewska, 1986; Damborenea, 1987a; M. A. Conti & Monari, 1991; Holzapfel, 1998; Delvene, 2003).

Mineralogy.—Aragonitic (Carter, 1990a, p. 150). Outer shell layer: aragonite (irregular prismatic). Middle and inner shell layers: aragonite (homogeneous).

Genus TRIGONUCULA Ichikawa, 1949, p. 267

Type species.—*Trigonucula sakawana* Ichikawa, 1949, p. 268.

Stratigraphic range.—Upper Triassic (Carnian–upper Rhaetian) (Hayami, 1975; Hautmann, 2001b). Both Cox and others (1969) and Sepkoski (2002) assigned a Upper Triassic range to this genus. This is here maintained, despite references from the Jurassic and Cretaceous: *Trigonucula yunshanensis* Yu & Li (in Z. Li & Yu, 1982, p. 94, fig. 13–14) and *Trigonucula? yunshanensis* (Gu, Li, & Yu, 1997, p. 15, pl. 2,8–9). Nevertheless, both the hinge and shell outline of these species are totally different from those described for *Trigonucula sakawana* and therefore probably do not belong to the genus (Jingeng Sha, personal communication, 2008). Dickins and McTavish (1963) mention the genus (*Trigonucula* sp.) in the Lower Triassic (Scythian), but this will not be taken into account for two reasons: (1) it was not included in Cox and others (1969); and (2) the figures in Dickins and McTavish (1963) are impossible to compare due to their poor quality; also the authors pointed out in their discussion (p. 129): “In shape *Trigonucula* sp. is not unlike *Nucula* sp. *juv. ind.* Spath (1930, p. 53, pl. 12,12) from the Lower Triassic (Otoceratan) of Greenland.”

Paleogeographic distribution.—Tethys and Circumpacific (Fig. 1).

Tethys domain: Late Triassic: Norian of Iran (Hautmann, Aghababalu, & Krystyn, 2011); Rhaetian of Iran (Hautmann, 2001b).

Circumpacific domain: Late Triassic: Carnian of Japan (Ichikawa, 1949; Hayami, 1975; Kobayashi & Tamura, 1983b).

Paleoautecology.—B, D, Is, FM; Sb. A relatively quick shallow burrower and detritivorous mode of life is attributed to this genus, similar to the living nuculids (Reid, 1998). Hautmann (2001b, p.

26) described divaricate ornamentation of the shell in his emended diagnosis of the genus. This type of ornamentation has been studied from a functional point of view by several authors (e.g., S. M. Stanley, 1969; Seilacher, 1972), and it is now known that it facilitates excavation (Checa & Jiménez-Jiménez, 2003b).

Mineralogy.—Aragonitic. No specific data about the *Trigonucula* mineralogy and shell microstructure is known, but a totally aragonitic mineralogy is assumed, according to the diagnosis of subclass Paleaeotaxodonta given by Allen and Hannah (1986).

Genus NUCULOMA

Cossmann in Cossmann & Thiéry, 1907, p. 124

Type species.—*Nucula castor* d’Orbigny, 1850, p. 339.

Stratigraphic range.—Upper Triassic (Rhaetian)–Lower Cretaceous (Valanginian) (Laws, 1982; Kaim, 2001). Although *Nuculoma* was regarded as a typical Jurassic genus (Cox & others, 1969; Sepkoski, 2002), it was found in the Rhaetian of New York Canyon (Laws, 1982; Guex & others, 2003, 2004; Lucas & Tanner, 2004; Lucas & others, 2007) and in the Lower Cretaceous of several localities (Kaim, 2001; Marinov & others, 2006; X. Li, 1990). Accordingly, its stratigraphic range is here extended.

Although originally used for Jurassic forms, several Recent species were also included in *Nuculoma*. There is no revision of these living species to test which ones are really consistent with the diagnosis, but they will not be taken into account here, because, according to Hansson (1998, p. 93), living species should be included in *Ennucula* Iredale, 1931 [*Ennucula* Iredale, 1931 = *Nuculoma*: auct., non Cossmann in Cossmann & Thiéry, 1907 (*Nucula castor* d’Orbigny, 1850 - Jurassic fossil)].

Paleogeographic distribution.—Tethys and Circumpacific (Fig. 1). Available information suggests that the genus appeared in the Circumpacific domain, specifically in the Rhaetian of Nevada (Guex & others, 2004), and, during the Early Jurassic, it spread to the Tethys (Hallam, 1972, 1977) and Boreal domains (Zakharov & others, 2006). Later, during the Jurassic, its distribution expanded not only to the European Tethys (X. Li & Grant-Mackie, 1994; Holzapfel, 1998), but also to the Proto-Atlantic (Liu, 1995).

Circumpacific domain: Late Triassic: Rhaetian of Nevada (Hallam & Wignall, 2000); Early Jurassic: Hettangian of Nevada (Hallam & Wignall, 2000).

Tethys domain: Early Jurassic: Sinemurian of Europe (Hallam, 1977).

Paleoautoecology.—B, D, Is, FM; Sb. Fürsich (1982) compared *Nuculoma* with Recent *Nucula*, and he assigned it a similar mode of life, moving just below the sediment surface, feeding on the detritus taken with palp proboscis, like other nuculids.

Mineralogy.—Aragonitic (Carter, 1990b, p. 307). Outer shell layer: aragonite (prismatic). Middle and inner shell layers: aragonite (nacreous).

Superfamily NUCULANOIDEA

Adams & Adams, 1858 in 1854–1858

Family NUCULANIDAE Adams & Adams, 1858 in 1854–1858

Genus NUCULANA Link, 1807, p. 155

Type species.—*Arca rostrata* Chemnitz, 1784, pl. 55, fig. 550–551.

Remarks.—*Nuculana* is a genus especially difficult to identify since the external characters alone, in absence of inner views, are

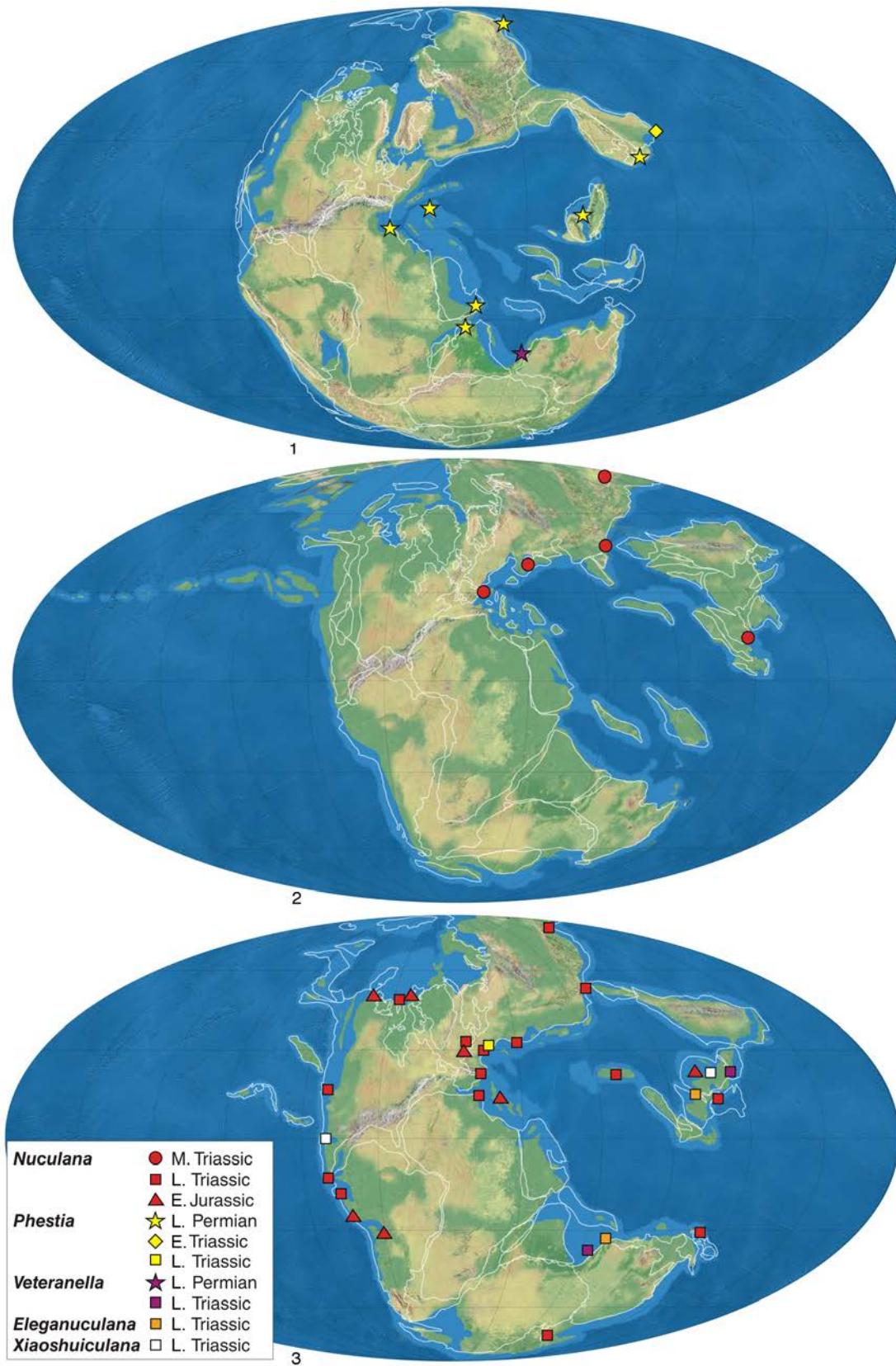


Figure 2. Paleogeographical distribution of Nuculanidae (*Nuculana*, *Phestia*, *Veteranella*, *Eleganuculana*, *Xiaoshuiculana*). 1, Early Triassic; 2, Middle Triassic; 3, Late Triassic–Early Jurassic.

undistinguishable from those of other genera, such as *Phaenodesmia* Bittner, 1894, *Phestia* Chernyshev, 1951, *Veteranella* (*Veteranella*) Patte, 1926, or *V. (Glyptoleda)* Fletcher, 1945; hence many Paleozoic and Mesozoic specimens attributed to *Nuculana* probably belong to other genera (Boyd & Newell, 1979; Damborenea, 1987a; Carter, 1990a; Z. Fang & Cope, 2004).

Leda Schumacher, 1817, is a junior objective synonym of *Nuculana* (both genera have the same type species). Although this was pointed out by Cox and others (1969), some authors still use the name *Leda* (e.g., Fürsich & Wendt, 1977; Ruban, 2006a).

Stratigraphic range.—Middle Triassic (Anisian)—Holocene (Tamura & others, 1975). Although there are references for this genus from the Paleozoic, we follow McAlester (in Cox & others, 1969), who considered its range to be from the Triassic to the present (see Nakazawa & Newell, 1968, p. 37–38 for discussion of this genus). Sepkoski (2002) extended it to the lower Induan, but the only mention from the Lower Triassic is *Nuculana (Dacryomya)* sp. from Japan in Nakazawa (1961); however, this was referred to as *Phestia* sp. by Nakazawa and Newell (1968). Therefore, the first appearance is regarded as Anisian (Tamura & others, 1975). Furthermore, the record is fairly continuous throughout the entire study interval (see Paleogeographic Distribution, below). However, not all authors agree about the presence of *Nuculana* in this time interval. Carter (1990a, p. 151) stated that *Nuculana* did not appear until the Cretaceous. In our opinion, a thorough review of this genus is needed, but it is beyond the scope of this paper, and we will tentatively use the proposed range.

Paleogeographic distribution.—Cosmopolitan (Fig. 2). Although the genus is also present in the Early Jurassic from both the Circumpacific and the Austral domains, these records are Pliensbachian in age (Damborenea, 1987a; Aberhan, 1994a, 1998a).

Tethys domain: Middle Triassic: Anisian of Malaysia (Tamura & others, 1975), northern Vietnam (Komatsu, Huyen, & Huu, 2010); Ladinian of Afghanistan (Farsan, 1975), Spain (Niemeyer, 2002), western Caucasus (Ruban, 2006a); Late Triassic: China (Cowper-Reed, 1927); Carnian of Italy (S. Conti, 1954), Slovenia (Jurkovek, 1978), China (Wen & others, 1976; Lu, 1981; Gou, 1993; J. Yin, Enay, & Wan, 1999); Norian of Iran (Hautmann, 2001b; Repin, 2001); Norian–Rhaetian of England (Hallam & El Shaarawy, 1982; Hallam, 2002); Rhaetian of Italy (Sirna, 1968), Iran (Hautmann, 2001b; Repin, 2001), Spain (Márquez-Aliaga, Plasencia, & Ros, 2005), China (J. Yin, Enay, & Wan, 1999), Austria (Tomašových, 2006a, 2006b); Early Jurassic: Hettangian of China (J. Yin, Enay, & Wan, 1999); Hettangian–Sinemurian of England (Liu, 1995); Sinemurian of Turkey (M. A. Conti & Monari, 1991).

Circumpacific domain: Late Triassic: Carnian of Mexico (Alencaster de Cserna, 1961), Peru (Jaworski, 1922; Cox, 1949); Norian of Nevada (Laws, 1982).

Boreal domain: Middle Triassic: northern Siberia (Dagys & Kurushin, 1985), Primorie (Kiparisova, 1972); Late Triassic: Carnian of Primorie (Kiparisova, 1972); Triassic–Jurassic: northeastern Asia (Kurushin, 1990). Holocene species have a wide distribution in the boreal domain and in cold-temperate regions.

Austral domain: Late Triassic: Carnian of New Zealand (Marwick, 1953), Carnian–Norian of New Guinea (Skwarko, 1967); Rhaetian of New Zealand (Grant-Mackie, 1960).

Paleoautoecology.—B, D, Is, FM; Sb. Holocene species of this genus are very fast burrowers (Gordillo & Aitken, 2000), moving in the surface of the sediment, with a detritivorous trophic regime (Damborenea, 1987a; M. A. Conti & Monari, 1991; Holzapfel, 1998; Hautmann, 2001b).

Mineralogy.—Aragonitic (Carter, 1990b, p. 311–312, for Recent species). All shell layers: aragonite (homogeneous).

Genus PHESTIA Chernyshev, 1951, p. 9

Type species.—*Leda inflatiformis* Chernyshev, 1939, p. 116.

Remarks.—We regard *Polidevcia* Chernyshev, 1951, p. 25, as a subgenus of *Phestia* (see discussion for *Polidevcia* in Genera not Included, p. 168).

The generic name was first proposed in Chernyshev, 1943, p. 35, but no type species was designated, and it remained a nomen nudum until the type was designated by this author in 1951.

Stratigraphic range.—Middle Ordovician (lower Llanvirn)—Upper Triassic (Carnian) (Carter, 1990a; Z. Fang & Cope, 2004). Cox and others (1969) assigned this genus a Devonian–Lower Triassic range, and Sepkoski (2002), considered it was present from the Devonian (Givetian) to Lower Triassic (data taken from Skelton & Benton, 1993), but the range is extended in this paper. The first occurrence of the genus was Middle Ordovician (Llanvirnian [=overlaps with Darriwilian stage]), according to Z. Fang and Cope (2004), although doubtfully because the figured specimen is an external mold, and the internal features are unknown. Thus, although reference to *Phestia* seems justified, the same authors note that it externally resembles *Glyptoleda* (regarded in this paper as a subgenus of *Veteranella*). Carnian is used here as the upper limit, based on data provided by Carter (1990a, p. 153). This author considered that “*Nuculana*” *sulcellata*, from the Italian Carnian, would be better located within *Phestia*, since its form, ligament structure, and nacreous interior are typical of this genus. Nakazawa and Newell (1968) included *Nuculana (Dacryomya)* sp., figured by Nakazawa (1961, p. 270, pl. 14, 5–7), in *Phestia*, and thus extended the range of this genus to the Triassic of southwestern Japan. Hautmann and others (2005) mentioned *Phestia?* cf. *perlonga* (Mansuy) from the upper Rhaetian of southern Tibet, but this is the type species of *Mesoneilo* Vu Khuc, 1977a, p. 676, to which the authors did not refer in their paper. This very doubtful record will not be taken into account here.

Paleogeographic distribution.—Tethys, Circumpacific, and Boreal (Fig. 2). Cox and others (1969) regarded *Phestia* as a cosmopolitan genus, but, although it was very widespread during the Paleozoic, during the studied time interval, it was only present in the Tethys, the Boreal, and the Circumpacific domains.

Tethys domain: late Permian: Iran (Teichert, Kummel, & Sweet, 1973), Tunisia and India (Boyd & Newell, 1979), southern China (L. Li, 1995; Clapham & Bottjer, 2007), Oman (Dickins, 1999); Late Triassic: Carnian of Italy (Carter, 1990a).

Circumpacific domain: late Permian: Japan (Nakazawa & Newell, 1968; Murata & Bando, 1975; Hayami & Kase, 1977); Early Triassic: Japan (Nakazawa & Newell, 1968).

Boreal domain: late Permian: northeastern Russia (Biakov, 1998, 2002, 2006, 2007; Klets & others, 2006).

Paleoautoecology.—B, D, Is, FM; Sb. *Phestia* most probably had a mode of life similar to the living *Nuculana*, but it lacked a pallial

sinus, so it possibly did not have true siphons (as *Nuculana* has). Instead, it may have had pseudosiphons created by ciliary connections between the undulations of the mantle (see Bradshaw, 1999, p. 75–76). The genus was regarded as a superficial burrowing detritivore that used the palp proboscis to collect food particles (Hoare, Heaney, & Mapes, 1989; Bradshaw, 1999). R. Zhang and Yan (1993) agreed with this and provided a reconstruction of its mode of life, showing the similarity to *Palaeoneilo*. The elongated anterior part and the anterior pedal muscle scars, which can be observed in some specimens, suggest it had a large foot that would allow it to burrow effectively (Mángano & others, 1998). These authors associated the ichnofossil *Lockeia ornata* with *Phestia*, from which they concluded that *Phestia* was a vagrant detritivorous capable of moving subhorizontally in the sediment.

Mineralogy.—Aragonitic (Carter, 1990a, p. 154–155). Outer shell layer: aragonite (prismatic). Middle and inner shell layers: aragonite (nacreous).

Genus VETERANELLA Patte, 1926, p. 158

Type species.—*Nuculana (Veteranella) strenua* Patte, 1926, p. 158.

Stratigraphic range.—Lower Permian (Artinskian)–Upper Triassic (Norian) (Kutassy, 1931; Waterhouse, 1964). The stratigraphic range is here extended with respect to Sepkoski (2002), because we include *Glyptoleda* and *Nucundata* as subgenera of *Veteranella*, according to Cox and others (1969) (see discussion for *Glyptoleda* and *Nucundata* in Genera not Included, p. 161, 166).

Cox and others (1969) assigned a Permian–Triassic range to *Veteranella*; Sepkoski (2002) considered *Nucundata* to be present in the Permian following Cox and others (1969), *Glyptoleda* in the late Guadalupian following Waterhouse (1987), and a Norian range for *Veteranella* following Hallam (1981). J. Chen, Liu, and Lan (1983) mentioned *Glyptoleda* and other genera attributed to their new subfamily Veteranellinae from Devonian to Permian, but none of these genera was listed as being present before the Carboniferous (Z. Fang & Cope, 2004).

The oldest record of the genus (referred to *Nucundata* and *Glyptoleda*) is lower Permian (Artinskian–Kungurian) of New Zealand (Waterhouse, 1964). The genus was also mentioned from Lower Jurassic age; e.g., Kurushin (1990) quoted *Veteranella* from the Triassic–Jurassic boundary, confirming its presence in lower Hettangian beds, and Zhakarov and others (2006) mentioned *Glyptoleda* from the Pliensbachian, but none of them justified the presence of this genus in the Lower Jurassic, because they neither figured the specimens nor included the original source of their data. The youngest record is Upper Triassic: *Veteranella (Ledoides)* Chen, Wen, & Lan in Wen & others, 1976, from Carnian–Norian of Tibet (Kobayashi & Tamura, 1983a), from Carnian of China (Wen & others, 1976), and from Norian of eastern Tethys (Hallam, 1981).

Paleogeographic distribution.—Tethys (Fig. 2). *Veteranella* had a wide distribution in Boreal and Austral domains during the early and middle Permian (Waterhouse, 1964, 1983; Biakov, 1998, 2006), but it was not found there during the late Permian.

Tethys domain: late Permian: Changhsingian of Nepal (Waterhouse & Chen, 2006); Late Triassic: China (Kutassy, 1931); Carnian of China (Wen & others, 1976); Carnian and Norian of southern Tibet (Kobayashi & Tamura, 1983a); Norian of Xizang (Tibet) (Z. Fang & others 2009).

Paleoautoecology.—B, D, Is, FM; Sb. *Veteranella reidi* (Fletcher, 1945) (Permian) is the oldest species with oblique chevron-type ornamentation, which became common among bivalves during the Cenozoic, and is interpreted as an adaptation to rapid escape from potential predators and for minimizing shell damage during burrowing (Checa & Jiménez-Jiménez, 2003a). Numerous studies demonstrated that this type of ornamentation facilitates excavation (S. M. Stanley, 1969, 1970; Seilacher, 1972), so this genus is regarded as a fast burrower.

Mineralogy.—Aragonitic (Carter, Barrera, & Tevesz, 1998). Data provided for subclass Protobranchia. All shell layers: aragonite. Inner shell layer: usually nacreous.

Genus ELEGANUCULANA

J. Chen & Yang, 1983, p. 355 [358]

Type species.—*Eleganuculana nyeruensis* J. Chen & Yang, 1983, p. 356.

Stratigraphic range.—Upper Triassic (Norian) (J. Chen & Yang, 1983). J. Chen and Yang (1983) described *Eleganuculana* including only the type species from Norian of Knagmar region in Xizang province (southern China). J. Chen, Liu, and Lan (1983) mentioned the same species from the Norian of Tibet.

Paleogeographic distribution.—Eastern Tethys (Fig. 2).

Tethys domain: Late Triassic: Norian of southern China (J. Chen & Yang, 1983), Tibet (J. Chen, Liu, & Lan, 1983).

Paleoautoecology.—B, D, Is, FM; Sb. Similar to *Nuculana*.

Mineralogy.—Aragonitic (Carter, Barrera, & Tevesz, 1998). No data are available for *Eleganuculana*. Protobranchia shell mineralogy is fully aragonitic (Carter, Barrera, & Tevesz, 1998).

Genus XIAOSHUICULANA J. Chen in J. Chen, Liu, & Lan, 1983, p. 622, 626

Type species.—*Reticulana elegansa* Li & Li in R. Zhang, Wang, & Zhou, 1977, p. 9.

Stratigraphic range.—Upper Triassic. *Xiaoshuiculana* was described by J. Chen (in J. Chen, Liu, & Lan, 1983) from Upper Triassic of China (Guangdong province), including only the type species. McRoberts (1997a) described a new species: *X. tozeri* McRoberts, 1997a, from the lower Rhaetian Antimonio Formation of Sonora (Mexico).

Paleogeographic distribution.—Tethys and Circumpacific (Fig. 2).

Tethys domain: Late Triassic: China (J. Chen, Liu, & Lan, 1983).

Circumpacific domain: Late Triassic: Rhaetian of Mexico (McRoberts, 1997a).

Paleoautoecology.—B, D, Is, FM; Sb. *Xiaoshuiculana* is externally similar to *Nuculana*, but its rostrum is more elongated, and the shell bears oblique ribs (McRoberts, 1997a). These ribs would primarily strengthen the shell and probably also favored efficient excavation (Checa & Jiménez-Jiménez, 2003a).

Mineralogy.—Aragonitic (Carter, Barrera, & Tevesz, 1998). Data provided for subclass Protobranchia.

Family MALLETIIDAE Adams & Adams, 1858 in 1854–1858

Genus PHAENODESMIA Bittner, 1894, p. 188

Type species.—*Phaenodesmia klipsteiniana* Bittner, 1894, p. 188.

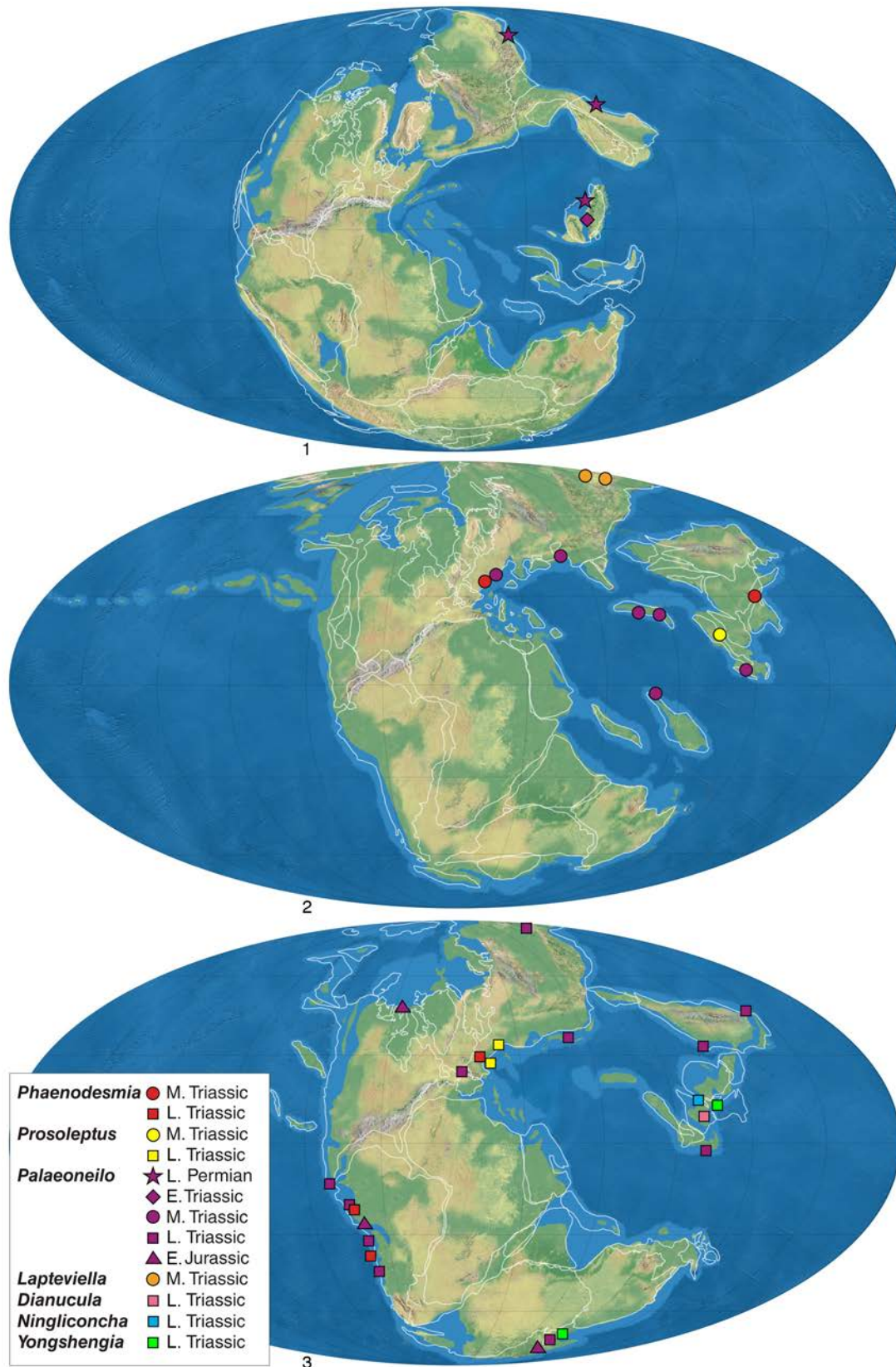


Figure 3. Paleogeographical distribution of Mallettiidae (*Phaenodesmia*, *Prosoleptus*, *Palaeoneilo*, *Lapteviella*, *Dianucula*, *Ningliconcha*, *Yongshengia*). 1, Early Triassic; 2, Middle Triassic; 3, Late Triassic–Early Jurassic.

Stratigraphic range.—Middle Triassic (Anisian)—Upper Triassic (Rhaetian) (Hallam, 1981; F. Stiller, personal communication, 2008). Cox and others (1969) assigned a Triassic range in Europe to this genus. Sepkoski (2002), allegedly based on data provided by Hallam (1981), assigned it an Anisian–Norian range. However, Hallam (1981) considered that *Phaenodesmia* was present in Carnian and Norian (including Rhaetian) deposits. The oldest record is from Anisian beds of the Alps (Diener, 1923) and southwestern China (F. Stiller, personal communication, 2008).

Paleogeographic distribution.—Tethys and Circumpacific (Fig. 3).

Tethys domain: Middle Triassic: Anisian of southwestern China (F. Stiller, personal communication, 2008), southern Alps (Diener, 1923); Late Triassic: Carnian of southern Alps (Diener, 1923).

Circumpacific domain: Late Triassic: South America (Hallam, 1981), Peru (Jaworski, 1922; Körner, 1937); Carnian of Chile (Nielsen, 2005).

Paleoautoecology.—B, D, Is, FM; Sb. We assign to this genus the same mode of life as other nuculids.

Mineralogy.—Aragonitic (Carter, Barrera, & Tevesz, 1998). Data provided for subclass Protobranchia.

Genus PROSOLEPTUS Beushausen, 1895, p. 95

Type species.—*Nucula lineata* Goldfuss, 1837 in 1833–1841, p. 153.

Stratigraphic range.—Middle Triassic (Anisian)—Upper Triassic (Carnian) (Fürsich & Wendt, 1977; Komatsu, Huyen, & Huu, 2010). Cox and others (1969) considered that *Prosoleptus* was present in the European Triassic. Sepkoski (2002) assigned it a Middle Triassic(?)–Carnian range following Hallam (1981), who mentioned *Prosoleptus* from Ladinian and Carnian deposits of western Tethys.

Fürsich and Wendt (1977) found *P. lineata* (Goldfuss, 1837 in 1833–1841) in the Cassian Formation of the southern Alps. This formation is regarded as upper Ladinian–Carnian in age, and probably for this reason, Hallam (1981) mentioned it from the Ladinian. Although Fürsich (in PBDB, 2005) confirmed that *P. lineata* occurs only in Carnian beds, it was recently reported from Anisian beds of northern Vietnam (Komatsu, Huyen, & Huu, 2010).

Paleogeographic distribution.—Tethys and ?Boreal (Fig. 3). *Prosoleptus* was present in the Tethys domain and probably also in northern Siberia (Carnian) (Kurushin, 1984).

Tethys domain: Middle Triassic: Anisian–Ladinian of northern Vietnam (Komatsu, Huyen, & Huu, 2010); Late Triassic: Carnian of Italy (south of the Alps) (Fürsich & Wendt, 1977), Germany (Goldfuss, 1863).

Paleoautoecology.—B, D, Is, FM; Sb. We assign the same mode of life as other nuculids.

Mineralogy.—Aragonitic (Carter, 1990a, p. 159–160; Carter, Lawrence, & Sanders, 1990, p. 315–316). All layers: aragonite (homogeneous).

Genus PALAEONEILO Hall & Whitfield, 1869, p. 6

The original spelling was *Palaeoneilo* Hall & Whitfield, 1869, p. 6, see McAlester, 1968, p. 41. For the authorship of the paper where this genus was named, see McAlester, 1968, p. 62.

Type species.—*Nuculites constricta* Conrad, 1842, p. 249.

Remarks.—There is some confusion in the literature among the genera *Palaeoneilo*, *Praesacella* Cox, 1940, and *Mesosacella* Chavan, 1947, p. 197 (see discussion in Damborenea, 1987a, p. 54). The problem stems from the fact that there are both Paleozoic and Mesozoic records of this genus and in the presence or absence of resilifer in different species referred to it. Some authors (cf. Damborenea, 1987a, p. 54; Aberhan, 1998a, p. 67) referred Paleozoic species to *Palaeoneilo* and Mesozoic species to *Mesosacella*, but Cox (1937a) stated that there is no reason to separate the Paleozoic and Mesozoic species in different genera; this last criterion is followed here (but see Duff, 1978). Hodges (2000) regarded *Palaeoneilo* as a morphologically conservative genus that changed very little in general external shape through time.

Stratigraphic range.—Lower Ordovician (Tremadocian)—Lower Jurassic (Toarcian) (Gahr, 2002; Sánchez, 2002). Cox and others (1969) mentioned the range of this genus as Ordovician to the end of the Mesozoic, with a cosmopolitan distribution. Later, Sepkoski (2002) assigned it an Ordovician (upper Arenigian)—Jurassic (?upper Pliensbachian) range, following Pojeta (1971).

The first appearance is from the Lower Ordovician of Argentina (Sánchez, 2002). However, there are some problems with its last appearance. We accept Gahr's youngest record (2002) from the Toarcian; other younger records will not be taken into account, since almost all have some descriptive problems. For instance, Sha and Fürsich (1993) mentioned *Palaeoneilo* sp. from the Upper Jurassic and Lower Cretaceous of China, but they did not figure or systematically describe it. Later (Sha & Fürsich, 1994; Sha & others, 1998), they studied specimens from the same area and referred them to several species of *Nuculana* (*Praesacella*) and *Mesosacella*, but none to *Palaeoneilo*, although they discussed the problems of differentiating *Palaeoneilo* and *Mesosacella*, and they even gave a series of guidelines to distinguish them. Hu, Jansa, and Wang (2008) also mentioned the genus from the Upper Jurassic–Lower Cretaceous interval, but not only did they not figure it, but they listed it as an ammonoid.

Paleogeographic distribution.—Cosmopolitan (Fig. 3). *Palaeoneilo* was a cosmopolitan genus during part of Paleozoic and Mesozoic, at least during the study interval considered.

Tethys domain: late Permian: southern China (L. Li, 1995; Y. Wang & others, 2006; Y. Yin & others, 2006; He, Feng, & others, 2007); Early Triassic: China (Z. Yang & Yin, 1979; L. Li, 1995; Sha & Grant-Mackie, 1996); Middle Triassic: Tethys (Hallam, 1981); Muschelkalk and Buntsandstein of Poland (Senkowiczowa, 1985); Anisian of southern China (Komatsu, Chen, & others, 2004); Anisian–Norian of Malaysia and Thailand (Tamura & others, 1975); Ladinian of Afghanistan (Farsan, 1975); Late Triassic: Tethys (Hallam, 1981); Carnian of China (Sha & Grant-Mackie, 1996), southern Alps (Diener, 1923; Kutassy, 1931; Fürsich & Wendt, 1977); Carnian–Norian of China (Wen & others, 1976; Lu & Chen, 1986; Gou, 1993); Norian of southwestern China (Lu, 1981), Singapore (Kobayashi & Tamura, 1968a); Rhaetian of Burma (Diener, 1923); Early Jurassic: Hettangian–Sinemurian of southwestern England (Hodges, 2000); Sinemurian–Pliensbachian of Europe (Hallam, 1987).

Circumpacific domain: late Permian: Japan (Nakazawa & Newell, 1968; Hayami & Kase, 1977); Late Triassic: Mexico, Chile, and Peru

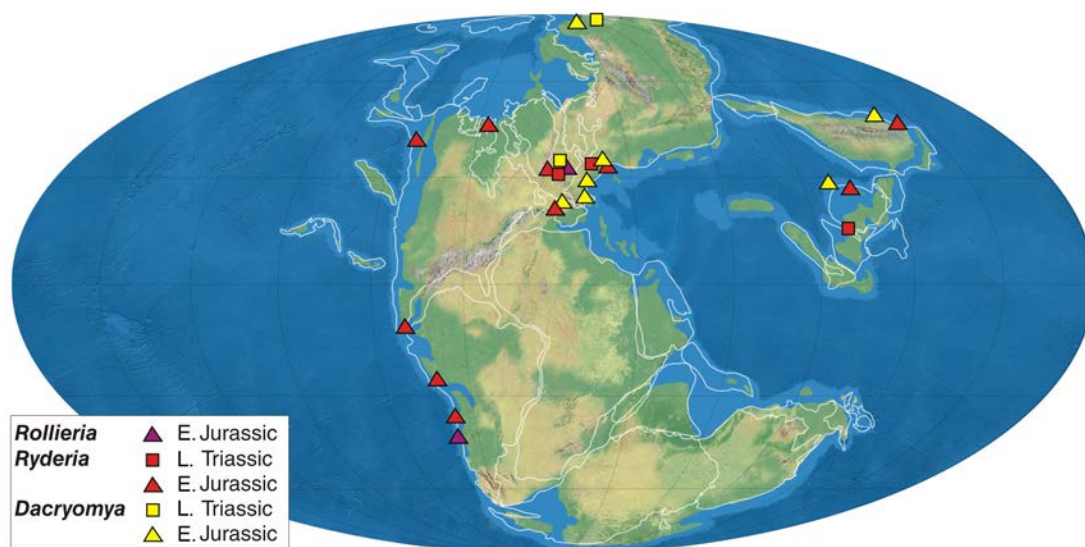


Figure 4. Paleogeographical distribution of Yoldiidae (*Rollieria*) and Polidevciidae (*Ryderia*, *Dacryomya*). Late Triassic–Early Jurassic.

(see references in Damborenea, 1987a); Carnian of Mexico (Diener, 1923), Japan (Hayami, 1975); Carnian–Norian of Japan (Onoue & Tanaka, 2005); Early Jurassic: Sinemurian of Chile (Covacevich, Pérez, & Escobar, 1991).

Boreal domain: late Permian: northeastern Russia (Biakov, 1998, 2007); Late Triassic: northeastern Russia (Polubotko & Repin, 1990).

Austral domain: Late Triassic: New Zealand (see references in Damborenea, 1987a), Rhaetian of New Zealand (MacFarlan, 1998) and Argentina (Damborenea & Manceñido, 2012); Early Jurassic: Pliensbachian of New Zealand (MacFarlan, 1998).

Paleoautoecology.—B, D, Is, FM; Sb. *Palaeoneilo* is regarded as a detritivorous bivalve, a superficial burrower living completely buried, very close to the sediment surface, like some living species of *Yoldia* (Damborenea, 1987a). It used a palp proboscis to feed on organic particles dispersed in the sediment (Hodges, 2000). Since in some species (e.g., *P. elliptica*) there is a shallow pallial sinus, presumably it had short siphons. Life position within the substrate most probably was with the posterior end up near the surface of the sediment, as interpreted for *Phestia* (see R. Zhang & Yan, 1993, p. 854, fig. 2). According to Hodges (2000), shell morphology indicates that *Palaeoneilo* was a quick burrower, and the foot could help to increase excavation speed.

Mineralogy.—Aragonitic (Carter & Tevesz, 1978; Carter, 1990a, p. 159–161; Carter, Lawrence, & Sanders, 1990, p. 315; Zhu & others, 1990). Outer shell layer: aragonite (homogeneous + fibrous prismatic). Middle and inner shell layers: aragonite (homogeneous).

Genus LAPTEVIELLA

Kurushin in Dagys & Kurushin, 1985, p. 47

Type species.—*Lapteviella prontchistshevi* Kurushin in Dagys & Kurushin, 1985, p. 47.

Stratigraphic range.—Middle Triassic (Anisian) (Dagys & Kurushin, 1985). *Lapteviella* is a monospecific genus described

by Kurushin (in Dagys & Kurushin, 1985) from the Anisian of northern Central Siberia. It is similar to *Mesoneilo* Vu Khuc, 1977a, but it differs by having a pallial sinus, prosogyrous beaks, and the anterior part of hinge shorter than the posterior. It is also comparable to *Palaeoneilo* (both have prosogyrous beaks, a similar arrangement of hinge teeth, shallow pallial sinus, concentric ornamentation, adductor muscle scars of similar shape, size, and position) (see fig. 6 and 10 in Dagys & Kurushin, 1985, and fig. 31 in Hodges, 2000). On the other hand, *Lapteviella* figures in Dagys and Kurushin (1985) show neither an internal septum nor the typical radial groove of *Palaeoneilo*.

Paleogeographic distribution.—Boreal (Fig. 3).

Boreal domain: Middle Triassic: Anisian of Siberia (Dagys & Kurushin, 1985; Klets, 2006) and northeastern Russia (Konstantinov, Sobolev, & Yaderkin, 2007).

Paleoautoecology.—B, D, Is, FM; Sb. Dagys and Kurushin (1985) indicated the presence of a smooth pallial sinus, from which the presence of short siphons could be inferred. We assign a mode of life similar to other members of the family Malletiidae, i.e., detritivorous, feeding from the substrate surface, and constantly moving to find new food sources.

Mineralogy.—Aragonitic (Carter, Barrera, & Tevesz, 1998), data provided for the subclass Protobranchia.

Genus DIANUCULA Guo, 1988, p. 113

Type species.—*Dianucula sulcata* Guo, 1988, p. 113.

Remarks.—Guo (1988) included *Dianucula* in the family Malletiidae and we follow him, although Z. Fang and others (2009) included it in the family Afghanodesmatidae Scarlato & Starobogatov, 1979.

Stratigraphic range.—Upper Triassic (Norian) (Guo, 1988). Guo (1988) proposed *Dianucula* from upper Upper Triassic beds, and included two new species, the type and *Dianucula ovata* Guo, 1988. The genus was recorded from Dapingzhang formation, which

is Norian in age (Feng & others, 2005). Sepkoski (2002) did not consider it in his compendium.

Paleogeographic distribution.—Eastern Tethys (Fig. 3).

Tethys domain: Late Triassic: Norian of southwestern China (Yunan province) (Guo, 1988).

Paleoautoecology.—B, D, Is, FM; Sb. We assign a mode of life similar to other members of the family Mallettiidae, i.e., detritivorous, feeding from the substrate surface, and constantly moving to find new food sources.

Mineralogy.—Aragonitic (Carter, Barrera, & Tevesz, 1998), data provided for subclass Protobranchia.

Genus NINGLICONCHA J. Chen & Stiller, 2008, p. 364

Type species.—*Ningliconcha ningliensis* J. Chen & Stiller, 2008, p. 365.

Stratigraphic range.—Upper Triassic (lower Norian) (J. Chen & Stiller, 2008). J. Chen and Stiller (2008) proposed the monospecific genus *Ningliconcha* and reported it from upper lower Norian of China (Yunnan province).

Paleogeographic distribution.—Eastern Tethys (Fig. 3).

Tethys domain: Late Triassic: Norian of southwestern China (Yunnan province) (J. Chen & Stiller, 2008).

Paleoautoecology.—B, D, Is, FM; Sb. We assign this genus a mode of life similar to the rest of nukulids. The cancellate shell sculpture, characteristic of *Ningliconcha* (J. Chen & Stiller, 2008), probably aided in burrowing, as it does in other nukulids. The pallial line is integripalliate, and it either did not have siphons or they were short.

Mineralogy.—Aragonitic (Carter, Barrera, & Tevesz, 1998), data provided for subclass Protobranchia.

Genus YONGSHENGIA J. Chen & Stiller, 2008, p. 360

Type species.—*Palaeoneilo cuneata* Chen in Ma & others, 1976, p. 195.

Stratigraphic range.—Upper Triassic (middle Norian) (J. Chen & Stiller, 2008). J. Chen and Stiller (2008) proposed *Yongshengia* based on *P. cuneata* Chen in Ma & others, 1976 (lower middle Norian of Yunnan) and tentatively included *Palaeoneilo mundeni* Fleming (in Fleming, Munden, & Suggate, 1954) from the Norian of New Zealand.

Paleogeographic distribution.—Eastern Tethys (Fig. 3).

Tethys domain: Late Triassic: Norian of southwestern China (Yunan province) (Ma & others, 1976; Guo, 1985; Zhu & others, 1990; J. Chen & Stiller, 2008).

Austral domain: Late Triassic: Norian of New Zealand (Fleming, Munden, & Suggate, 1954).

Paleoautoecology.—B, D, Is, FM; Sb. Similar to *Palaeoneilo*. *Yongshengia* is one of the largest nukuloids and had a large posterior pedal muscle scar (J. Chen & Stiller, 2008). Its large size was probably inconvenient to fast burrowing, but this could be compensated for by a large foot (inferred by the pedal muscle scar).

Mineralogy.—Aragonitic. Zhu and others (1990) studied the shell microstructure of "*Palaeoneilo cuneata*", and they described a probable aragonitic outer shell layer of homogeneous microstructure and aragonitic inner layers.

Family YOLDIIDAE Dall, 1908b

Genus ROLLIERIA Cossmann, 1920, p. 82

Type species.—*Nucula palmae* J. de C. Sowerby, 1824, p. 117.

Remarks.—Cox and others (1969) and other workers (Liu, 1995; Gahr, 2002) considered *Rollieria* as a subgenus of *Nuculana* Link, 1807, but here we regard it as a separate genus, following Hodges (2000, p. 36), who remarked that *Rollieria* lacks some of the characters of *Nuculana*: "... it does not possess the characteristic elongated posterior, lacks an escutcheon and is suboval in outline." The name *Rollieria* also was used for an ammonoid genus, *Rollieria* Jeannel, 1951, p. 98, but *Rollieria* Cossman, 1920, has priority.

Stratigraphic range.—Lower Jurassic (Hettangian)—Lower Cretaceous (Hodges, 2000; Jingeng Sha, personal communication, 2008). Cox and others (1969) assigned it a Jurassic range, as did Sepkoski (2002), based on data from Hallam (1977). The oldest record is Hettangian (Hallam, 1972, 1976, 1977, 1987, 1990; Hodges, 2000). Sowerby described the type species from sediments of Carboniferous age, but Hodges (2000, p. 35–36) doubted the presence of *Rollieria* at that time, based on the fact that the genus was never found again in sediments older than Jurassic.

Paleogeographic distribution.—Tethys and Circumpacific (Fig. 4).

Tethys domain: Early Jurassic: Hettangian—Sinemurian of southwestern Britain (Hodges, 2000; Mander, Twitchett, & Benton, 2008; Hallam & Wignall, 2000), Europe (Hallam, 1976, 1977, 1987).

Circumpacific domain: Early Jurassic: South America (Dambo-renea, 2002b).

Paleoautoecology.—B, D, Is, FM; Sb. We assign a mode of life similar to other nukuloids. General morphology of the species of this genus suggests that it was a quick burrower (Hodges, 2000). *Rollieria* had a shallow pallial sinus, and thus probably had short siphons. We assume that the *Rollieria* mode of life was similar to *Palaeoneilo*.

Mineralogy.—Aragonitic (Carter, Barrera, & Tevesz, 1998), data provided for subclass Protobranchia.

Family POLIDEVCIIDAE Kumpera, Prantl, & Růžička, 1960

Genus RYDERIA Wilton, 1830, p. 72

Type species.—*Leda renevieri* Oppel, 1856 in 1856–1858, p. 215.

Remarks.—Although several authors include *Ryderia* as a subgenus of *Nuculana*, it is considered here as an independent genus, following Cox and others (1969). However, we regard *Teinonuculana* Zhang in Zhang, Wang, & Zhou, 1977, p. 9, as a synonym of *Ryderia* (see discussion of *Teinonuculana* in Genera not Included, p. 171).

Stratigraphic range.—Upper Triassic (Rhaetian)—Lower Jurassic (Toarcian) (Liu, 1995; J. Yin & McRoberts, 2006). Cox and others (1969) indicated that this genus was present in Europe during the Jurassic. Sepkoski (2002) restricted its range to the Lower Jurassic (lower Hettangian—upper Pliensbachian), following Hallam (1977, 1987). The oldest record we accept here is Rhaetian, according to Ivimey-Cook and others (1999) and J. Yin and McRoberts (2006). Hodges (2000) considered that the genus was present from Carboniferous to Early Jurassic times, but we did not find any mention older than Rhaetian nor any paper quoting this genus before the Late Triassic. Hodges did not provide references to his statement, and

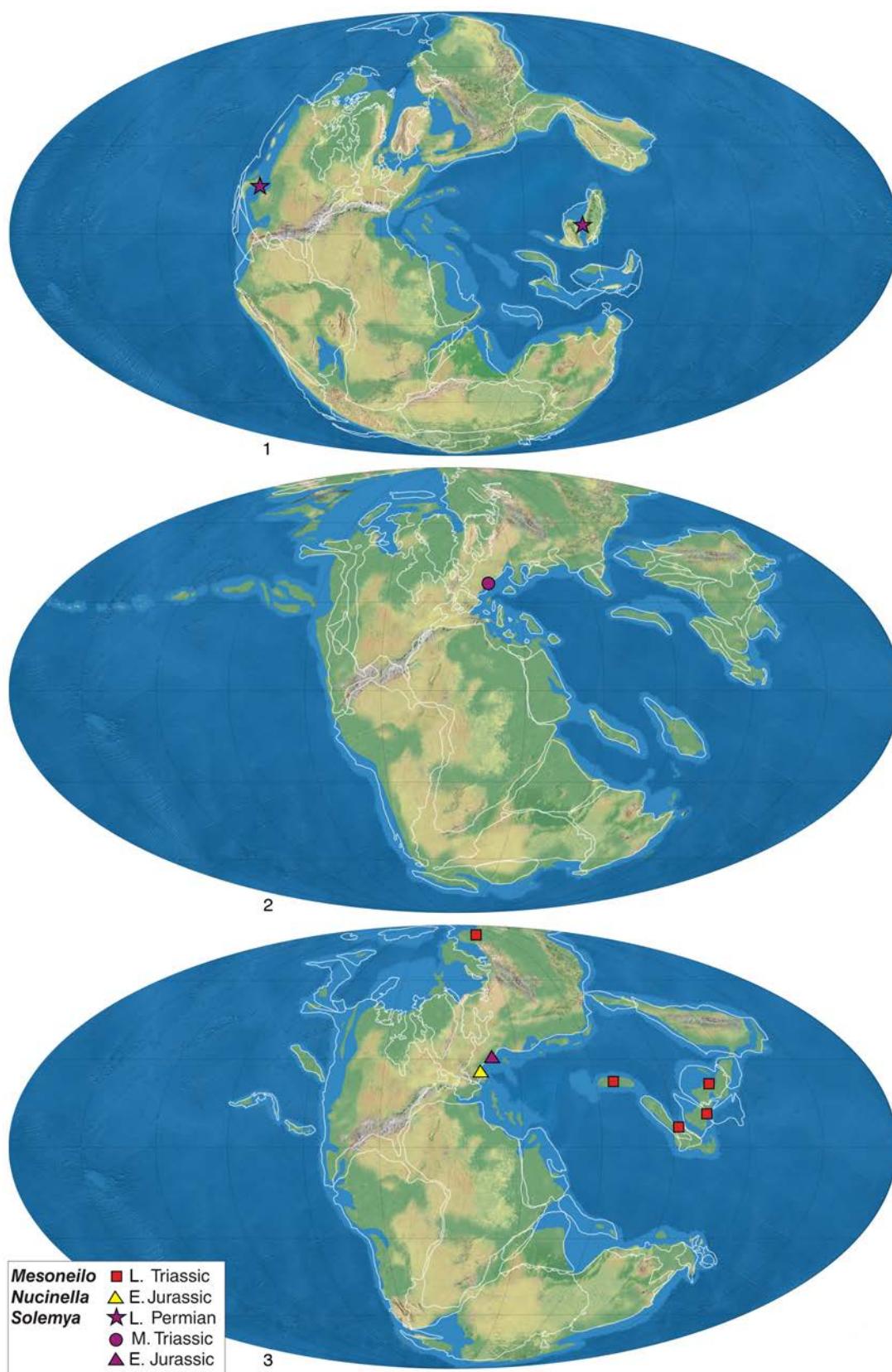


Figure 5. Paleogeographical distribution of Ctenodontidae (*Mesoneilo*), Nucinellidae (*Nucinella*) and Solemyidae (*Solemya*). 1, Early Triassic; 2, Middle Triassic; 3, Late Triassic–Early Jurassic.

thus it will not be taken into account here. The youngest record is from Toarcian beds (Liu, 1995; Fürsich & others, 2001).

Paleogeographic distribution.—Tethys and Circumpacific (Fig. 4).

Tethys domain: Late Triassic: Rhaetian of Tibet (China) (J. Yin & McRoberts, 2006), northeastern England (Ivimey-Cook & others, 1999), southwestern United Kingdom (Mander, Twitchett, & Benton, 2008), southern Germany (Hodges, 2000); Early Jurassic: Germany and China (Hodges, 2000); Hettangian and Sinemurian of Europe (Hallam, 1976, 1977, 1987), eastern Asia and Australasia–Indonesia (Hallam, 1977), southwestern England (Hodges, 2000), southern England (Liu, 1995); Sinemurian of Portugal (Liu, 1995).

Circumpacific domain: Early Jurassic: Canada (Aberhan, 1998a), South America (Hodges, 2000), western Japan (Hodges, 2000).

Paleoautoecology.—B, D, Is, FM; Sb. According to Hodges (2000), *Ryderia* was a fast burrower. Puri in Cox and others (1969) mentioned a wide and shallow pallial sinus, but Hodges remarked that he did not observe such a feature in any of the specimens he studied, after making a thorough revision of the genus. Moreover, Hodges (2000, p. 45) indicated that “The lack of a pallial sinus and the extremely elongated rostrum suggest that the exposed siphons were short and that the tip of the rostrum lay just below the sediment surface.” Like other nuculanids, it was probably detritivorous.

Mineralogy.—Aragonitic (Carter, Lawrence, & Sanders, 1990, p. 313; Carter, Barrera, & Tevesz, 1998). Outer and middle shell layers: aragonite (?). Middle shell layer: aragonite (?).

Genus DACRYOMYA Agassiz, 1842–1844, p. 500

Type species.—*Nucula lacryma* J. de C. Sowerby, 1824, p. 119.

Remarks.—*Dacryomya* is a particularly problematical genus for several reasons. For a long time this genus has been (and still is) regarded as a subgenus of *Nuculana*. Externally, it is very similar to other nuculanoids, such as *Ryderia*, *Nuculana*, or *Phestia*, and the differences between these genera and *Dacryomya* are often subjective when internal structures are not seen. For example, the four genera have a rostrate posterior, but in different degree: *Ryderia* has the longest rostrum, while *Dacryomya* has the shortest. Hodges (2000, p. 21) pointed out that *Dacryomya* is very similar to *Ryderia* and *Nuculana* and they can be confused, but *Dacryomya* “is distinguishable from *Ryderia* by its much greater inflation and shorter rostrum and from *Nuculana* by its much shorter rostrum and lack of marked ridges bordering the escutcheon.” Moreover, in Cox and others (1969, p. 239), *Phestia* was described as “Like *Nuculana*, but with prominent internal ridges,” but *Dacryomya* and *Ryderia* also have internal ridges. A thorough review of this genus is needed.

Furthermore, there is no consensus about the family affiliation of this genus: it was referred to Nuculanidae (Cox & others, 1969; Hayami, 1975), Nuculidae (Ivimey-Cook & others, 1999; Hodges, 2000) or Polidevciidae (Carter, 1990a; Delvene, 2000), where we provisionally include it.

Stratigraphic range.—Upper Triassic (Norian)–Upper Jurassic (Kimmeridgian) (Okuneva, 1985; Delvene, 2000). There are some Lower Triassic records of this genus (Nakazawa, 1961; Hayami, 1975), but they will not be taken into account here because Puri in Cox and others (1969) ignored them and assigned it a Middle Jurassic range. Carter (1990a) and Hodges (2000) regarded the first appearance as Lower Jurassic, but Ivimey-Cook and others

(1999) reported it from the Rhaetian and Okuneva (1985) from Norian beds. Sepkoski (2002) assigned it a Lower Triassic–Lower Jurassic range, following Hayami (1975), but these data will not be taken into account due to the descriptive issues already mentioned. The youngest age accepted is Upper Jurassic, according to Delvene (2000).

Paleogeographic distribution.—Tethys, Circumpacific, and Boreal (Fig. 4).

Tethys domain: Late Triassic: Rhaetian of England (Ivimey-Cook & others, 1999). Early Jurassic: England (Watson, 1982); Sinemurian of Europe (Hallam, 1976, 1977, 1987), England and Portugal (Liu, 1995), England, Germany, Switzerland, France, and Portugal (Hodges, 2000); Hettangian of China (Hodges, 2000).

Circumpacific domain: Early Jurassic: Japan (Goto, 1983).

Boreal domain: Late Triassic: Norian of Transbaykal region (Siberia) (Okuneva, 1985). Early Jurassic: northern Siberia and Arctic region (Zakharov & others, 2006).

Paleoautoecology.—B, D, Is, FM; Sb. Similar to *Palaeonucula*.

Mineralogy.—Aragonitic (Carter, 1990a, p. 153–156). Outer shell layer: aragonite (prismatic). Middle and inner shell layers: aragonite (nacreous).

Superfamily CTENODONTOIDEA Wöhrmann, 1894

Family CTENODONTIDAE Wöhrmann, 1894

Genus MESONEILO Vu-Khuc, 1977a, p. 676

Type species.—*Leda perlonga* Mansuy, 1914, p. 82.

Remarks.—Vu Khuc (1977a) included this new genus in the family Ctenodontidae because it possesses a continuous hinge; in other words, the hinge is not interrupted below the umbo. He distinguished *Mesoneilo* from *Phaenodesmia* or *Palaeoneilo* because the first has opisthogyrous beaks and more teeth in the anterior part of the hinge. However, other authors included the type species of *Mesoneilo* in *Nuculana* (Gou, 1993; Hautmann, 2001b, p. 30) or in *Phestia* (Hautmann and others, 2005), but none of them mentioned *Mesoneilo*. A review of this species is needed to solve this question. Furthermore, some authors suggested that the family Ctenodontidae was exclusively Paleozoic and it is not well defined (Carter, 1990a); all these provide strong arguments to revise the familial affiliation of this genus.

Stratigraphic range.—Upper Triassic (Norian–Rhaetian) (Vu Khuc, 1977a). The genus was reported from Norian of northern Vietnam but a Norian to Rhaetian (Upper Triassic) range was given (Vu Khuc, 1977a). Later Okuneva (1985) referred a specimen from Norian beds of Siberia (Transbaykal region) to *Mesoneilo perlonga*, but she did not see its hinge and assigned it on the basis of its external shape alone. We think this assignment is very uncertain due to the external similarity with other nuculanoid genera.

Paleogeographic distribution.—Tethys and ?Boreal (Fig. 5).

Tethys domain: Late Triassic: China (Gou, 1993); Norian–Rhaetian of northern Vietnam, Laos, Burma, and southern China (Vu Khuc, 1977a; Vu Khuc & Huyen, 1998), Iran (Hautmann, 2001b).

?Boreal domain: Late Triassic: Norian of Transbaykal region (northern Siberia) (Okuneva, 1985).

Paleoautoecology.—B, D, Is, FM; Sb. Similar to *Nuculana*.

Mineralogy.—Aragonitic (Carter, Barrera, & Tevesz, 1998). Data about the shell mineralogy of the genus and the family are not avail-

able. We assign an aragonitic mineralogy following Carter, Barrera, and Tevesz (1998) for subclass Protobranchia.

Superfamily MANZANELLOIDEA Chronic, 1952

Family NUCINELLIDAE Vokes, 1956

Genus NUCINELLA Wood, 1851 in 1851–1882, p. 72

Type species.—*Pleurodon ovalis* Wood, 1840, p. 230.

Stratigraphic range.—Lower Jurassic (Hettangian)–Holocene (Vokes, 1956; McRoberts, Newton, & Allasinaz, 1995). The oldest record of *Nucinella* is *N. liasina* (Bistram, 1903) from Hettangian beds of the border between Switzerland and Italy (near lake Lucano) (Vokes, 1956). McRoberts, Newton, and Allasinaz (1995) mentioned the same species from Hettangian beds of the Lombardian basin (Alps). Cox and others (1969), as well as Skelton and Benton (1993) and Sepkoski (2002), agreed with the same time range.

Paleogeographic distribution.—Eastern Tethys (Fig. 5). The genus is now widely distributed geographically (see Cox & others, 1969, p. 269), as it was during older times (e.g., Cretaceous of Georgia [Pojeta, 1988] or Japan [Amano, Jenkins, & Hikida, 2007]). Nevertheless, during the study interval, the genus was only reported from Italy. During the Toarcian, it was also reported from Germany and England (Aberhan, 1993; Harries & Little, 1999).

Tethys domain: Early Jurassic: Hettangian of Italy (Vokes, 1956; McRoberts, Newton, & Allasinaz, 1995).

Paleoautoecology.—B, D-Ch, Is, FM; Sb. *Nucinella* was a nonsiphonate, active burrower, as indicated by the lack of pallial sinus. It was most probably detritivorous, and it possibly had chemosymbiotic bacteria. According to Allen and Sanders (1969), at least the living species possesses large gills and tiny palps, similar to *Solemya*, which is not considered as detritivorous (S. M. Stanley, 1970). This suggests that *Nucinella* may have had a similar feeding habit, but the wide bathymetric range of the living species (between 9 and 900 m, though most live at approximately 400 m) challenges this assumption. The possibility that they have symbiotic relations with chemosynthetic bacteria is strongly supported by the fact that some living species do not even possess palps or intestine (e.g., *N. viridula* Kuznetsov & Schileyko, 1984, *N. maxima* (Thiele & Jaekel, 1931) (Beesley, Ross, & Wells, 1998).

Mineralogy.—Aragonitic (Carter, 1990a, p. 178). Outer shell layer: aragonite (prismatic). Middle and shell layers: aragonite (homogeneous).

Superfamily SOLEMYOIDEA Gray, 1840

Family SOLEMYIDAE Gray, 1840

Genus SOLEMYA Lamarck, 1818, p. 488

Type species.—*Solemya mediterranea* Lamarck, 1818, p. 488.

Remarks.—Cox and others (1969) regarded *Janeia* King, 1850, p. 177, as a subgenus of *Solemya*, but Pojeta (1988, p. 214–215) advised not to use that name since the generic concept lacks meaning. The genus *Acharax* Dall, 1908a, p. 2, is not included in the study interval, because no records from Triassic or Lower Jurassic deposits were found (see discussion in Genera not Included, p. 156).

Stratigraphic range.—Carboniferous (Upper Pennsylvanian)–Holocene (Pojeta, 1988). Cox and others (1969) assigned *Solemya* a Devonian–Holocene range, but Pojeta (1988) made an exhaustive revision of Paleozoic solemyoids and concluded that this genus ex-

tended from Pennsylvanian to Recent. We follow Pojeta, although other authors (Cope, 1997) extended its range back to the Devonian (Cope did not discuss this matter further), while others considered that the Paleozoic records are doubtful and regard the Jurassic as the first certain appearance (Imhoff & others, 2003; Little & Vrijenhoek, 2003). Ciriacks (1963) mentioned *Solemya* sp. from upper Permian deposits, but his assignation was only based on external shape. Seilacher (1990) described a new ichnofossil, *Solemyatuba*, that might be produced by *Solemya* or other related genera that live in a similar way. This ichnogenus has a wide distribution from Ordovician to Holocene (see Seilacher, 1990, p. 306–309). The only solemyoid genera known during Permian and Triassic times are *Solemya* and supposedly *Acharax*, and both have Recent representatives that are able to build Y-shaped tubes (S. M. Stanley, 1970; K. A. Campbell, Nesbitt, & Bourgeois, 2006); therefore, both are good candidates for *Solemyatuba* builders.

Paleogeographic distribution.—Tethys and Circumpacific (Fig. 5). During the time range of this review, *Solemya* was only reported from the Tethys, whereas it is mentioned from a wider geographic range at other moments of geologic time. Nevertheless, there is certain evidence (ichnogenus *Solemyatuba*) of its possible presence in Rhaetian beds of Germany and the Permian of Russia (Seilacher, 1990). During the middle Permian, it was reported from Russia and Siberia (Biakov, 2006; Ganelin & Biakov, 2006; Klets & others, 2006) and also from Middle and Late Jurassic from the Tethys (Fürsich, 1982; Komatsu, Saito, & Fürsich, 1993; Sha & Fürsich, 1994) and Austral domains (N. Hudson, 2003). There is a doubtful reference from the Late Triassic of Argentina (Damborenea & Manceñido, 2012).

Tethys domain: late Permian: Changhsingian of China (Teichert, 1990; M. Lin & Yin, 1991); Middle Triassic: Anisian of Hungary (Vörös & Pálffy, 2002); Early Jurassic: Germany (Seilacher, 1990).

Circumpacific domain: late Permian: Wyoming (United States) (Ciriacks, 1963).

Paleoautoecology.—B, Id, S-Ch, FM; Db. *Solemya* species have elongated and cylindrical shells with which they burrow deep Y-shaped tunnels (S. M. Stanley, 1970). Although their feeding behavior is not fully understood, and many strategies have been proposed: detritivorous (Cope, 1997), filter feeder (S. M. Stanley, 1970; Fürsich, 1982), or the use of both strategies (Liljedahl, 1984), it is clear that most of their food requirements are provided by chemosynthetic symbiotic bacteria (Cavanaugh, 1983). Many Holocene species have very small gut and palp proboscides (Reid, 1998) but have disproportionately large gills where they lodge the chemosymbiotic bacteria (Stewart & Cavanaugh, 2006). They live most of their life inside the Y-shaped tunnels and have a well-developed foot used for burrowing and swimming (Reid, 1998). In addition to the typical Y- or U-shaped galleries (described for *Solemya*), other types of burrows, such as I- and J-shaped, were attributed to *Acharax* (Campbell, Nesbitt, & Bourgeois, 2006). Even though they can swim, this is not their main mode of life; and the foot may also be functional to move inside their galleries (S. M. Stanley, 1970). The known species usually live in shallow water areas and are almost always associated with low-oxygen environments rich in sulfur and organic matter (S. M. Stanley, 1970; Pojeta, 1988; Seilacher, 1990). This habitat provides a barrier against oxygen-dependent predators (A. G. Fischer & Bottjer, 1995).

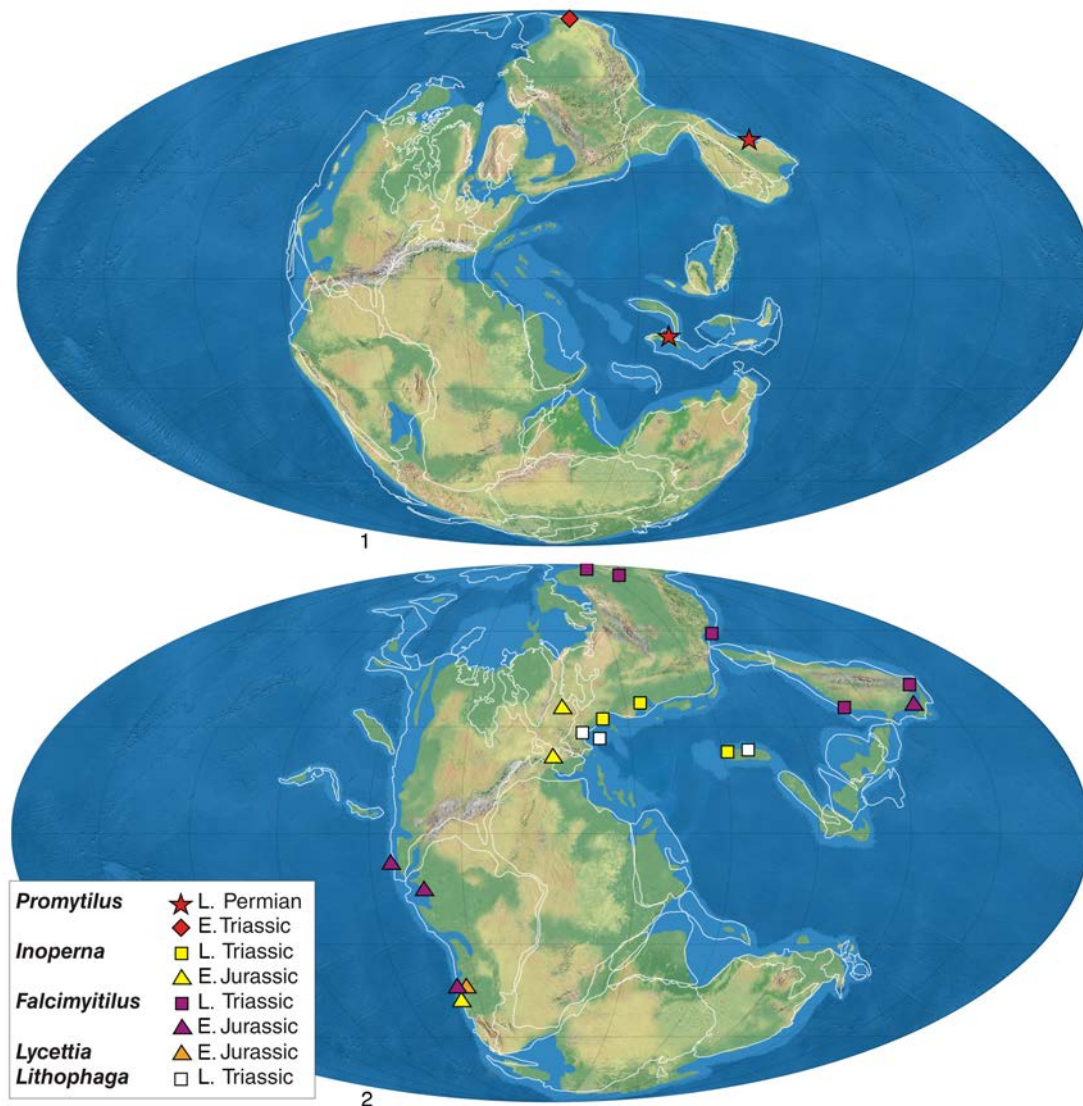


Figure 6. Paleogeographical distribution of Mytilidae (*Promytilus*, *Inoperna*, *Falcimytilus*, *Lycettia*, *Lithophaga*). 1, late Permian–Early Triassic; 2, Late Triassic–Early Jurassic.

Mineralogy.—Aragonitic (Carter, 1990a, p. 174). Outer shell layer: aragonite (prismatic). Middle and inner shell layers: aragonite (homogeneous).

Superfamily MYTILOIDEA Rafinesque, 1815

Family MYTILIDAE Rafinesque, 1815

Genus MODIOLUS Lamarck, 1799, p. 87

Type species.—*Mytilus modiolus* Linnaeus, 1758, p. 706.

Stratigraphic range.—Upper Devonian (Famennian)–Holocene (Cox & others, 1969). *Modiolus* is a long-ranging genus: having its origin in the Devonian, it is one of the oldest mussel genera with a good living representation (Cox & others, 1969). However, some authors believe that only Cenozoic to Holocene species should be referred to *Modiolus* (see Hodges, 2000).

Paleogeographic Distribution.—Cosmopolitan.

Paleoautoecology.—B, Se, S, Endo, Sed; By. As suggested by comparison with living *Modiolus* species, most fossil species are thought to have been semi-infaunal and endobysate (S. M. Stanley, 1970, 1972). There are many examples of fossil *Modiolus* found in life position that confirm that they were gregarious and lived semiburied and fixed by their byssus to pebbles and other hard objects buried in the sediment (Fürsich, 1980, 1982). The byssus emerges from the anterior part of the shell. They tend to inhabit intertidal and subtidal, high-energy environments (S. M. Stanley, 1970; Hodges, 2000). Seilacher (1984, p. 228–229), in his own terminology, qualified this genus as a “mud-sticker.”

Mineralogy.—Bimineralic (Hayami, Maeda, & Ruiz-Fuller, 1977; Carter, 1990a, p. 283). Outer shell layer: calcite (prismatic). Middle and inner shell layers: aragonite (nacreous).

Genus PROMYTILUS Newell, 1942, p. 37

Type species.—*Promytilus annosus* Newell, 1942, p. 38.

Stratigraphic range.—Carboniferous (Mississippian)–Lower Triassic (Induan) (Newell, 1942; Waller & Stanley, 2005). Cox and others (1969) assigned *Promytilus* a Carboniferous (Mississippian)–Permian range; Sepkoski (2002) assigned it to the Carboniferous (Mississippian)–Permian (upper Guadalupian), following Hayami and Kase (1977). But these last authors mentioned several *Promytilus* species reported by Nakazawa and Newell (1968) from middle and upper Permian (Changhsingian) of Japan (Tenjinnoki and Gujo formations), although Hayami and Kase (1977, p. 86) only indicate upper Permian (stage unknown). Boyd and Newell (1997) considered Gujo Formation to be of upper Permian age. The presence of *Promytilus* in Lower Triassic deposits was mentioned by Waller (in Waller & Stanley, 2005) based on *P. borealis* Kurushin, the original reference is Kurushin (in Dagens & others, 1989). In his original proposal of the genus, Newell (1942) noted that some Triassic and Jurassic specimens attributed to *Modiolus* could belong to *Promytilus* instead.

Paleogeographic distribution.—Boreal (Fig. 6). *Promytilus* had a cosmopolitan distribution during Carboniferous and early Permian times, and lived in the Tethys domain in the late Permian (Wuchiapingian of China: Clapham, & Bottjer, 2007; Malaysia: Nakazawa, 1973), but during the study interval, we only found references from the Boreal domain.

Boreal domain: Early Triassic: Taimyr Peninsula (Russia) (Kurushin in Dagens & others, 1989).

Paleoautoecology.—B, E, S, Epi, Sed; By. According to S. M. Stanley (1972), *Promytilus* represents an intermediate stage between *Mytilus* and *Modiolus* and most probably lived attached by its byssus to hard substrates in the intertidal zone, by analogy with the extant species "*Modiolus*" *pulex* (Lamarck, 1819), with which it has a great similarity (see fig. 8 and 9 in S. M. Stanley, 1972). As described by Newell (1942), *Promytilus* had a well-defined byssal sinus. According to Waller (in Waller & Stanley, 2005), *Promytilus* is mytiliform in most shell features but possesses an anterior lobe that is smaller and less developed than in *Modiolus* species.

Mineralogy.—Bimineralic (Newell, 1942; Nakazawa & Newell, 1968). Newell (1942) and Nakazawa and Newell (1968) indicated the presence of a calcitic outer shell layer with prismatic microstructure, but Carter (1990a) doubts that this was the original mineralogy. Outer shell layer: ?calcite (prismatic). Middle and inner shell layers: aragonite (nacreous).

Genus INOPERNA Conrad in Kerr, 1875, p. 5

Type species.—*Modiolus* (*Inoperna*) *carolinensis* Conrad in Kerr, 1875, p. 5.

Stratigraphic range.—Upper Triassic (Rhaetian)–Upper Cretaceous (Maastrichtian) (Abdel-Gawad, 1986; Repin, 1996). Cox and others (1969) assigned it a Lower Jurassic (upper Liassic)–Upper Cretaceous range. However, findings referred to the subgenus *Triasoperna* Repin, 1996, p. 367 [7], indicate that the stratigraphic range of this genus should be extended back to the Upper Triassic (Repin, 1996; Hautmann, 2001b).

Paleogeographic distribution.—Tethys and ?Austral (Fig. 6). Although *Inoperna* was not widely distributed during our study

interval, from Pliensbachian times and throughout all the Jurassic and Cretaceous, it had a cosmopolitan distribution (Freneix, 1965; Vörös, 1971; Hayami, 1975; Wen, 1982; Abdel-Gawad, 1986; Damborenea, 1987a; Liu, 1995; Holzapfel, 1998; Sha & others, 1998; Fürsich & others, 2001; Gahr, 2002; Delvene, 2003; Valls, Comas-Rengifo, & Goy, 2004).

Tethys domain: Late Triassic: Rhaetian of Iran (Repin, 1996; Hautmann, 2001b), northern Caucasus (Repin, 1996), Austria (Tomašových, 2006a, 2006b; Siblík & others, 2010); Early Jurassic: Hettangian of southwestern Great Britain (Hodges, 2000); Sinemurian of Portugal (Liu, 1995).

Austral domain: Early Jurassic: Hettangian–Sinemurian of Argentina (Damborenea, 1996a; Damborenea & Manceñido, 2005b).

Paleoautoecology.—B, Se, S, Endo, Sed; ?Bo. Because *Inoperna* was referred to the subfamily Lithophaginae, several authors suggested the possibility that it was a borer (Damborenea, 1987a; Hodges, 2000; Hautmann, 2001b). However, Pojeta and Palmer (1976) warned that although its morphology is similar to the current *Lithophaga*, which has a borer mode of life, this particular life habit cannot be certain unless we find the specimens within their holes. In addition, one of those authors found *Inoperna plicata* J. Sowerby (Middle Jurassic of England) in life position that indicates a semi-infaunal habit. Hodges (2000, p. 64) compared *Inoperna* with members of the living genus *Adula* H. Adams & A. Adams, 1857 in 1854–1858, and he suggested that, like them, *Inoperna* could be a mechanical borer, boring into the substrate with its anterior part and then fixed inside it by the byssus. Most authors regard *Inoperna* as semi-infaunal endobryssate (Fürsich & others, 1995, 2001; Hautmann, 2001b; Gahr, 2002; Delvene, 2003).

Mineralogy.—Bimineralic (Carter, 1990a, p. 185). There is no information about *Inoperna* shell mineralogy. We use the data provided for the subfamily Lithophaginae.

Outer shell layer: calcite (homogeneous-prismatic). Middle shell layer: aragonite (nacreous). Inner shell layer: aragonite (nacreous-prismatic).

Genus FALCIMYTILUS Cox, 1937c, p. 343

Type species.—*Mytilus suprajurensis* Cox, 1925, p. 142.

Stratigraphic range.—Upper Triassic (Carnian)–Upper Jurassic (Tithonian) (Kelly, 1984). Cox and others (1969) assigned it a Jurassic range, regardless of previous records that reported the genus from the Upper Triassic of Japan (Kobayashi & Ichikawa, 1950; Nakazawa, 1956; Hayami, 1958a). The latest undoubted record accepted here dates from Tithonian times (Kelly, 1984). Other authors, such as J. D. Taylor, Cleavelly, and Morris (1983), mentioned *Falcimylus lanceolatus* Sowerby from Lower Cretaceous (Albian), but they neither figured nor described the specimens, they just included them in a list of bivalve shells perforated by gastropods.

Paleogeographic distribution.—Tethys, Circumpacific, and Boreal (Fig. 6). During the study interval, the genus was known from the eastern Tethys, and later in the Jurassic, it was reported also from western Tethys (Hallam, 1976, 1996). The genus is often recorded from this area from Middle and Upper Jurassic beds (Fürsich, 1982; Kelly, 1984; Jaitly, 1988; Liu, 1995, 1999; Holzapfel, 1998; Sha & others, 1998).

Tethys domain: Late Triassic: Carnian–Norian of China (J. Chen, 1982a).

Circumpacific domain: Late Triassic: Carnian of Japan (Kobayashi & Ichikawa, 1950; Nakazawa, 1956; Hayami, 1975); Early Jurassic: Mexico (Damborenea in Damborenea & González-León, 1997); Hettangian of Japan (Hayami, 1958a); Hettangian–Sinemurian of ?South America (Damborenea, 1996a).

Boreal domain: Late Triassic: northern Siberia (Dagys & Kurushin, 1985) and eastern Siberia (Kobayashi & Tamura, 1983b); Carnian of Primorie (Kiparisova, 1972); Norian of Russia (Zabaykal region) (Okuneva, 1985).

Paleoautoecology.—B, E, S, Epi, Sed; By. As indicated by its mytiliform outline and its triangular cross section, *Falcimyltilus* probably lived as epibyssate on hard substrates, as living *Mytilus* species do (Fürsich, 1982; Damborenea, 1987a).

Mineralogy.—Unknown (Carter, 1990a, p. 283; 1990b, p. 400). Outer shell layer: calcite and/or aragonite (?). Middle shell layer: aragonite (nacreous). Inner shell layer: aragonite (nacreous-prismatic).

Genus LYCETTIA Cox, 1937c, p. 345

Type species.—*Mytilus lunularis* Lycett, 1857, p. 128.

Stratigraphic range.—Lower Jurassic (Sinemurian)–Upper Cretaceous (Maastrichtian) (Cox & others, 1969; Damborenea, 1996a). Cox (1937c) proposed *Lycettia* and reported it from the Jurassic. Cox and others (1969) considered it was present in the Jurassic and Upper Cretaceous. This discontinuous range is due to the fact that *Cuneolus* Stephenson, 1941, p. 156, is regarded as a synonym of *Lycettia* in Cox and others (1969). The type species of *Cuneolus* (*Dreissena tippiana* Conrad, 1858, p. 328) is typical from Upper Cretaceous beds (Carter, 1990a). Since then, the genus was also reported from Lower Cretaceous deposits (Hayami, 1975; Villamil, Kauffman, & Leanza, 1998; Komatsu & Maeda, 2005).

Paleogeographic distribution.—Austral (Fig. 6). During the earliest Jurassic, *Lycettia* was only present in the Austral Domain, but during the rest of the Jurassic, it was also reported from the Tethys (Damborenea, 1987a; Liu, 1995; Fürsich & others, 2001; Gahr, 2002).

Austral domain: Early Jurassic: Sinemurian of Argentina (Damborenea, 1996a; Damborenea & Manceñido, 2005b; Damborenea & Lanés, 2007).

Paleoautoecology.—B, E, S, Epi, Sed; By. *Lycettia* presents some characters that indicate an epibyssate mode of life: external shape triangular in lateral view, the absence of anterior lobe and triangular cross section (S. M. Stanley, 1972). These features are taken to the extreme in this genus, which most probably lived fixed by the byssus to hard substrates in high-energy environments (Damborenea, 1987a). These hard substrates may be other bivalve shells, as *Myoconcha* from Middle Jurassic (Damborenea, 1987a), or *Steinmanella quintucoensis* (Weaver) from the Lower Cretaceous (Villamil, Kauffman, & Leanza, 1998).

Mineralogy.—Aragonitic (Carter, 1990b, p. 395–396). Outer shell layer: aragonite (prismatic). Middle shell layer: aragonite (nacreous). Inner shell layer: aragonite (prismatic-nacreous).

Genus LITHOPHAGA Röding in Bolten, 1798, p. 156

Type species.—*Mytilus lithophagus* Linnaeus, 1758, p. 705.

Stratigraphic range.—Upper Triassic (Norian)–Holocene (Kleemann, 1994). Cox and others (1969) considered the reports of this genus from Carboniferous age to be doubtful, and thus they attributed it a continuous range from Miocene to Recent. These doubtful data are surely from Newell (1942), who pointed out that, although *Lithophaga* was not very common in the Paleozoic, several species were described from Carboniferous and Permian beds around the world. However, Kleemann (1990) argued that the specimens attributed to *Lithophaga* from Carboniferous and Triassic age are indeed more than doubtful: they are externally similar to *Lithophaga*, but they probably did not have an endolithic mode of life. Kleemann (1994) and Carter and Stanley (2004) found specimens of *Lithophaga* in life position in holes bored inside Upper Triassic corals (as happens in many living species). Since the presence of *Lithophaga* in pre-Upper Triassic sediments cannot be assured, we will consider that the genus ranges from Upper Triassic to the present. Linck (1972) reported *Lithophaga* sp. cf. *vermiculata* Linck from Carnian beds, but he only assigned his specimen to *Lithophaga* on the basis of its external features, and he did not find it in life position, so we cannot really be sure that it was *Lithophaga*. Ivimey-Cook and others (1999) found borings that could belong to *Lithophaga* in Rhaetian deposits from England.

Paleogeographic distribution.—Tethys (Fig. 6). If finding specimens within their borings is a prerequisite to refer them to *Lithophaga*, then it is very difficult to know what the actual distribution of the genus was. In our study interval, it was reported from Tethys, but at other times (and also Recent), it had a cosmopolitan distribution (Cox & others, 1969).

Tethys domain: Late Triassic: Norian of Germany (Carter & Stanley, 2004); Rhaetian of Austria (Kleemann, 1994; Carter & Stanley, 2004), Iran (Hautmann, 2001b).

Paleoautoecology.—B, Is, S, By, Sed; Bo. Living *Lithophaga* species are borers in hard substrates, especially in dead and live coral skeletons (Kleemann, 1994; Scott, 1988). They are regarded as chemical borers, because they disaggregate the substrate with the aid of special chemical substances, although it appears that in some species, like *Lithophaga nigra* (d'Orbigny, 1853), this is supplemented by mechanical boring (L. Fang & Shen, 1988). Regarding fossil species, *Lithophaga* shells are reported in coral boreholes (Kleemann, 1994; Waller & Stanley, 2005), so the same mode of life is assumed for them. Savazzi (2001) mentioned a possible macrosymbiotic relationship between *Lithophaga* species burrowing into live corals and the corals themselves, as the coral provides protection and reduces competition with other borers that only bore on nonliving substrates. There is no evidence that the bivalve uses the coral as a food source.

Mineralogy.—Bimineralic (Carter, 1990a, p. 285). Outer shell layer: calcite (homogeneous-prismatic). Middle shell layer: aragonite (nacreous). Inner shell layer: aragonite (nacreous-prismatic).

Family MYSIDIPELLIDAE Cox, 1964

Although Hautmann (2008) proposed that this family should be included in the superfamily Ambonychioidea, we follow Cox and others (1969), Carter (1990a), Amler (1999), Amler, Fischer, and Rogalla (2000), Waller and Stanley (2005), and Bouchet and Rocroi

(2010) to refer it to the Mytiloidea (see discussions in Hautmann, 2001b, 2008; Waller & Stanley, 2005). Some disagreement has arisen in recent years about which genera should be included in this family, and this is summarized below.

Cox (1964) proposed the family and included within it *Protopis* Kittl, 1904, p. 718 (= *Joannina* Waagen, 1907, p. 94) and two new genera, *Mysidiella* Cox, 1964, p. 44 (*pro Mysidia* Bittner, 1891, p. 113, *non* Westwood, 1840) and *Tommasina* Cox, 1964, p. 44 (*nom. nov.* for *Mytiliconcha* Tommasi, 1911, *non Mytiliconcha* Conrad, 1862). Waller (in Waller & Stanley, 2005) proposed the synonymy *Protopis* (= *Tommasina*) and advised the exclusion of *Protopis* and its synonyms (*Joannina* and *Tommasina*) from the family Mysidiellidae, but he did not suggest a new allocation. Waller (in Waller & Stanley, 2005) proposed the inclusion of *Botulopsis* Reis, 1926 (emended by him) and his new genus *Promysidiella* Waller in Waller & Stanley, 2005. Stiller and Chen (2006), following Cox but without mentioning Waller's paper (in Waller & Stanley, 2005), added to the genera in the family (*Protopis*, *Mytiliconcha*, and *Mysidiella*), their three new genera from the Anisian of China: *Leidapoconcha* Stiller & Chen, *Waijiaoella* Stiller & Chen, and *Qingyaniola* Stiller & Chen. These authors regarded the name *Mytiliconcha* as valid, and, since Conrad's and Tommasi's names differ in one letter, we agree with Vokes (1980) in regarding *Tommasina* as an unnecessary name.

On the other hand, Hautmann (2008) proposed the new family Healeyidae, which includes *Healeyia* Hautmann, 2001b, *Joannina* (which he regarded as valid for substantial differences with *Protopis*), and, with some hesitation, *Protopis* and the three genera created by Stiller and Chen (2006): *Leidapoconcha*, *Waijiaoella*, and *Qingyaniola*. In turn, he suggested that *Mysidiella*, *Promysidiella*, and *Botulopsis* should remain in Mysidiellidae, following Waller (in Waller & Stanley, 2005), but including this family within the Ambonychioidea. Hautmann (2008) based these conclusions on the study of the microstructure of one of his specimens of *Mysidiella imago* Hautmann, 2001b, where he found that the outer shell layer was subdivided into several sublayers (from outside to inside): prismatic, foliar, and coarsely prismatic. He argued that the foliar sublayer and the size of the prisms of the outer sublayer support an origin from myalinids rather than from mytilids. Nevertheless, although no microstructure studies are known for *Promysidiella cordillerana* (Newton), Newton (in Newton & others, 1987, fig. 13, p. 16) proposed that "abraded specimens exhibit an inner, very fine radial structure, representing silica replacement of primary fibrous prismatic microstructure, homologous to that occurring in outer ostracum of modern *Mytilus*, as well as Permian mytiloids (Newell, 1942)."

Waller (in Waller & Stanley, 2005) differentiated Mysidiellidae from Myalinidae, because they had different microstructure in the outer shell layers (fibrous prismatic and columnar prismatic, respectively) and different types of ligament (opisthodontic and duplivincular, respectively). But he did not study the microstructural shell details under the electronic microscope, and based his assumption on: "it superficially appears very similar to the microstructure of the outer shell layer of many modern mytilids" (Waller in Waller & Stanley, 2005, p. 8). Hautmann's (2008) proposal seems more solidly supported because it is based on microstructural studies and also on

the revision of holotypes and several collections but, in our view, a lot of work is still needed to clarify this question. It is evident that the problems of this family are far from settled, and we therefore include all related genera in this family without further systematic discussions.

We follow Waller and Stanley (2005) and Stiller and Chen (2006) in the allocation of their genera into Mysidiellidae, and we also maintain the inclusion of *Protopis* and its synonyms. Meanwhile, in the absence of new studies, we believe it is still risky to accept the new family proposed by Hautmann (2008) with its original generic composition. We regard *Joannina* as a valid genus, following Hautmann (2008).

Genus MYSIDIELLA Cox, 1964, p. 44

nom. nov. pro Mysidia Bittner, 1891, *non* Westwood, 1840, p. 83
Type species.—*Mysidia orientalis* Bittner, 1891, p. 113.

Stratigraphic range.—Upper Triassic (Carnian–Rhaetian). Cox and others (1969) assigned this genus a Ladinian–Rhaetian range, as did also Sepkoski (2002) and Stiller and Chen (2006). The Ladinian record surely refers to *Mysidia taramellii* De Toni, 1913, because it is the only one from that stage (data from Diener, 1923); but Waller (in Waller & Stanley, 2005), in his revision of family Mysidiellidae and based on the illustrations provided by De Toni, assigned this species to *Botulopsis* Reis, 1926, p. 124. Moreover, they also considered that *Mysidiella cordillerana* Newton in Newton and others, 1987, p. 16, and *Mysidiella americana* (Körner, 1937) should belong to *Promysidiella* Waller in Waller & Stanley, 2005, p. 10. They renamed the specimens described by Newton (in Newton & others, 1987) as *Krumbeckiella* sp. cf. *timorensis* (Krumbeck, 1924) as their new species *Mysidiella newtonae* Waller & Stanley, 2005. Sente and Vörös in Budai and others (2003) reported ?*Mysidiella* sp. from Anisian beds, but this will not be taken into account because the material was not figured.

Paleogeographic distribution.—Tethys and Circumpacific (Fig. 7).

Tethys domain: Late Triassic: Carnian of Greece (Diener, 1923), China (Wen & others, 1976); Norian of Turkey (Diener, 1923), China (Kobayashi & Tamura, 1983a); Norian–Rhaetian of Iran (Hautmann, 2001b).

Circumpacific domain: Late Triassic: Carnian of British Columbia (Waller & Stanley, 2005), of Japan (Nakazawa, 1994); Norian of Oregon, United States (Wallowa Terrane) (Waller & Stanley, 2005).

Paleoautoecology.—B, E, S, Epi, Sed; By. The deep byssal notch (see diagnosis in Waller & Stanley, 2005) present in species attributed to this genus indicates an epibyssate mode of life. Their external morphology is similar to mytilid shells, and thus they probably lived in high-energy environments (Newton in Newton & others, 1987). The anterior part of the valves is flat, suggesting the animal lived orthothetically rested, i.e., with the commissure at a nearly right angle to the substrate surface (Hautmann, 2001b, 2008).

Mineralogy.—Bimineralic (Hautmann, 2008). According to Hautmann (2001b), the outer shell layer consists of foliated calcite, but Waller (in Waller & Stanley, 2005) did not find evidence of this type of microstructure in their specimens referred to *Mysidiella* species. Hautmann (2008), following a suggestion by Waller (in

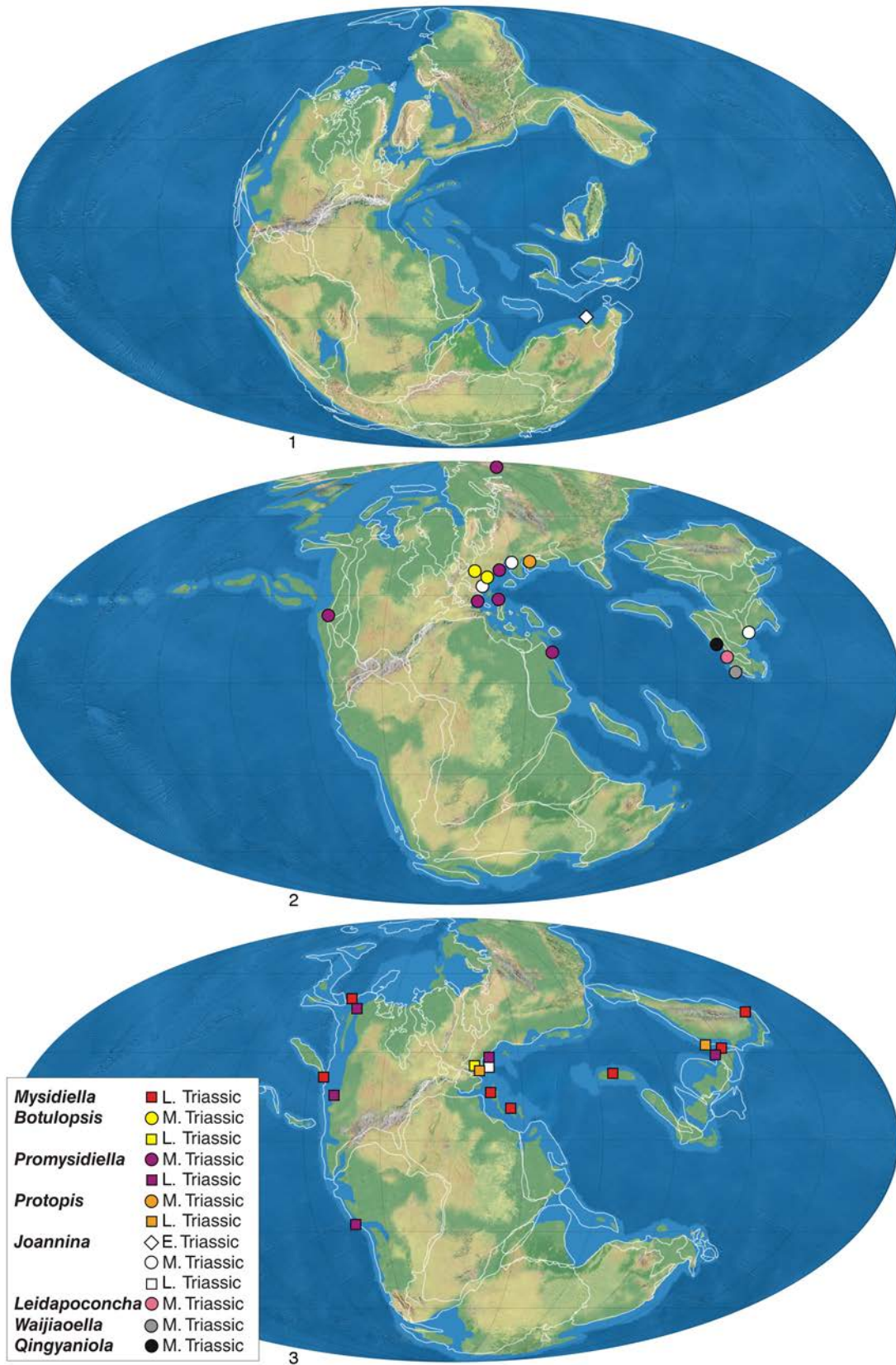


Figure 7. Paleogeographical distribution of Mysidiellidae (*Mysidiella*, *Botulopsis*, *Promysidiella*, *Protopsis*, *Joannina*, *Leidapoconcha*, *Waijiaoella*, *Qingyaniola*). 1, Early Triassic; 2, Middle Triassic; 3, Late Triassic–Early Jurassic.

Waller & Stanley, 2005), studied the microstructure in tangential section (rather than in radial section, as he had done previously: Hautmann, 2001b) and found that the outer shell layer of *Mysidiella imago* Hautmann, 2001b, had several sublayers with prismatic, foliar, and coarsely prismatic microstructure (from outer to inner sublayers). Outer shell layer: calcite (prismatic). Middle and inner shell layers: aragonite (?).

Genus BOTULOPSIS Reis, 1926, p. 124

Type species.—*Botulopsis reisi* Waller in Waller & Stanley, 2005, p. 13 [= *Botulopsis cassiana* Reis, 1926, non *Botulopsis cassiana* (Bittner, 1895)].

Remarks.—We include *Botulopsis* in Mysidiellidae following Waller (in Waller & Stanley, 2005).

Stratigraphic range.—Middle Triassic (Ladinian)—Upper Triassic (Carnian) (Waller & Stanley, 2005). Cox and others (1969) assigned this genus an Upper Triassic range; Sepkoski (2002) considered *Botulopsis* present in Ladinian and Carnian times, based on data provided by Hallam (1981). Waller (in Waller & Stanley, 2005) emended the generic diagnosis and renamed the type species *Botulopsis cassiana* Reis, 1926, as *Botulopsis reisi* Waller in Waller & Stanley, 2005, present in Ladinian beds. Furthermore, Waller (in Waller & Stanley, 2005) included other two species within the genus: *Botula? cassiana* Bittner, 1895 (Carnian) and *Mysidia taramellii* De Toni, 1913 (Ladinian). Hautmann (2008) pointed out that *Botulopsis* was reported from Rhaetian deposits of Germany, and if that reference is correct, the range for this genus should be extended. Stiller (2001) mentioned *Botulopsis cassiana* from the Anisian of China, but this assignation is wrong (Stiller, personal communication, 2008).

Paleogeographic distribution.—western Tethys (Fig. 7).

Tethys domain: Middle Triassic: Ladinian of Austria (Kutassy, 1931), Italy (Reis, 1926; Waller & Stanley, 2005); Late Triassic: Carnian of the Alps (Bittner, 1895; Diener, 1923; Waller & Stanley, 2005).

Paleoautoecology.—B, E, S, Epi, Sed; By. *Botulopsis* was probably an epibyssate bivalve, on account of its external shell shape, which is quite inflated, and its shallow byssal gape, but possibly it did not inhabit high-energy environments, as *Mysidiella* did.

Mineralogy.—Bimineralic (Waller & Stanley, 2005). *Botulopsis* shell microstructure is not known; data used here are taken from the diagnosis of the family Mysidiellidae in Waller and Stanley (2005). Outer shell layer: calcite (fibrous prismatic). Middle and inner shell layers: aragonite (?).

Genus PROMYSIDIELLA

Waller in Waller & Stanley, 2005, p. 10

Type species.—*Mysidiella cordillerana* Newton in Newton & others, 1987, p. 16.

Stratigraphic range.—Middle Triassic (lower Anisian)—Upper Triassic (lower Norian) (Waller in Waller & Stanley, 2005; Newton in Newton & others, 1987). The type species comes from lower Norian beds, but Waller (in Waller & Stanley, 2005) included also the following species: *Mysidia americana* Körner, 1937, *Mytilus eduliformis* Schlotheim, 1820, *Mytilus otiosus* McLearn, 1947, and two new species: *Promysidiella planirecta* Waller in Waller & Stanley, 2005, and *P. desatoyensis* Waller in Waller & Stanley, 2005. Waller (in

Waller & Stanley, 2005) also pointed out that some species attributed to *Mytilus* Linnaeus, 1758, from the European Muschelkalk could be included in *Promysidiella*. In the same paper (Waller in Waller & Stanley, 2005, p. 10), he assigned it a Lower Triassic (Spathian)—Upper Triassic (Norian) range, but this is probably an error, because in the discussion he said, “. . . the oldest known *Promysidiella*, *P. eduliformis* (Schlotheim, 1820) from the lower Middle Triassic.” Hautmann (2008) stated that *eduliformis* did not appear until early Anisian. There is, however, a Lower Triassic record of this species, although its systematic affiliation needs confirmation: Z. Yang & Yin (1979) mentioned *Mytilus eduliformis* from the upper Scythian Shihchienfeng Group of Shaanxi province (northern China), and Hautmann and others (2011) mentioned *Promysidiella?* sp. from southern China.

Paleogeographic distribution.—Tethys, Circumpacific, and ?Boreal (Fig. 7).

Tethys domain: Middle Triassic: Anisian—Ladinian of Spain (Mal-lada, 1880; Schmidt, 1935; Virgilli, 1958; Márquez-Aliaga, 1983, 1985; Budurov & others, 1991), Italy (Posenato, 2002; Posenato & others, 2002), Germany (Ürlich, 1992), Jordan (Hautmann, 2008); Late Triassic: China (Gou, 1993), Germany (Warth, 1990).

Circumpacific domain: Middle Triassic: Ladinian of Nevada (United States) (Waller & Stanley, 2005); Late Triassic: Carnian of Peru (Körner, 1937), British Columbia (Canada) (Waller & Stanley, 2005); early Norian of Oregon (United States) (Newton, 1986; Newton & others, 1987).

?Boreal domain: Middle Triassic: Anisian of northern Siberia (Dagys & Kurushin, 1985), although we should check if this is taxonomically correct.

Paleoautoecology.—B, E, S, Epi, Sed; By. Newton (in Newton & others, 1987) suggested that the type species was epibyssate with a life style similar to Recent mytilids; based on its external shape, she inferred that it probably lived on hard substrates in high-energy open environments. Some species, such as *P. desatoyensis*, probably lived gregariously as the living *Mytilus edulis* Linnaeus does, according to taphonomic analysis of several individuals found in proximity to each other (Waller in Waller & Stanley, 2005). Waller (in Waller & Stanley, 2005) also argued that this species could have had a pendent mode of life, because some features (broad and flat anterior part, anterior margin concave, deep byssal invagination, and byssal notch) indicate that it was strongly attached by the byssus. However, he also suggested an epibyssate mode of life on hard substrates, but solitary (i.e., not forming clusters) for another species, *P. planirecta*.

Mineralogy.—Bimineralic (Newton in Newton & others, 1987, p. 16; Carter, 1990a, p. 286; Waller & Stanley, 2005, p. 10; but see Hautmann, 2008, p. 556). Outer shell layer: calcite (fibrous prismatic). Middle and shell layers: aragonite (?).

Genus PROTOPIS Kittl, 1904, p. 718

Type species.—*Opis (Protopis) triptycha* Kittl, 1904, p. 718.

Remarks.—We regard *Mytiliconcha* Tommasi, 1911 (= *Tommasina* Cox, 1964) as a synonym of *Protopis* following Waller (in Waller & Stanley, 2005) (see discussion for *Tommasina* in Genera not Included, p. 171). Waller (in Waller & Stanley, 2005, p. 9) removed *Protopis* from the Mysidiellidae and this was further discussed by Hautmann (2008, p. 559), who reillustrated the

original specimens of the type species and placed *Protopis* within the Modiomorphoidea (p. 562).

Stratigraphic range.—Middle Triassic (Anisian)—Upper Triassic (Carnian) (Waller & Stanley, 2005; Hautmann, 2008). Hautmann (2008) reviewed the genus *Protopis* and included there only the type species. Some species traditionally placed within this genus were transferred to *Joannina* by the author (see discussion for *Joannina* below). Therefore he assigned the genus to the Anisian. However, he did not refer to other species, as *Protopis qinghaiensis* Wen, from Carnian–Norian of Qinghai (data provided by Stiller & Chen, 2006). These authors suggested that this species might be included in *Waijiaoella* Stiller & Chen, 2006, based on its overall shape, but they noted a revision was needed. Waller (in Waller & Stanley, 2005) included *Tommasina* Cox, 1964 (see discussion in Genera not Included, p. 171) as a synonym of *Protopis*. *Tommasina*, or more correctly *Mytiliconcha* Tommasi, 1911, p. 35 (see Vokes, 1980), is also monospecific, including only the type, *Mytiliconcha orobica* Tommasi, 1911, from Carnian beds (Cox, 1964; Cox & others, 1969; Stiller & Chen, 2006). Waller (in Waller & Stanley, 2005) indicated its presence in Ladinian times, but this is most probably an error, because the only data source is Tommasi, 1911. Skelton and Benton (1993, p. 243) mentioned as first appearance of the family Mysidiellidae *Protopis triptycha* Kittl, 1904, from Scythian of the Werfen layers in the Austrian Alps, but it is not possible to verify this record because the authors did not indicate the original source.

Paleogeographic distribution.—Tethys (Fig. 7).

Tethys domain: Middle Triassic: Anisian of the Balkans (Hautmann, 2008); Late Triassic: Carnian of the Alps (Italy) (Cox, 1964; Cox & others, 1969; Stiller & Chen, 2006), China (Stiller & Chen, 2006).

Paleoautoecology.—B, E, S, Epi, Sed; By. We assign this genus an epibyssate mode of life, like most mysidiellids. The species here recognized within *Protopis* are *Opis (Protopis) triptycha* Kittl, 1904 (type species of *Protopis*) and *Mytiliconcha orobica* Tommasi, 1911 (type species of *Tommasina*, considered synonym of *Protopis*). These species lack the typical anterior lobe of *Joannina* species and show morphological features similar to other Mysidiellidae, so we suggest they had the same mode of life.

Mineralogy.—Bimineralic(?). There are no data about shell mineralogy and microstructure of this genus. Provisionally, we assign it bimineralic mineralogy.

Genus JOANNINA Waagen, 1907, p. 94

Type species.—*Joannina joannae* Waagen, 1907, p. 94.

Remarks.—Krumbeck (1924) included *Joannina* as a synonym of *Protopis* and Cox (1964) and Cox and others (1969), among others, accepted this situation, which Waagen (1907) already suspected (Hautmann, 2008). However, Hautmann (2008, p. 559–560) revised the holotypes of the type species of *Joannina* and *Protopis*, and he found differences that justify the separation of both genera. This author included within *Joannina* its type species and tentatively *Protopis timorensis* Krumbeck, 1924, from the Lower Triassic of Timor, *Joannina waageni* Schnetzer, 1934, and *Joannina aberrans* Schnetzer, 1934, both from the Anisian of Austria.

Stratigraphic range.—Lower Triassic (?Induan)—Upper Triassic (Carnian) (Krumbeck, 1924; Stiller & Chen, 2006). The oldest re-

cord is from the Lower Triassic (Krumbeck, 1924), and the youngest, *Protopis joannae*, from Carnian beds (Waagen, 1907; Stiller & Chen, 2006). This species was also mentioned by Hautmann (2008) from Ladinian [data provided by Waagen, 1907], and although Kochanová, Mello, and Siblík (1975, pl. 8,5) mentioned *Protopis* sp. cf. *joannae* from the Carnian of the Carpathians, the figured material is only a very poorly preserved fragment, not enough to ascertain if it really belongs to this species. Sha, Chen, and Qi (1990) also mentioned *Protopis?* sp. cf. *P. timorensis* Krumbeck, but according to Stiller and Chen (2006), this specimen is badly preserved and thus of doubtful relationship.

Paleogeographic distribution.—Tethys (Fig. 7).

Tethys domain: Early Triassic: ?Induan of Timor (Krumbeck, 1924); Middle Triassic: Anisian of Austrian Alps (Hautmann, 2008), China (Komatsu, Chen, & others, 2004), Hungary (Szente & Vörös in Budai & others, 2003); Ladinian of the Alps (Hautmann, 2008); Late Triassic: Carnian of the Alps (Stiller & Chen, 2006).

Paleoautoecology.—B, Se, S, Endo, Sed; By. According to Hautmann (2008, fig. 5), one of the main differences between *Joannina* and *Protopis* is that the former has a distinct anterior lobe. Furthermore, he pointed out that *Joannina* is modioliform, and thus he suggested an endobyssate mode of life, with the byssus emerging “between this anterior shell lobe and the main body of the shell, a faint radial shell fold creates a gape between both valves for the passage of the byssus” (Hautmann, 2008, p. 559, and see his fig. 5.1). *Joannina* is externally similar to *Leidapoconcha*, which probably had also an endobyssate mode of life.

Mineralogy.—Bimineralic(?). *Joannina* shell mineralogy or microstructure has not been studied. Due to the taxonomic problems already discussed, we cannot refer to the predominant mineralogy in the family (see explanation in Mineralogy of *Leidapoconcha* below). We provisionally assign it bimineralic mineralogy.

Genus LEIDAPOCONCHA Stiller & Chen, 2006, p. 215

Type species.—*Leidapoconcha gigantea* Stiller & Chen, 2006, p. 216.

Stratigraphic range.—Middle Triassic (Anisian) (Stiller & Chen, 2006). *Leidapoconcha* has only been reported from sediments dated as lower upper Anisian (Stiller & Chen, 2006). It is a monotypic genus.

Paleogeographic distribution.—Eastern Tethys (Fig. 7).

Tethys domain: Middle Triassic: Anisian of southwestern China (Guizhou) (Stiller & Chen, 2006).

Paleoautoecology.—B, Se, S, Endo, Sed; By. According to the environment suggested for the deposits where *Leidapoconcha*, *Waijiaoella*, and *Qingyaniola* were found, they lived in fully marine, shallow water, and low-energy settings (Stiller & Chen, 2006). The authors also suggested an endobyssate or epibyssate mode of life for these genera, on the basis of their external morphology, since all of them have byssal gapes. Nevertheless, we think that a semi-infaunal, endobyssate, and sedentary mode of life is more feasible, similar to that proposed for *Healeyia* by Hautmann (2001b).

Mineralogy.—Bimineralic(?). No data about the shell mineralogy and microstructure of this genus are available. Both Waller (in Waller & Stanley, 2005) and Hautmann (2008) agree that the family Mysidiellidae probably had a bimineralic shell, with calcitic outer shell layer and aragonitic middle and inner layers,

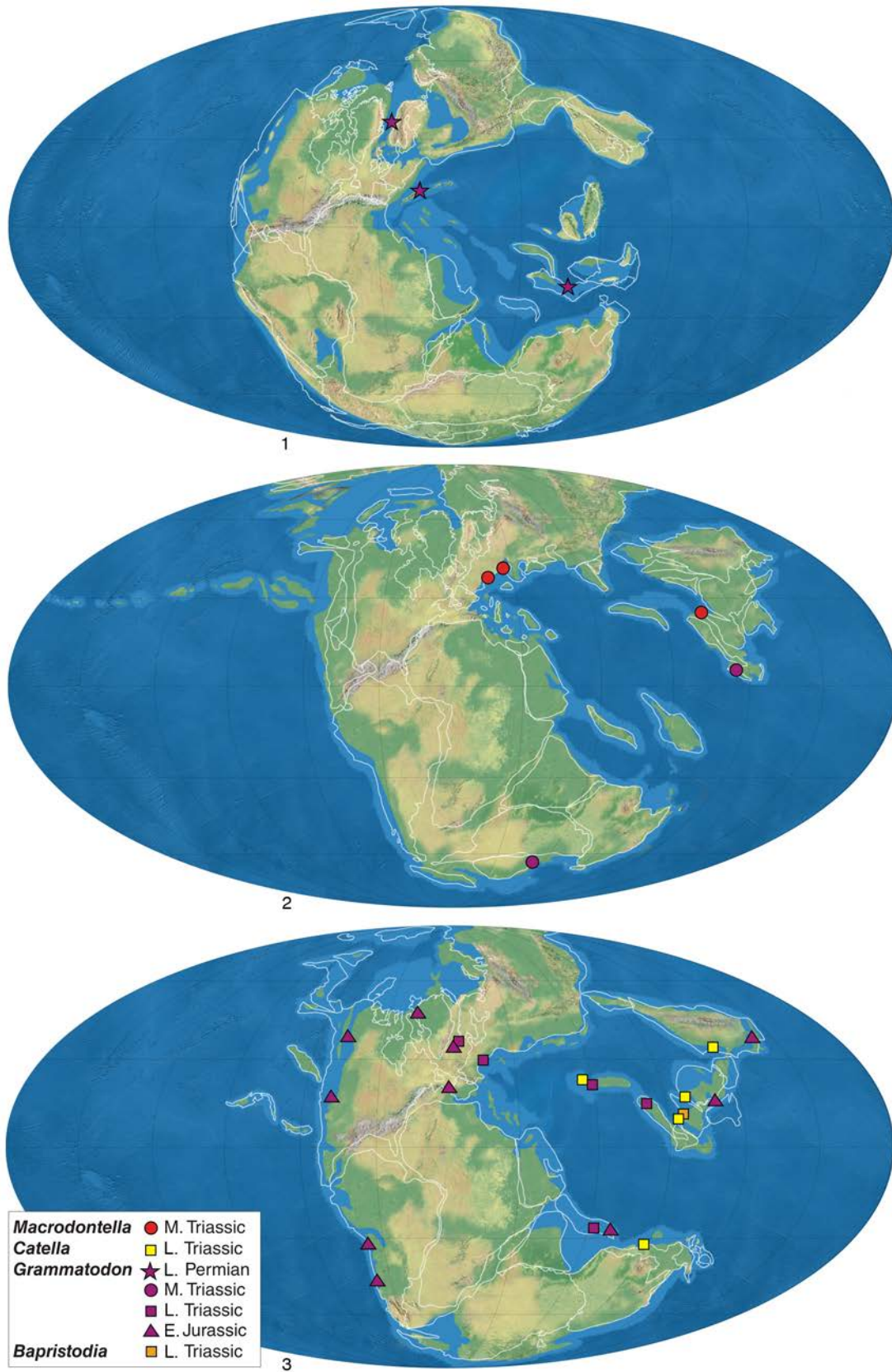


Figure 8. Paleogeographical distribution of Parallelodontidae (*Macrodonella*, *Catella*, *Grammatodon*, *Bapristodia*). 1, late Permian; 2, Middle Triassic; 3, Late Triassic–Early Jurassic.

but they disagree about the outer shell layer microstructure. However, Hautmann (2008) included *Leidapoconcha*, *Waijiaoella*, and *Qingyaniola* in his new family Healeyidae. No microstructural studies have been done on its type genus (*Healeyia*), but an original aragonitic mineralogy is suggested by the fact that the shell is often found completely recrystallized (Hautmann, 2008). Stiller and Chen (2006) indicated the presence of recrystallized calcite in the shell of the specimens they studied.

Genus WAIJIAOELLA Stiller & Chen, 2006, p. 218

Type species.—*Waijiaoella elegans* Stiller & Chen, 2006, p. 219.

Stratigraphic range.—Middle Triassic (Anisian) (Stiller & Chen, 2006). *Waijiaoella* was only reported from sediments dated as lower upper Anisian (Stiller & Chen, 2006). The genus includes two species, the type and *Waijiaoella speciosa* Stiller & Chen, 2006.

Paleogeographic distribution.—Eastern Tethys (Fig. 7). See *Leidapoconcha* (p. 26).

Paleoautoecology.—B, Se, S, Endo, Se. See *Leidapoconcha* (p. 26).

Mineralogy.—Bimineralic(?). See *Leidapoconcha* (p. 26).

Genus QINGYANIOLA Stiller & Chen, 2006, p. 222

Type species.—*Qingyaniola mirabilis* Stiller & Chen, 2006, p. 223.

Stratigraphic range.—Middle Triassic (Anisian) (Stiller & Chen, 2006). See *Leidapoconcha* (p. 26).

Paleogeographic distribution.—Eastern Tethys (Fig. 7). See *Leidapoconcha* (p. 26).

Paleoautoecology.—B, Se, S, Endo, Se. See *Leidapoconcha* (p. 26).

Mineralogy.—?Bimineralic. See *Leidapoconcha* (p. 26).

Superfamily ARCOIDEA Lamarck, 1809 Family PARALLELODONTIDAE Dall, 1898

Newell in Cox and others (1969, p. 256) pointed out that the phylogeny of this group is not well known, and several decades later, the problems to distinguish their genera still persist, although many authors have recently discussed this topic (see e.g., Damborenea, 1987a; Amler, 1989; Carter, 1990a; Stiller, 2006). The trouble is mainly focused on *Parallelodon* Meek & Worthen, 1866, *Grammatodon* Meek & Hayden, 1860, and *Cosmetodon* Branson, 1942. The general shell shape, the teeth (especially their arrangement), and ornamentation are features that were commonly used as criteria to distinguish these taxa (Manceñido, González, & Damborenea, 1976). Although it seems that the orientation of hinge teeth is a good criterion, it is not enough, since, as has been shown, in some *Parallelodon* species, the teeth may change their orientation during ontogeny (Newton in Newton & others, 1987; Hautmann, 2001b). In this regard, Stiller (2006, p. 12) concluded that “the convergence direction of the long posterior pseudolaterals appears to be taxonomically more reliable than the direction of the short anterior cardinals; the anterior ends of the posterior teeth intersect the dorsal shell margin in the Paralleodontinae and the ventral margin of the hinge plate in the Grammatodontinae.” The difficulty of applying these criteria is that hinge teeth are not observed in most specimens. A thorough review of this family is needed, but it is beyond the scope of this paper.

Genus MACRODONTILLA Assmann, 1916, p. 616

Type species.—*Macrodontella lamellosa* Assmann, 1916, p. 616.

Remarks.—Although Assmann (1916) included *Macrodontella* in the family Arcidae, we follow Newell in Cox and others (1969) and later authors (e.g., Sha, Chen, & Qi, 1990) and refer it to the Paralleodontidae.

Stratigraphic range.—Middle Triassic (Anisian). Assmann (1916) described this monotypic genus from lower Muschelkalk (probably Anisian) from the Erzführender Dolomit Formation in Silesia (Poland). Cox and others (1969) assigned it a Middle Triassic range. *Macrodontella* was reported from middle Anisian beds from Poland (Malinowskiej, 1979). The genus was also doubtfully recorded from Chinese Anisian deposits (Sha, Chen, & Qi, 1990).

Paleogeographic distribution.—Tethys (Fig. 8).

Tethys domain: Middle Triassic: Poland (Assmann, 1916; Cox & others, 1969), Anisian of Poland (Malinowskiej, 1979), China (?Qinghai province) (Sha, Chen, & Qi, 1990).

Paleoautoecology.—B, E-Se, S, Epi-Endo, Sed; By. Sha, Chen, and Qi (1990) suggested an epibyssate and suspensivorous mode of life; however, Aberhan and others (2004) assigned it a semi-infaunal mode of life. Because it is a monotypic genus with reduced distribution, it is difficult to obtain good illustrations to help settle this question.

Mineralogy.—Aragonitic (Carter, 1990a, p. 189). No data about shell mineralogy-microstructure of *Macrodontella* are available. Data provided for the family Paralleodontidae (Carter, 1990a).

Genus CATELLA Healey, 1908, p. 13

Type species.—*Grammatodon (Catella) laticlava* Healey, 1908, p. 13.

Stratigraphic range.—Upper Triassic (Carnian)–Lower Paleogene (Danian) (Wen & others, 1976; Heinberg, 1999). Healey (1908) described *Catella* as a subgenus of *Grammatodon* from the Rhaetian of Burma. Cox and others (1969) assigned it an Upper Triassic–Jurassic range, and Sepkoski (2002) assigned a Triassic (Norian)–Paleocene (Thanetian) range, and presumably got his data from Heinberg (1978), but in this last paper, the figure with the ranges of genera seems to indicate Danian, not Thanetian. The youngest record is Paleocene (Danian) (Heinberg, 1999), because we were not able to corroborate the range offered by Sepkoski (2002). The oldest record considered for almost all authors for *Catella* is Norian (Wen & others, 1976; Hallam, 1981; J. Zhang, 1983; Hautmann, 2001b). Nevertheless, Guo (1988) proposed a new subgenus, *Catella (Oceanopieris)*, from the Carnian of Yunnan (China), which was considered a junior synonym of *Catella* by Z. Fang and others (2009). *Catella* shows a seemingly discontinuous distribution through time. Although it was widely mentioned from the Upper Triassic (see next section), it is not reported again until the Upper Jurassic (X. Li, 1990; Monari, 1994) and later in the Upper Cretaceous (Heinberg, 1999).

Paleogeographic distribution.—Eastern Tethys (Fig. 8).

Tethys domain: Late Triassic: Carnian of Yunnan (China) (Guo, 1988); Norian of Yunnan (China) (J. Zhang, 1983), Himalaya (southern Tibet) (Wen & others, 1976; J. Yin & Enay, 2000; Hautmann,

2001b); Norian–Rhaetian of Iran (Hautmann, 2001b); Rhaetian of Burma (Healey, 1908), Indochina (Kutassy, 1931).

Paleoautoecology.—B, Se, S, Endo, Sed; By. Several aspects of the shell shape, such as the reduced anterior part of the shell, absence of ventral flattening, external modioliform appearance, and presence of byssal sinus, suggest that *Catella* was probably an endobyssate semi-infaunal bivalve (Heinberg, 1999; Hautmann, 2001b).

Mineralogy.—Aragonitic (Carter, 1990a, p. 184–185). There are no data about *Catella* shell mineralogy or microstructure. Data provided for superfamily Arcoidea.

Genus PARALLELONDON Meek & Worthen, 1866, p. 17
nom. nov. pro Macrodon Buckman [Lycett MS] in Murchison, Buckman, & Strickland, 1844, *non* Schinz, 1822, p. 482, *nec* Müller, 1842, p. 308

Type species.—*Macrodon rugosus* Buckman in Murchison, Buckman, & Strickland, 1844, p. 99.

Stratigraphic range.—Middle Devonian–Upper Cretaceous (Amler & Winkler Prins, 1999). Traditionally, all Paleozoic members of the family Parallelodontidae were referred to *Parallelodon* (Newell in Cox & others, 1969); however, Manceñido, González, and Damborenea (1976) and Yancey (1985) noticed that many of these species should be referred to *Grammatodon* (*Cosmetodon*) instead. The same happens with some Mesozoic species referred to *Parallelodon*, which would better be allocated in *Grammatodon* (*Grammatodon*) (Damborenea, 1987a). Many Paleozoic species were described based on poorly preserved material or with little morphological discussion (Amler, 1989; Anelli, Rocha-Campos, & Simões, 2006). In practice, it is hard to distinguish between *Parallelodon* and *Grammatodon* (Boyd & Newell, 1979). For this reason, the range assigned here is provisional for these two genera, awaiting revision of Paleozoic material.

Paleogeographic distribution.—Cosmopolitan.

Paleoautoecology.—B, E, S, Epi, Sed; By. There are endobenthic and epibenthic species within this genus (S. M. Stanley, 1972). Those with a modioliform appearance are presumably endobyssate. Others are quadrangular and morphologically very similar to epifaunal Recent arcids. Some species, such as *P. monobensis* Nakazawa, 1955, have a large ventral sinus indicating an epibyssate mode of life. Other species, such as *P. groeberi* Damborenea, 1987a, and *P. riccardii* Damborenea, 1987a, were also epifaunal and probably attached to hard substrates with a strong byssus, as living *Arca* species do (S. M. Stanley, 1970; Damborenea, 1987a). *Parallelodon riccardii* might even have been a nestler (Damborenea, 1987a), as suggested by its elongated and laterally compressed shell (Thomas, 1978). However, *P. tenuistriatus* (Meek & Worthen, 1866) and *P. hirsonensis* (Archiac, 1843) were probably endobyssate (Quiroz-Barroso & Perrilliat, 1998; Fürsich & others, 2001). They are often found associated with corals and sponges (Damborenea, 1987a; Newton in Newton & others, 1987). But they could also live attached on rocks in open substrates (Newton in Newton & others, 1987). J. Yin and McRoberts (2006) suggested that representatives of the genus had an epibyssate and suspensivorous mode of life. We assign *Parallelodon* the predominant mode of life of species attributed to this genus.

Mineralogy.—Aragonitic (Carter, 1990a, p. 189–190). Outer shell layer: aragonite (prismatic). Middle shell layer: aragonite (cross-lamellar). Inner shell layer: aragonite (complex cross-lamellar).

Genus GRAMMATODON Meek & Hayden, 1860, p. 419

Type species.—*Arca* (*Cucullaea*) *inornata* Meek & Hayden, 1859, p. 51.

Remarks.—We regard *Cosmetodon* Branson, 1942, p. 248, as a subgenus of *Grammatodon*, following most authors (Fürsich, 1982; Kelly, 1984; Yancey, 1985; Damborenea, 1987a; Gardner & Campbell, 1997; Ivimey-Cook & others, 1999; Hautmann, 2001b; Nakazawa, 2002; Delvene, 2003). Some authors (Tashiro, 1986; Stiller, 2006) argued that *Cosmetodon* is a separate genus. Two other subgenera are included in our study range: *Grammatodon* and *Indogrammatodon* Cox, 1937b.

Stratigraphic range.—Lower Permian (Artinskian)–Upper Cretaceous (Maastrichtian) (Yancey, 1985; Carter, 1990a). Newell in Cox and others (1969) included all Paleozoic members of the family Parallelodontidae within *Parallelodon*, but as stated above, there are certain specimens that should be attributed to *Grammatodon* instead (Manceñido, González, & Damborenea, 1976; Yancey, 1985). In the absence of a good review of Paleozoic members of this family, the first appearance is from the Permian Pacific margin (Manceñido, González, & Damborenea, 1976; Yancey, 1985) and the last appearance is from Upper Cretaceous age (Carter, 1990a). Sepkoski (2002) assigned it a Jurassic (Hettangian)–Cretaceous (?Cenomanian) range, following Cox and others (1969) and Hallam (1977).

Paleogeographic distribution.—Cosmopolitan (Fig. 8).

Tethys domain: late Permian: Malaysia (Nakazawa, 2002), Greece (Clapham & Bottjer, 2007); Middle Triassic: Anisian of Malaysia (Tamura & others, 1975); Late Triassic: Carnian of Malaysia (Tamura & others, 1975); Norian of Iran (Repin, 2001); Norian–Rhaetian of Iran (Hautmann, 2001b); Rhaetian of Burma (Healey, 1908), north-eastern England (Penarth Group) (Ivimey-Cook & others, 1999), Tibet (Hautmann & others, 2005), Austria (Tomašových, 2006a); Early Jurassic: Tibet (Gou, 2003); Hettangian of Tibet (Hautmann & others, 2005); Sinemurian of Vietnam (Hayami, 1964; Sato & Westermann, 1991), Portugal and southern England (Liu, 1995), China (Stiller, 2006).

Circumpacific domain: Early Jurassic: western United States (Oregon) (Fraser, Bottjer, & Fischer, 2004); Hettangian of Japan (Hayami, 1958d); Hettangian–Sinemurian of Japan (Hayami, 1975); Sinemurian of Chile (Aberhan, 1994a) and Canada (Aberhan, 1998a).

Austral domain: Middle Triassic: Ladinian of New Zealand (Marwick, 1953); Early Jurassic: Argentina (Damborenea, 1987a; Damborenea & Lanés, 2007); Hettangian–Sinemurian of Neuquén Basin (Damborenea & Manceñido, 2005b).

Boreal domain: late Permian: Norway (Nakazawa, 1999); Early Jurassic: Hettangian of Greenland (Liu, 1995).

Paleoautoecology.—B, E, S, Epi, Sed; By. The assignment of one specific mode of life to this genus is difficult. Duff (1978) and Damborenea (1987a) found several inconsistencies, depending on which features of the shell were observed. According to authors and

species, *Grammatodon* was interpreted as epibyssate (Fürsich, 1982; Fürsich & others, 2001; Hautmann, 2001b; Delvene, 2003; J. Yin & Grant-Mackie, 2005; Aberhan, Kiessling & Fürsich, 2006; Stiller, 2006; Tomašových, 2006a), semi-infaunal (Fürsich, 1982; Pugaczewska, 1986; Delvene, 2003) or infaunal (Duff, 1978; Damborenea, 1987a; Gardner & Campbell, 1997; Harries & Little, 1999). According to S. M. Stanley (1972), the members of the subfamily Grammatodontinae would be rather epibyssate as suggested by their elongated shell by comparison with living species. However, in the same genus, we find species (such as *G. toyorensis* Hayami, 1959) with dorsally inflated shells and no evidence of byssal gape, which could be interpreted as shallow burrowers (Damborenea, 1987a); others [such as *G. (Cosmetodon) mediodepressum* (Krumbeck, 1913)] with an elongated ventral margin, which were probably epibyssate (Hautmann, 2001b), and finally, others [such as *G. (Cosmetodon) keyserlingii* (d'Orbigny, 1850) or *G. (C.) marshallensis* (Winchell, 1862)] showing a modioliform shape with an expanded posterior part, which are interpreted as semi-infaunal (S. M. Stanley, 1972; Fürsich, 1982). Having said that, we assign the prevailing inferred mode of life, i.e., epibyssate, to the genus.

Mineralogy.—Aragonitic (Carter, 1990b, p. 326). Outer shell layer: aragonite (cross-lamellar). Middle shell layer: aragonite (?). Inner shell layer: aragonite (cross-lamellar).

Genus BAPRISTODIA Guo, 1988, p. 115

Type species.—*Bapristodia serrata* Guo, 1988, p. 116.

Stratigraphic range.—Upper Triassic (Norian) (Guo, 1988). Guo (1988) proposed *Bapristodia*, a monospecific genus, from the Maichuqing formation dated as Norian (H. Yao & others, 2007).

Paleogeographic distribution.—Eastern Tethys (Fig. 8).

Tethys domain: Late Triassic: Norian of southwestern China (Yunan) (Guo, 1988).

Paleoautoecology.—B, E, S, Epi, Sed; By. We assign it the most common mode of life in the family Parallelodontidae. The external morphology of *B. serrata* is similar to some epibyssate species of *Grammatodon*, although no evidence of byssal gape is mentioned in the diagnosis offered by Guo (1988) [translated English version in Z. Fang & others, 2009].

Mineralogy.—Aragonitic (Carter, 1990a, p. 184–185). There are no data about the shell mineralogy or microstructure of *Bapristodia*. Data provided for superfamily Arcoidea (Carter, 1990a).

Family CUCULLAEIDAE Stewart, 1930

Genus CUCULLAEA Lamarck, 1801, p. 116

Type species.—*Cucullaea auriculifera* Lamarck, 1801, p. 116.

Remarks.—One of the subgenera of *Cucullaea* lived during the study interval: *Idonearca* Conrad, 1862, p. 289 (type species, *Cucullaea tippiana* Conrad, 1858, p. 328).

Stratigraphic range.—Lower Jurassic (Hettangian)–Holocene (Hayami, 1958d; Beesley, Ross, & Wells, 1998). *Cucullaea* had its origin during the Early Jurassic and reached its greatest diversity during the Late Cretaceous, followed by a gradual decline until the present. Although Cox and others (1969) assigned it a discontinuous range [Jurassic (Liassic)–Cretaceous, Holocene], *Cucullaea* was present during the Cenozoic (Griffin, 1991; Griffin & Nielsen, 2008). The oldest record is from the Hettangian (Hayami, 1958d, 1975). It is

currently represented by a single species, *C. labiata* (Lightfoot, 1786), with an Indo-Pacific distribution (Beesley, Ross, & Wells, 1998).

Paleogeographic distribution.—Circumpacific (Fig. 9). Although during other times this genus was widely distributed, during the Early Jurassic (Hettangian and Sinemurian), it was only found in northwestern Pacific. During the Pliensbachian and Toarcian, it was distributed in the Arctic region (Zakharov & others, 2006), South America (A. F. Leanza, 1940, 1942; Damborenea, 1987a; Aberhan, 1994a), and Europe (Fürsich & others, 2001; Gahr, 2002).

Circumpacific domain: Early Jurassic: Hettangian of Japan (Hayami, 1958d, 1975).

Paleoautoecology.—B, Is-Se, S, SM; Sb. The species referred to *Cucullaea* have a very inflated quadrangular shell, with a truncated posterior end, indicative of a slow shallow-burrowing mode of life, as in modern species of *Anadara* (S. M. Stanley, 1970). The only extant species, *C. labiata*, lives at depths down to 200 m, buried in sand, with the anterior part downward (Beesley, Ross, & Wells, 1998). Damborenea (1987a) noted that shells of *C. jaworskii* A. F. Leanza and *C. rothi* A. F. Leanza (Lower Jurassic) lack epizoan organisms, whereas other epifaunal invertebrates from the same beds bear abundant epifauna. Thus we regard *Cucullaea* as a shallow infaunal or even semi-infaunal bivalve (see Damborenea, 1987a, p. 75).

Mineralogy.—Aragonitic (Carter, 1990b, p. 326). Outer shell layer: aragonite (prismatic or cross-lamellar). Middle shell layer: aragonite (cross-lamellar). Inner shell layer: aragonite (complex cross-lamellar).

Superfamily LIMOPSOIDEA Dall, 1895

Family PHILOBRYIDAE Bernard, 1897

Genus EOPHILOBRYOIDEA Stiller & Chen, 2004, p. 414

Type species.—*Eophilobryoidella sinoanisica* Stiller & Chen, 2004, p. 414.

Stratigraphic range.—Middle Triassic (upper Anisian) (Stiller & Chen, 2004). *Eophilobryoidella* is particularly abundant in the middle part of the Leidapo Member of Qingyan formation. Up to now, the family Philobryidae was believed to range from the Eocene to the present time, but this finding extends its stratigraphic range back to the Middle Triassic. Therefore, the idea that this family evolved from the family Limopsidae, which has a Cretaceous origin, is invalidated (Stiller & Chen, 2004; Oliver & Holmes, 2006).

Paleogeographic distribution.—Eastern Tethys (Fig. 9).

Tethys domain: Middle Triassic: late Anisian of southwestern China (Guizhou province) (Stiller & Chen, 2004).

Paleoautoecology.—B, E, S, Epi, Sed; By. Living members of family Philobryidae are suspensivorous and live at depths that can exceed 1000 m, almost always attached (epibyssate) to other organisms (Beesley, Ross, & Wells, 1998). Stiller and Chen (2004) interpreted that *Eophilobryoidella* had a similar mode of life, although a byssal notch is not observed. These authors suggested that species of this genus were epibyssate, because they found epizoan organisms attached to the shells while the bivalve was alive. According to the environment in which these organisms lived, they concluded the species of *Eophilobryoidella* preferred shallow, low energy and normal salinity waters.

Mineralogy.—Aragonitic (Carter, 1990a, p. 195; Carter, 1990b, p. 328). There is no information about *Eophilobryoidella* shell mineral-

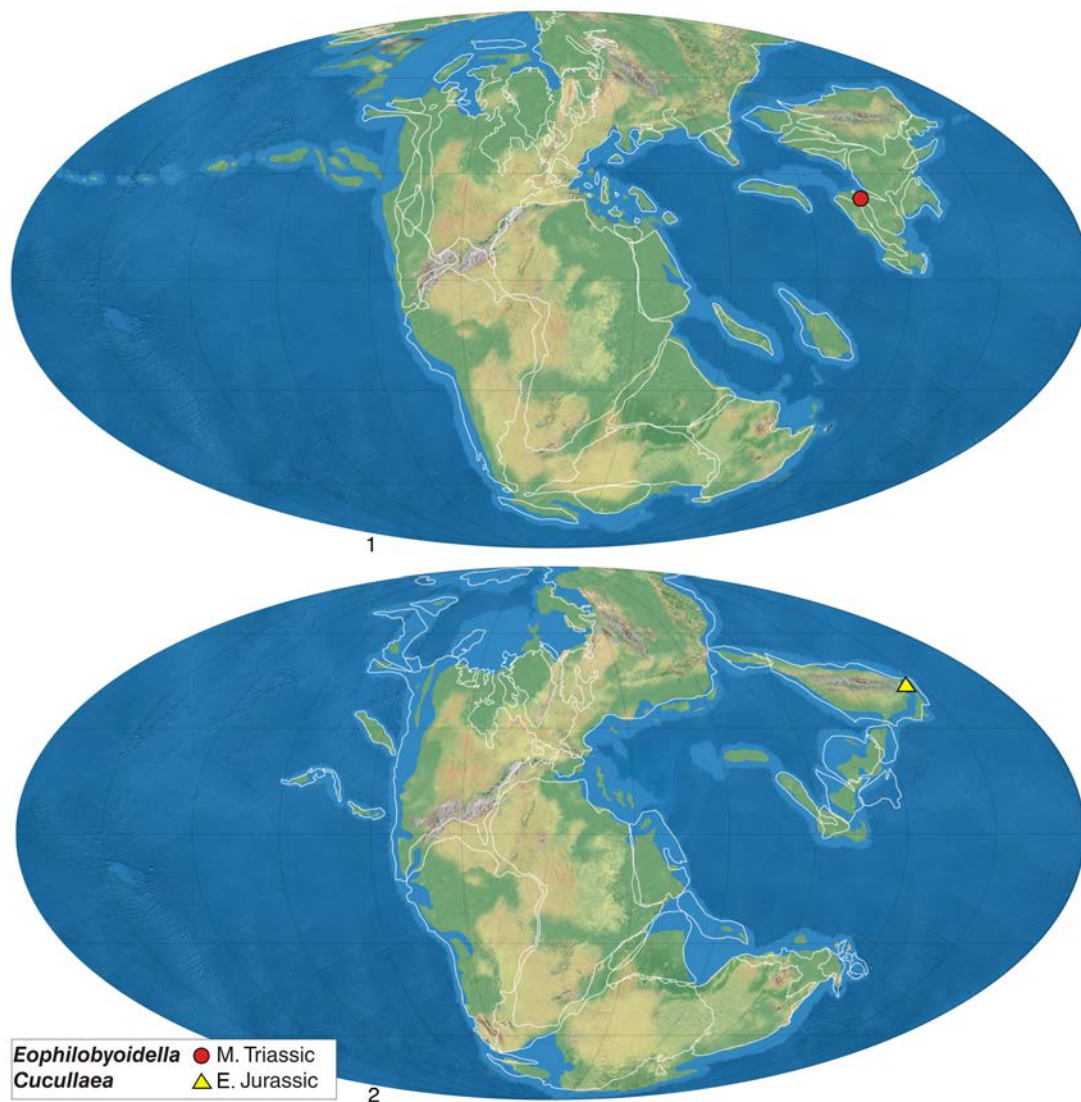


Figure 9. Paleogeographical distribution of Cucullaeidae (*Cucullaea*) and Philobryidae (*Eophilobryoidella*). 1, Middle Triassic; 2, Early Jurassic.

ogy or microstructure. Data from Recent Philobryidae specimens are used. Outer shell layer: aragonite (?). Middle shell layer: aragonite (cross-lamellar). Inner shell layer: aragonite (complex cross-lamellar).

Family PICHLERIIDAE Scarlato & Starobogatov, 1979

Genus HOFERIA Bittner, 1894, p. 190

Type species.—*Lucina duplicata* Münster, 1841, in Goldfuss, 1833–1841, p. 227.

Stratigraphic range.—Upper Triassic (Carnian). There are some *Hoferia* records from the Ladinian (Hallam, 1981; Kobayashi & Tamura, 1983a; Sepkoski, 2002), but none of these figure or indicate the original source of the data, and all of them are referred to the Alps. *Hoferia* was listed from the Cassian Formation in the southern Alps; according to Fürsich and Wendt (1977, fig. 2), this unit is upper Anisian to the lower part of the upper Carnian in age. Nevertheless, Fürsich (in PBDB, 2005) provided data from this paper, and he clearly assigned a Carnian age to *Hoferia* specimens. In addition, Kobayashi and Tamura (1983a) also mentioned *Hoferia*

from the Norian of Yunnan, but they did not provide any bibliographic reference. The only quotation of this genus from Yunnan is Cowper-Reed (1927), but from the Carnian. The last author only had a badly preserved internal mold of a right valve, and he included the specimen in *Hoferia*, because it shows a characteristic anterior lobe. We assign here a Carnian range to *Hoferia*.

Paleogeographic distribution.—Tethys (Fig. 10).

Tethys domain: Late Triassic: Carnian of the Italian Alps (Leonardi, 1943; Fürsich & Wendt, 1977), Yunnan (China) (Cowper-Reed, 1927).

Paleoautoecology.—B, Is, S, Endo, SM; Sb. The family Pichleriidae includes members of both shallow burrowers and those with epibyssate attached. *Hoferia* presents a byssal groove (see diagnosis in Cox & others, 1969, p. 265), and thus it must have been byssate. The globose shell suggests it was an endobyssate shallow burrower that lived near the surface or even semi-infaunally.

Mineralogy.—Aragonitic (Carter, 1990a, p. 196). There are no specific data for *Hoferia*, but we provisionally use those provided by

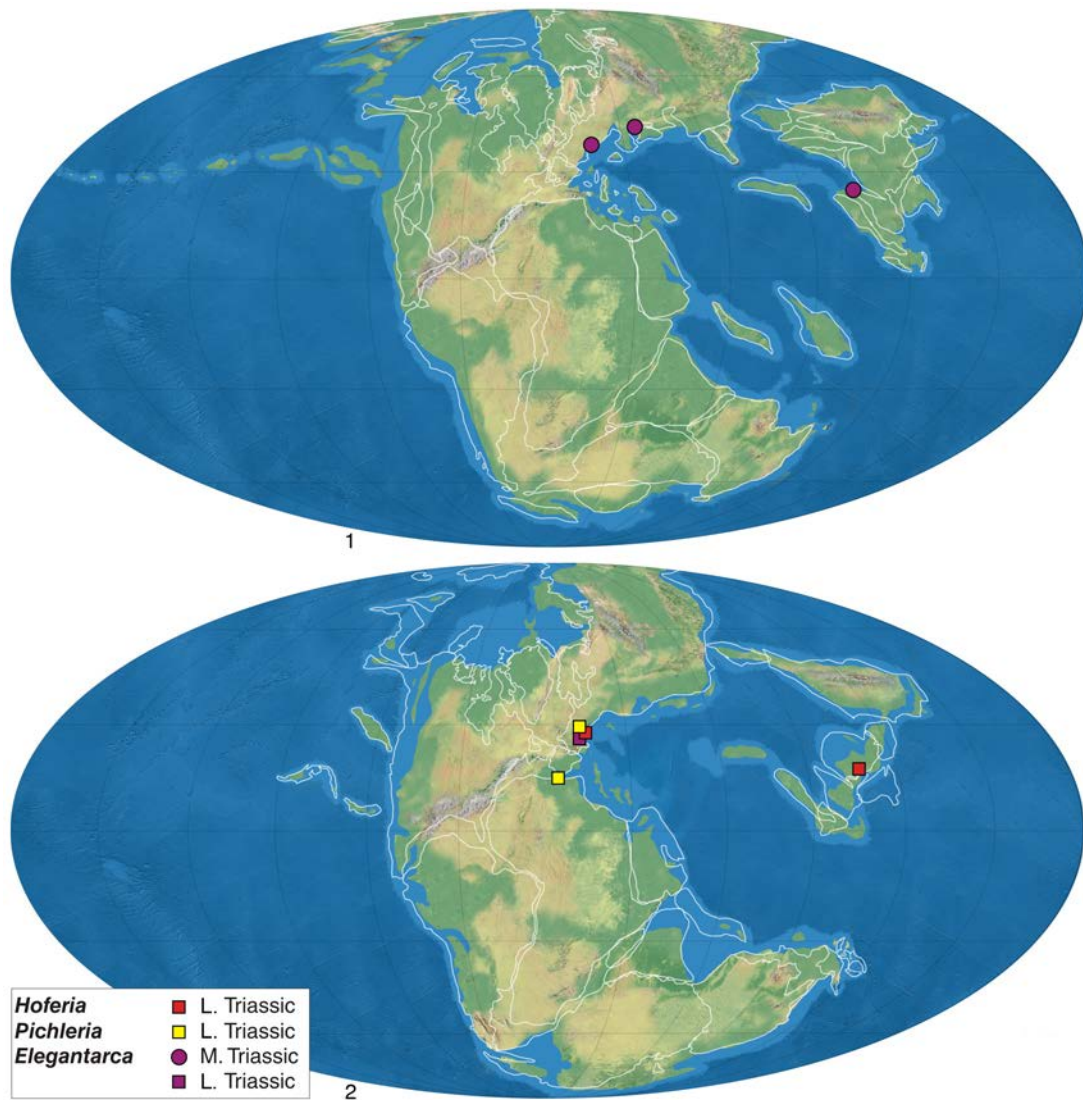


Figure 10. Paleogeographical distribution of Pichleriidae (*Hoferia*, *Pichleria*, *Elegantarca*). 1, Middle Triassic; 2, Late Triassic–Early Jurassic.

Carter (1990a) for the family Pichleriidae, provided by the analysis of *Pichleria*, a genus closely related to *Hoferia* (see above).

Genus PICHLERIA Bittner, 1894, p. 189

Type species.—*Cucullaea auingeri* Laube, 1865, p. 62.

Stratigraphic range.—Upper Triassic (Carnian) (Cox & others, 1969). Cox and others (1969) assigned *Pichleria* to the Upper Triassic, and Sepkoski (2002) to the Triassic (upper Ladinian–Carnian), following Hallam (1981) (see discussion for *Hoferia*). Wen and others (1976) mentioned *Pichleria* from the Norian of China, but the figured specimens (pl. 7, 6–13) are members of family Limidae.

Paleogeographic distribution.—Tethys (Fig. 10).

Tethys domain: Late Triassic: Carnian of southern Alps (Italy) (Bittner, 1894, 1895; Diener, 1923; Leonardi, 1943; Corazzari & Lucchi-Garavello, 1980), southern Tunisia (Desio, Rossi Ronchetti, & Vigano, 1960).

Paleoautoecology.—B, Is–Se, S, Sed; ?. The shell morphology indicates that *Pichleria* probably lived semi-infaunally or infaunally near the substrate surface. Byssal notch and sinus appear to be absent.

Mineralogy.—Aragonitic (Carter, 1990a, p. 196). Outer shell layer: aragonite (prismatic). Middle shell layer: aragonite (nacreous). Inner shell layer: aragonite (prismatic).

Genus ELEGANTARCA Tomlin, 1930, p. 23

Type species.—*Arcoptera elegantula* Bittner, 1895, p. 126.

Remarks.—Cox and others (1969) regarded *Elegantarca* (*nom. nov. pro Arcoptera* Bittner, 1895, p. 126, *non* Heilprin, 1887, p. 98) as a synonym of *Hoferia*, but Stiller (personal communication, 2005) argued to maintain them as separate genera, due to differences in orientation, number, and shape of the hinge teeth and other morphological disparities. In his own words: “*Elegantarca* shows some distinct morphological differences to *Hoferia*. Outer shell shape:

Elegantarca has a large posterodorsal wing separated from the body of shell by a distinct but generally blunt posterior umbonal ridge (this diagonal ridge is lacking in *Hoferia*); *Elegantarca* in many cases is distinctly produced posteroventrally, *Hoferia* generally is shorter and more rounded. However, more important are differences in the hinge structure: *Hoferia* has a hinge with at least 10 short, taxodont teeth, which are radially arranged in two groups (Bittner, 1895; Broili, 1904; Cox & others, 1969); *Elegantarca* has very few, strong, radial teeth below the umbo, and one anterior and one posterior elongated tooth (about parallel to the hinge margin) (Broili 1904). The Chinese *Elegantarca subareata* Chen, Ma, & Zhang, 1974 has a hinge like the bivalves figured by Broili (1904, *Arcoptera*)."

Vokes (1980) regarded *Bittnerella* Dall, 1898, p. 613 (*nom. nov. pro Arcoptera* Bittner, 1895) as a valid name with priority over *Elegantarca*, but *Bittnerella* was included in the synonymy of *Hoferia* by Cox and others (1969), and now the name *Bittnerella* Dagens, 1974, p. 77, is used for a brachiopod genus.

Stratigraphic range.—Middle Triassic (Anisian)—Upper Triassic (Carnian) (Bittner, 1895; Komatsu, Chen, & others, 2004). The oldest known record of *Elegantarca* dates from Anisian times (Komatsu, Chen, & others, 2004; Stiller, personal communication, 2005) and the youngest from the Carnian (Bittner, 1895).

Paleogeographic distribution.—Tethys (Fig. 10).

Tethys domain: Middle Triassic: Anisian of southern China (Anonymous, 1974; Komatsu, Chen, & others, 2004; Stiller, personal communication, 2005), Bosnia (Diener, 1923); Ladinian of southern Alps (Italy) (Diener, 1923); Late Triassic: Carnian of southern Alps (Italy) (Bittner, 1895; Broili, 1904; Waagen, 1907).

Paleoautoecology.—B, Se, S, Endo, Sed; By. See *Hoferia*. Komatsu, Chen, and others (2004) regarded it as endobysate semi-infaunal.

Mineralogy.—Aragonitic (Carter, 1990a, p. 196). See *Hoferia*.

Superfamily AMBONYCHIOIDEA Miller, 1877

Family MYALINIDAE Frech, 1891

Genus MYALINA de Koninck, 1842 in 1841–1844, p.125

Type species.—*Myalina goldfussiana* de Koninck, 1842 in 1841–1844, p. 126.

Stratigraphic range.—Carboniferous (lower Mississippian)—upper Permian, ?Lower Triassic (McRoberts, personal communication, 2005). Both Cox and others (1969) and Sepkoski (2002) assigned a Carboniferous (Lower Mississippian)—upper Permian range to this genus, but previously and subsequently, several authors mentioned *Myalina* from the Lower Triassic (e.g., Kiparisova, 1938; Newell & Kummel, 1942; Ciriacks, 1963; Dagens & Kurushin, 1985; Schubert, 1993; Schubert & Bottjer, 1995; McRoberts & Newell, 2005). All these references are better regarded as belonging to *Promyalina*, *Myalinella*, or even *Promytilus* (McRoberts, personal communication, 2005; McRoberts, 2005). So we leave the Triassic record of this genus as doubtful pending a good review of the problem. According to McRoberts (personal communication, 2005), no myalinid reached the Middle Triassic, since the only genus mentioned for that age (*Aviculomyalina*) should in fact be included in the Pteriidae or Malleidae.

Paleogeographic distribution.—Circumpacific (Fig. 11). *Myalina* had a cosmopolitan distribution, but from the late Permian, we only find records from the Tethys and Circumpacific domains. The family Myalinidae had significant diversity and abundance during

the Carboniferous and Permian, but at the Permian–Triassic extinction, this family was decimated, later to disappear by the end of the Early Triassic (McRoberts, 2005). The doubtful Early Triassic records belong to the Circumpacific and Boreal domains.

Circumpacific domain: late Permian: western United States (Newell, 1942; Walter, 1953; McRoberts & Newell, 2005), Japan (Nakazawa & Newell, 1968; Hayami & Kase, 1977).

Paleoautoecology.—B, E, S, Epi, Sed; By. Species attributed to this genus have different morphologies and, consequently, their mode of life can be semi-infaunal (endobysate) to epifaunal (epibysate) (S. M. Stanley, 1972, fig. 12). Upper Permian specimens have reduced anterior lobes and, in some cases, bear a byssal sinus (*M. lamellosa* McRoberts & Newell, 2005; *M. plicata* McRoberts & Newell, 2005; *M. copei* Whitfield, 1902; see diagnosis in McRoberts & Newell, 2005), characters that indicate a byssate mode of life. Nevertheless, their thick and heavy shells were probably not functional for byssus attachment, and they were not active (Newell, 1942). According to McRoberts and Newell (2005), *M. lamellosa* probably lived lying on its anterior side, with an almost vertical commissure, lightly resting on its left valve. The species had a gregarious mode of life and is found in groups, as are many Recent mussels (Newell, 1942). Substrate type should also be taken into account: in soft substrates, they commonly adopt an endobysate mode of life to become stable, while on hard substrates, they were frequently epibysate.

Mineralogy.—Bimineralic (Newell, 1942, p. 33–34; Carter, 1990b, p. 331). Outer shell layer: calcite (prismatic-homogeneous). Inner shell layer: aragonite (nacreous).

Genus MYALINELLA Newell, 1942, 60

Type species.—*Myalina meeki* Dunbar, 1924, p. 201.

Remarks.—Newell (1942) described *Myalinella* as a subgenus of *Myalina*, pointing out the differences between *Myalinella* and other myalinids, such as *Myalina* (*Myalina*). Later, the same author (in Cox & others, 1969), raised *Myalinella* to genus level.

Stratigraphic range.—Carboniferous (Visean)—Lower Triassic (upper Olenekian) (R. Zhang & Pojeta, 1986; Fraiser & Bottjer, 2007a). Newell in Cox and others (1969) assigned a Carboniferous (Pennsylvanian)—Lower Triassic range to this genus and recorded it from Europe, United States, India, and Greenland. However, R. Zhang and Pojeta (1986) reported the first record of *Myalinella* from the Visean of China. The youngest record is Olenekian (Newell, 1942; Schubert, 1993; Schubert & Bottjer, 1995; Fraiser & Bottjer, 2007a).

Paleogeographic distribution.—Tethys, Boreal, and Circumpacific (Fig. 11). *Myalinella* had a wide distribution, but, during the late Permian, it seems restricted to few records; for instance, it was extensively mentioned from the western coast of the United States from the Permian until Guadalupian times (e.g., Newell, 1942; Ciriacks, 1963), but, from then on, it is only recorded from the Lower Triassic (e.g., Schubert, 1993), possibly due to lack of upper Permian deposits in this area. Even though during the early Permian it was present in the Tethys (e.g., Zheng, 1993), it seems to have been absent from this domain during the late Permian. However, it was recently reported from the Lower Triassic (Hautmann & others, 2011). Fraiser and Bottjer (2007a) studied several Lower Triassic sections from Japan and Italy, and they did not report *Myalinella*, but they did find another genus of the same family (*Promyalina*).

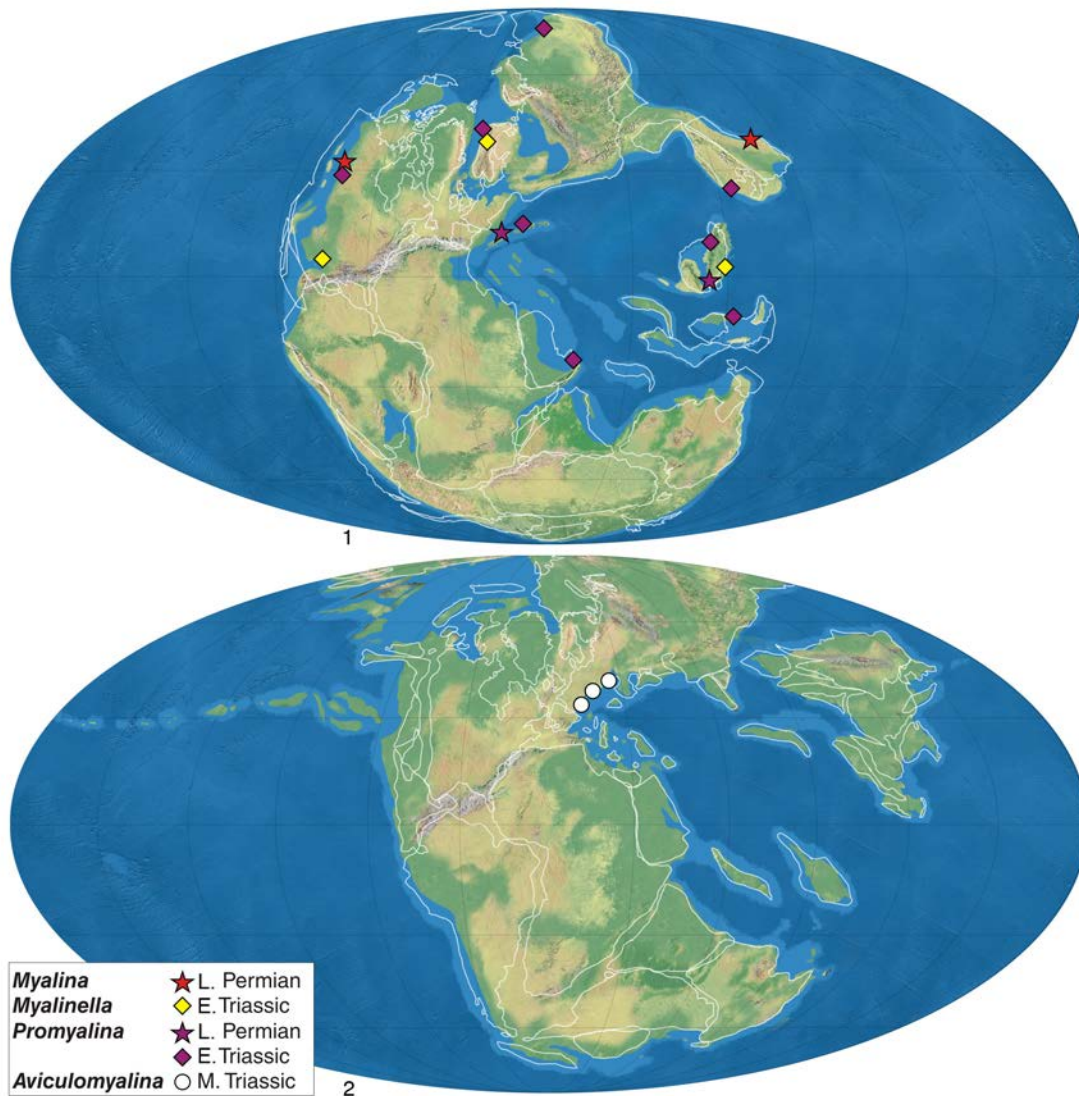


Figure 11. Paleogeographical distribution of Myalinidae (*Myalina*, *Myalinella*, *Promyalina*, *Aviculomyalina*). 1, late Permian–Early Triassic; 2, Middle Triassic.

Tethys domain: Early Triassic: Induan of southern China (Hautmann & others, 2011).

Boreal domain: Early Triassic: Greenland (Newell, 1942).

Circumpacific domain: Early Triassic: United States (Schubert, 1993; Schubert & Bottjer, 1995; Fraiser & Bottjer, 2007a).

Paleoautoecology.—B, Se, S, Endo, Sed; By. Specimens of this genus are usually found with closed valves, suggesting that they lived in low energy areas and/or were buried (Newell, 1942). They tolerated a wide salinity range (Newell, 1942), and they were found in fully marine (Kues, 2004) to estuarine environments (Mack & others, 2003). The shell shows some features indicative of a probable endobyssate and semi-infaunal mode of life: they have an anterior lobe and a byssal sinus, and their shells are small and fragile (Newell, 1942; McRoberts & Newell, 2005).

Mineralogy.—Bimineralic (Newell, 1942, p. 33–34). There are no available data about *Myalinella* shell microstructure. Newell (1942) indicated that, unlike most myalinids, *Myalinella* exhibits the same

structure in both valves. We assign the type present in members of the family Myalinidae.

Genus PROMYALINA Kittl, 1904, p. 690

Type species.—*Promyalina hindi* Kittl, 1904, p. 690.

Stratigraphic range.—upper Permian (upper Changhsingian)–Lower Triassic (upper Olenekian) (Fraiser & Bottjer, 2007a; He, Feng, & others, 2007). Cox and others (1969) assigned a Lower Triassic range to this genus, and they also doubtfully considered its presence in upper Permian beds. Although some authors (Sepkoski, 2002; McRoberts, 2005; McRoberts & Newell, 2005) only took into account the Lower Triassic records, others (Farabegoli, Perri, & Posenato, 2007, fig. 7; He, Feng, & others, 2007, fig. 5.18) accepted the late Permian records (late Changhsingian) from the Tethys domain. *Promyalina* showed a maximum abundance at the beginning of the Early Triassic, and it went extinct at the end of the same epoch.

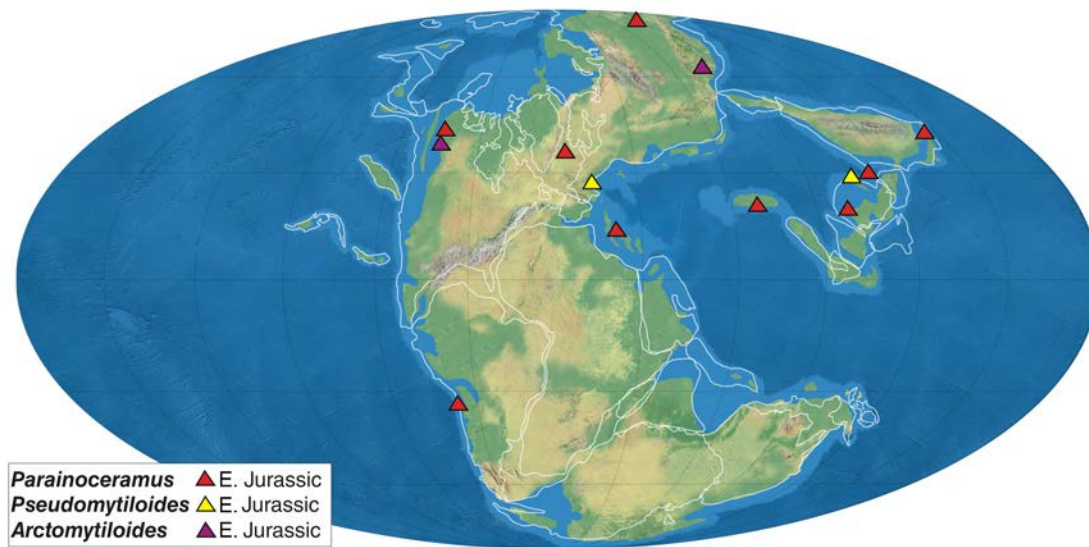


Figure 12. Paleogeographical distribution of Inoceramidae (“*Parainoceramus*,” *Pseudomytiloides*, *Arctomytiloides*). Late Triassic–Early Jurassic.

Paleogeographic distribution.—Tethys, Circumpacific, and Boreal (Fig. 11).

Tethys domain: late Permian: Italy (Farabegoli, Perri, & Posenato, 2007), Changhsingian of southern China (He, Feng, & others, 2007); Early Triassic: China (Z. Yang & Yin, 1979; C. Chen, 1982; F. Wu, 1985; Lu & Chen, 1986; Ling, 1988; Komatsu, Huyen, & Chen, 2006, 2007), northern Vietnam (Komatsu, Huyen, & Chen, 2006, 2007); Induan of Oman (Krystyn & others, 2003; Twitchett & others, 2004), south of China (Hautmann & others, 2011); Induan–early Olenekian of Italy (Broglio-Loriga & others, 1990; Fraiser & Bottjer, 2005a, 2007a; Posenato, 2008a).

Circumpacific domain: Early Triassic: early Olenekian of Japan (Nakazawa, 1961; Hayami, 1975; Fraiser & Bottjer, 2007a); Olenekian of western United States (Ciriacks, 1963; Boyd, Nice, & Newell, 1999; Boyer, Bottjer, & Droser, 2004; Fraiser & Bottjer, 2007a).

Boreal domain: Early Triassic: northern Siberia (Dagys & Kuru-shin, 1985); Induan of Greenland (Wignall, Morante, & Newton, 1998; Wignall & Twitchett, 2002).

Paleoautoecology.—B, Se, S, Endo, Sed; By. *Promyalina* was one of the more widely distributed genera during the Early Triassic worldwide. Together with *Eumorphotis* and *Unionites*, it dominated the bivalve fauna of the seas at the beginning of the Triassic (Fraiser & Bottjer, 2005b, 2007a). It showed a typical opportunistic behavior, being more abundant when conditions were adverse but disappearing as soon as environmental conditions were restored, probably by competition with more specialized taxa. Morphological characteristics indicate a probable semi-infaunal and endobyssate mode of life, similar to *Myalina* (Schubert, 1993). Posenato (2008a) suggested an epibyssate mode of life.

Mineralogy.—Bimineralic (McRoberts & Newell, 2005). No data are available for shell mineralogy or microstructure of the species of this genus. We use data for the family Myalinidae (see McRoberts & Newell, 2005). Outer shell layer: calcite (prismatic-homogeneous). Inner shell layer: aragonite (nacreous).

Genus AVICULOMYALINA Assmann, 1916, p. 608

Type species.—*Aviculomyalina lata* Assmann, 1916, p. 608.

Remarks.—Both McRoberts (2005) and Waller (in Waller & Stanley, 2005) pointed out that *Aviculomyalina* could be better located within the Pteriidae or Malleidae. We keep it in Myalinidae until this matter is adequately discussed.

Stratigraphic range.—Middle Triassic (Anisian) (Cox & others, 1969). Assmann (1916) described the genus from the Lower Muschelkalk (probably Anisian), in the “Erzführender Dolomit” Formation of Silesia. Other authors also reported it from Anisian beds (Malinowskij, 1979; Sepkoski, 2002). The range of this genus could be extended to Carnian and Norian if *Aviculomyalina? williamsi* (McLearn, 1941) were considered to belong to this genus, as proposed by Waller (in Waller & Stanley, 2005), rather than to *Mysidioptera* as proposed by Newton (in Newton & others, 1987).

Paleogeographic distribution.—Tethys (Fig. 11).

Tethys domain: Middle Triassic: Anisian of Poland (Assmann, 1916; Malinowskij, 1979), Alps (?Switzerland) (Zorn, 1971).

Paleoautoecology.—B, E, S, Epi, Sed; By. An epibyssate mode of life is suggested by some shell features, such as the external shell morphology, the presence of byssal gape, and the flattened anterior margin (Newton in Newton & others, 1987).

Mineralogy.—Bimineralic. There is no information about *Aviculomyalina* shell mineralogy or microstructure, but we regard it equivalent to *Promyalina*.

Family INOCERAMIDAE Giebel, 1852

The family Inoceramidae is especially problematic, due partly to its great morphological variability, and partly to the lack of consensus among specialists about the taxonomically significant characters. It is often difficult to discern between the different genera assigned to this family because, if internal characters are not shown, the external

shape is extremely variable, even within species (Crame, 1982). This is the consequence of convergent evolution resulting from functional and ecological constraints, the presence of few easily distinguishable characters, the great variability within species, and also the high evolutionary rates they exhibit. As a result, the group has a rich fossil record with a long history but with the serious drawback of a wide disparity of concepts used by successive specialists (Harries & Crampton, 1998).

Genus "PARAINOCERAMUS" Cox, 1954, p. 47

ex Voronetz, 1936, p. 23, 34, nom. nud.

Type species.—*Parainoceramus bulkuriensis* Voronetz, 1936, p. 24, 34.

Remarks.—The generic name *Parainoceramus* was proposed by Voronetz (1936, p. 23, 34) on the basis of badly preserved specimens from sediments then dated as Carnian from northern Siberia. The author included four species in this new genus, but he did not designate a type, and thus this name was not available. Years later, Cox (1954) completed the requirements for the validity of the name by designating *P. bulkurensis* Voronetz as the type (ICZN, 1999, Art. 13B, 50). He did not see Voronetz's material, but, nevertheless, he included within *Parainoceramus* two other species that are widely distributed in the European Jurassic: "*Crenatula ventricosa*" J. de C. Sowerby, 1823, and *Inoceramus substriatus* Münster, 1835, in Goldfuss, 1833–1841. On the basis of his knowledge of these last species, he emended Voronetz's original diagnosis to include an anterior auricle and anterior teeth on some species. Cox's (1954) concept of the genus *Parainoceramus* was followed by nearly all later authors dealing with Jurassic material (e.g., Hayami, 1960; Speden, 1970; Duff, 1978; Damborenea, 1987b; J. Chen, 1988; M. A. Conti & Monari, 1991; Monari, 1994), who added more Jurassic species from around the world. Nevertheless, it is all too evident that this was reluctantly done in many instances, in the absence of a better alternative. Another point overlooked in the *Treatise* (Cox & others, 1969, p. 320) and by later authors is that Emel'yantsev and others (1960; see also Muromtseva, 1979; and Astafieva, 1986) had redated the beds where Voronetz's original material was found to be upper Permian (Wuchiapingian and Changhsingian), and thus the stratigraphic range of *Parainoceramus sensu* Cox (1954) should be upper Permian (Siberia), Hettangian to Tithonian (cosmopolitan), with no record during the Triassic. A breakthrough was provided by Astafieva (1986, 1993), who revised Voronetz's original material and concluded that the type species should be referred to the Paleozoic genus *Kolymia* Licharew in Licharew & Einor, 1941. Thus, several widely distributed and common Jurassic species (*Parainoceramus sensu* Cox *non* Voronetz) remain without a genus to be referred to. We will provisionally use here the name "*Parainoceramus*" in this sense, until a proper solution is developed (Ros, Damborenea, & Márquez-Aliaga, 2009), and we record its first appearance in the earliest Jurassic. When the material is not well preserved, it is difficult to distinguish between *Parainoceramus* in this sense and *Pseudomytiloides* Koschelkina, 1963 (Aberhan, 1998a; Stiller, 2006).

Stratigraphic range.—Lower Jurassic (Hettangian)–Upper Jurassic (Tithonian) (Escobar, 1980; Kelly, 1984). Both Cox and others (1969) and Sepkoski (2002) regarded the first appearance of "*Parainoceramus*" to be Upper Triassic following Voronetz (1936),

ignoring that Emel'yantsev, Kravtsova, and Puk (1960) had already corrected the dating of the beds from which Voronetz described his specimens from Carnian to upper Permian. We assign the Lower Jurassic (Hettangian) as the oldest record (Escobar, 1980; Damborenea, 1996a), taking into account only the species assigned to this genus *sensu* Cox (1954). The youngest record is from the Tithonian (Kelly, 1984; Fozy, Kázmér, & Szente, 1994; Liu, 1995).

Paleogeographic distribution.—Tethys, Boreal, and Circumpacific (Fig. 12). "*Parainoceramus*" was cosmopolitan during the Early Jurassic (especially during the Pliensbachian), but during the Middle and Late Jurassic, it appears to have had a bipolar distribution (possibly Boreal and Austral domains) (Damborenea, 1996b). For further information, see Damborenea (1987b, p. 142–146).

Tethys domain: Early Jurassic: Tibet (Gou, 1985), China (J. Chen, 1982a, 1988); Hettangian of Vietnam (Hayami, 1964); Hettangian–Sinemurian of China (Stiller, 2006); Sinemurian of southern England (Liu, 1995), Turkey (M. A. Conti & Monari, 1991), China (Y. Wang & Smith, 1986).

Boreal domain: Early Jurassic: Sinemurian of northern Siberia (Hallam, 1977).

Circumpacific domain: Early Jurassic: Japan (Hayami, 1960); Hettangian–Sinemurian of Canada (Aberhan, 1998a); Hettangian of Chile (Escobar, 1980).

Paleoautoecology.—B, E, S, Epi, Sed; By. The shell morphology of species attributed to "*Parainoceramus*" is variable, and it largely depends on the type of environment. Some species, such as "*P. jinjiensis*" Chen, 1988, or "*P. subtilis*" (Lahusen), are mytiliform, and they were probably epibyssate (Duff, 1978; Stiller, 2006), but other species, such as "*P. apollo*" (A. F. Leanza, 1942), are modioliform with a well-developed anterior lobe, and they possibly had an endobenthic mode of life (Damborenea, 1987b). Other genera of the same family, such as *Pseudomytiloides*, were interpreted as pseudoplanktonic, at least in the early stages (Hayami, 1969a; Etter, 1996). "*Parainoceramus*" species are found in a wide array of facies types, since they could inhabit different environments, but they are especially abundant in anoxic facies (black shales) (Damborenea 1987b; Harries & others, 1996).

Mineralogy.—Biminerale (Carter, 1990a, p. 200; Carter, 1990b, p. 330). Outer shell layer: calcite (prismatic). Middle and inner shell layers: aragonite (nacreous).

Genus PSEUDOMYTILOIDES Koschelkina, 1963, p. 129

Type species.—*Mytiloides marchaensis* Petrova, 1947, p. 130.

Stratigraphic range.—Lower Jurassic (Hettangian)–Middle Jurassic (Aalenian) (Etter, 1996; Stiller, 2006). Cox and others (1969) assigned a Jurassic range to this genus. The oldest record is from Hettangian deposits (Stiller, 2006) and the youngest from Aalenian beds (Etter, 1996). The genus was also mentioned from the Upper Triassic (Norian–Rhaetian) of northeastern Asia (Kurushin, 1990; Polubotko & Repin, 1990), but without indication of the original sources and with no illustrations, so these records remain doubtful.

Paleogeographic distribution.—Tethys (Fig. 12). This genus was especially abundant during the Toarcian. During the earliest Jurassic, it was only reported from the Tethys; but it was also recorded from the Boreal domain by Pliensbachian and Toarcian times (Zakharov & others, 2006). Poulton (1991) reported *Pseudomytiloides* (?) sp.

from ?Hettangian beds of Canada, but it was only one specimen questionably referred to this genus.

Tethys domain: Early Jurassic: Hettangian–Sinemurian of China (Stiller, 2006); Sinemurian of southwestern France (Liu, 1995).

Paleoautoecology.—B-Ps, E, S, Epi, Sed-FaM; By. *Pseudomytiloides dubius* (J. de C. Sowerby, 1823) is particularly linked to the black shale facies, associated with anoxic conditions, since its abundance decreases as soon as the normal environmental conditions are restored after the early Toarcian extinction event (Harries & Little, 1999; Fürsich & others, 2001; Caswell, Coe, & Cohen, 2009). A pseudoplanktonic mode of life was proposed for this species and *P. matsumotoi* (Hayami, 1960) (Hayami, 1969a; Tanabe 1983; Seilacher, 1990). This was based on many forms of evidence: they are often found in anoxic facies (Hayami, 1969a), attached to pieces of wood (Hayami, 1969a; Tanabe 1983; Seilacher, 1990), and to ammonoid shells and other bivalves (Tanabe, 1983). However, some authors (e.g., Wignall & Simms, 1990; Etter, 1996) suggested that this interpretation is inadequate since the species abundance is too high to be derived only from floating logs. They proposed that *P. dubius* had a benthic epibyssate mode of life instead, but it could occasionally live as facultative pseudoplanktonic, with the capacity to attach to various substrates, such as floating objects, and tolerate low oxygen environments (see also Caswell, Coe, & Cohen, 2009). Some authors proposed that certain species of *Pseudomytiloides* might contain chemosymbionts that would help them live in these inhospitable settings (Harries & Crampton, 1998). Other species, such as *P. yinhangensis* Chen, 1988, were found in well-oxygenated, quiet, and near-shore environments (Stiller, 2006). The epibyssate mode of life is clearly suggested by their mytiliform shells and their long and flat anteroventral margin (Tanabe, 1983).

Mineralogy.—Bimineralic (Carter, 1990a, p. 200). There are no specific data for *Pseudomytiloides*. Data used here provided by Carter (1990a) for family Inoceramidae. Outer shell layer: calcite (prismatic). Middle and inner shell layers: aragonite (nacreous).

Genus ARCTOMYTILOIDES Polubotko, 1992, p. 64

Type species.—*Pseudomytiloides rassocheensis* Polubotko, 1968b, p. 61.

Stratigraphic range.—Lower Jurassic (Sinemurian–?Toarcian) (Aberhan, 1998a). The genus was described by Polubotko (1992). It was reported from the Sinemurian of northeastern Russia, and it includes the following species besides the type: *A. sinuosus* (Polubotko, 1968b), *A. kelimiarensis* Polubotko, 1992, and *A. (?) turomtchensis* Polubotko, 1992. Subsequently, Aberhan (1998a) doubtfully reported it from Toarcian beds.

Paleogeographic distribution.—Boreal and Circumpacific (Fig. 12).

Boreal domain: Early Jurassic: Sinemurian of northeastern Russia (Polubotko, 1968b, 1992).

Circumpacific domain: Early Jurassic: Sinemurian–Toarcian of ?Canada (Aberhan, 1998a).

Paleoautoecology.—B, E, S, Epi, Sed; By. Its mytiliform shell indicates an epibyssate mode of life, similar to some living species of the family Mytilidae.

Mineralogy.—Bimineralic (Carter, 1990a, p. 200). No data about *Arctomytiloides* shell mineralogy and microstructure are available. Data provided for the family Inoceramidae (see any genera in this family).

Superfamily PTERIOIDEA Gray, 1847

Family PTERIIDAE Gray, 1847

Genus PTERIA Scopoli, 1777, p. 397

Type species.—*Mytilus hirundo* Linnaeus, 1758, p. 706.

Remarks.—*Pteroperna* Morris & Lycett, 1853 in 1851–1855, is a subgenus, and *Rhynchopterus* Gabb, 1864, is a junior synonym of *Pteria* s.l. (see discussion for *Pteroperna* and *Rhynchopterus* in Genera not Included, p. 169 and 170).

Stratigraphic range.—Lower Triassic (Olenekian)–Holocene (Hayami, 1975; Beesley, Ross, & Wells, 1998). *Pteria* ranges from Triassic to Holocene times (Cox & others, 1969; Sepkoski, 2002). The earliest record found is *P. ussurica* (Kiparisova, 1938) from the Induan (Hayami, 1975). There are some pre-Triassic records (see PBDB, on-line), but most of them were published before Cox and others (1969). M. Wang (1993) described *Pteria? yonganensis* M. Wang, 1993, from upper Permian beds, but the generic assignment was only tentative, since he had few specimens and their differences with *Pteria* were important. Tëmkin (2006) doubted the origin of *Pteria* in the Early Triassic because many so-called winged shells that probably belong to other families (even Bakevelliidae or Isognomonidae) were referred to this genus.

Paleogeographic distribution.—Tethys, Circumpacific, and Boreal (Fig. 13). In the past, *Pteria* was a widespread genus; today it is common in warm seas (Cox & others, 1969; Beesley, Ross, & Wells, 1998), and was apparently not known from the Austral domain.

Tethys domain: Early Triassic: China (Z. Yang & Yin, 1979; S. Yang, Wang, & Hao, 1986; Ling, 1988; L. Li, 1995; Shen, He, & Shi, 1995; Tong & others, 2006; Komatsu, Huyen, & Chen, 2007); Middle Triassic: Anisian of the Alps (Switzerland) (Zorn, 1971), southern China (Komatsu, Chen, & others, 2004; Komatsu, Akasaki, & others, 2004); Anisian–Ladinian of northern Vietnam (Komatsu, Huyen, & Huu, 2010); Late Triassic: Carnian of Italy (Allasinaz, 1966; Fürsich & Wendt, 1977; Corazzari & Lucchi-Garavello, 1980), Germany (Linck, 1972); Norian of China (Lu, 1981); Norian–Rhaetian of Iran (Hautmann, 2001b); Rhaetian of Italy (Allasinaz, 1962; Gelati & Allasinaz, 1964; Gaetani, 1970); Early Jurassic: Hettangian of Italy (Allasinaz, 1962), China (J. Yin & McRoberts, 2006); Hettangian–Sinemurian of Italy (Gaetani, 1970); Sinemurian of eastern Asia (Hallam, 1977), Portugal (Liu, 1995).

Circumpacific domain: Early Triassic: Japan (Nakazawa, 1971; Hayami, 1975; Kashiyama & Oji, 2004); Late Triassic: Norian of Japan (Nakazawa, 1964); Early Jurassic: Hettangian of Japan (Hayami, 1975; Kondo & others, 2006; Fraiser & Bottjer, 2007a), ?Chile (Aberhan, 1994a).

Boreal domain: Late Triassic: Carnian of Primorie (Kiparisova, 1972).

Paleoautoecology.—B, E, S, Epi, Sed; By. Extant *Pteria* species often live attached to corals, usually by a strong byssus (S. M. Stanley, 1970, 1972). In many fossil specimens, the byssal notch is present (e.g., Damborenea, 1987b, *Pteroperna* sp.) and the shell morphology is similar enough to living species shells to assume they had a similar mode of life. They are often found forming groups of several individuals, probably as the result of a gregarious mode of life, as happens in modern species (S. M. Stanley, 1970).

Mineralogy.—Bimineralic (Carter, 1990b, p. 336, for living species). Outer shell layer: calcite (simple prismatic). Middle and inner shell layers: aragonite (nacreous).

Genus ARCAVICULA Cox, 1964, p. 47

Type species.—*Avicula arcuata* Münster in Goldfuss, 1835 in 1833–1841, p. 128.

Stratigraphic range.—Lower Triassic (lower Olenekian)–Upper Triassic (?Rhaetian) (Sha & Grant-Mackie, 1996; Newton in Newton & others, 1987). Although many authors assigned it a Middle Triassic (Ladinian)–Upper Triassic (Carnian) range (Cox & others, 1969; Hallam, 1981; Sepkoski, 2002; Tëmkin, 2006), *Arcavicula* was also mentioned from the Lower Triassic (Sha & Grant-Mackie, 1996) and with some uncertainty from the Norian (Newton in Newton & others, 1987). Newton (in Newton & others, 1987) provisionally referred her specimens to *Arcavicula* sp. due to the hinge details, but she related them to *Rhaetavicula* on account of their external similarity. It is also evident that some species were attributed to *Pteria* regardless of their internal characters. Newton (1988) later confirmed this reference. Laws (1982) mentioned but did not figure *Arcavicula* sp. from Upper Triassic (upper Norian = Rhaetian, according to Dagens & Dagens, 1994) from Nevada. There are no specific Middle Triassic *Arcavicula* records, although several authors (e.g., Cox & others, 1969; Hallam, 1981; Sepkoski, 2002; Tëmkin, 2006) mentioned this genus among their materials.

Paleogeographic distribution.—Tethys and Circumpacific (Fig. 13).

Tethys domain: Early Triassic: early Olenekian of China (Sha & Grant-Mackie, 1996); Late Triassic: Carnian of southern Alps and Apennines (Italy) (Broglia-Loriga, Ietto, & Posenato, 1993), Alps and Sicily (Diener, 1923; Kutassy, 1931), early Carnian of Lombardy (Italy) (Allasinaz, 1966), southern Alps (Italy) (Bittner, 1895); Norian of ?China (Kobayashi & Tamura, 1983a).

Circumpacific domain: Late Triassic: Norian of Oregon (United States) (Newton & others, 1987; Newton, 1988); Rhaetian of ?Nevada (United States) (Laws, 1982).

Paleoautoecology.—B, E, S, Epi, Sed; By. The presence of anterior auricle and byssal sinus in some specimens, and their external morphology, indicate that species of this genus most likely lived epibyssate or shallowly buried in the sediment in the adult stage, by comparison with living Pterioidea (Newton in Newton & others, 1987).

Mineralogy.—Bimineralic (Carter, 1990b, p. 335). Outer shell layer: calcite (simple prismatic). Middle and inner shell layers: aragonite (nacreous).

Genus RHAETAVICULA Cox, 1962, p. 594

Type species.—*Avicula contorta* Portlock, 1843, p. 126.

Remarks.—Cox (1962) pointed out the similarities between *Rhaetavicula* and *Oxytoma*, and he proposed that *Rhaetavicula* could even be a member of the family Oxytomidae, but *Rhaetavicula* lacks the deep byssal groove located under the right anterior auricle, which is typical of that family. Based on the information provided by the shell mineralogy of *Rhaetavicula* (calcitic outer layer and alleged aragonitic inner layer), it is probably referable to Pteriidae. Nevertheless, if further studies confirm an inner calcitic layer, it should be referred to the Oxytomidae instead (Cox, 1962). There are no

studies on this subject (Carter, 1990a). Previous to 1962, when Cox described this genus, the type species of *Rhaetavicula* was assigned to different genera: *Avicula*, *Pseudomonotis*, *Cassianella*, and *Pteria*.

Stratigraphic range.—Upper Triassic (Rhaetian). *Rhaetavicula contorta* is a Rhaetian guide fossil (see references in paleogeographic distribution). During that stage, it was widely distributed, especially in the Tethys domain.

Paleogeographic distribution.—Tethys and Circumpacific (Fig. 13). Though *Rhaetavicula* was reported from the Austral domain (New Zealand), Cox (1962, p. 594) referred this record to *Oxytoma*. Although Hallam (1981, 1990) also listed it from Austral regions, the record will not be taken into account here because this information could not be confirmed.

Tethys domain: Late Triassic: Rhaetian of England (Cox, 1962; Castell & Cox, 1975; Warrington & Ivimey-Cook, 1990; Ivimey-Cook & others, 1999; Wignall & Bond, 2008), Italy (Allasinaz, 1962; Sirna, 1968; Bice & others, 1992; McRoberts, 1994), Hungary (Vörös, 1981), Burma (Vu Khuc & Huyen, 1998), southern Tibet (Hallam & others, 2000; J. Yin & Enay, 2000), Iran (Hautmann, 2001b), western Carpathians (Slovakia) (Tomašových, 2004; Michalik & others, 2007), Alps (Austria) (Tomašových, 2006a, 2006b; McRoberts, 2010), Spain (Goy & Márquez-Aliaga, 1998).

Circumpacific domain: Late Triassic: Rhaetian of Nevada (United States) (Cox & others, 1969; Hallam & Wignall, 2000).

Paleoautoecology.—B, E, S, Epi-Un, Sed; By-R. According to Cox (1962), *Rhaetavicula* lacked a byssal notch, and he assumed that the byssus emerged between the two valves by a narrow gape. Since the shell is strongly inequivalve (convex left valve and flat right valve) and by similarities to living Pterioidea, it probably had an epibyssate mode of life. Another possibility is that the byssus was atrophied in adults (and thus the byssal notch is absent), and then it would live reclined on its left valve, similar to members of the family Cassianellidae (Hautmann, 2001b).

Mineralogy.—Bimineralic (Carter, 1990a, p. 206). Outer shell layer: calcite (prismatic). Middle and inner shell layers: aragonite (?).

Genus STEFANINIA Cox in Cox & others, 1969, p. 306

[ex Venzo, 1934, p. 165]

Type species.—*Gervilleia? ogilviae* Bittner, 1895, p. 88.

Remarks.—*Stefaninia* was named by Venzo (1934), but his description did not fulfill the nomenclatorial rules (ICZN Code, 1999), since no type species was assigned and no diagnostic features were given (Stenzel, 1971, p. 1215). Cox in Cox and others (1969, p. 306) designated the type species and provided its diagnosis.

Stratigraphic range.—Middle Triassic (upper Ladinian)–Upper Triassic (Carnian). Bittner (1895) described the type species from the Saint Cassian Formation, regarded as Carnian in age (Fürsich & Wendt, 1977). Cox and others (1969) assigned a Ladinian age, probably on the basis of Venzo's paper (1934; see above).

Paleogeographic distribution.—western Tethys (Fig. 13).

Tethys domain: Middle Triassic: late Ladinian of Italy (Cox & others, 1969); Late Triassic: Carnian of Italy (Bittner, 1895).

Paleoautoecology.—B, E, S, Epi, Sed; By. Its external morphology and the presence of byssal notch indicate a probable byssate mode of life. Possibly, like other members of the family, it spent the early

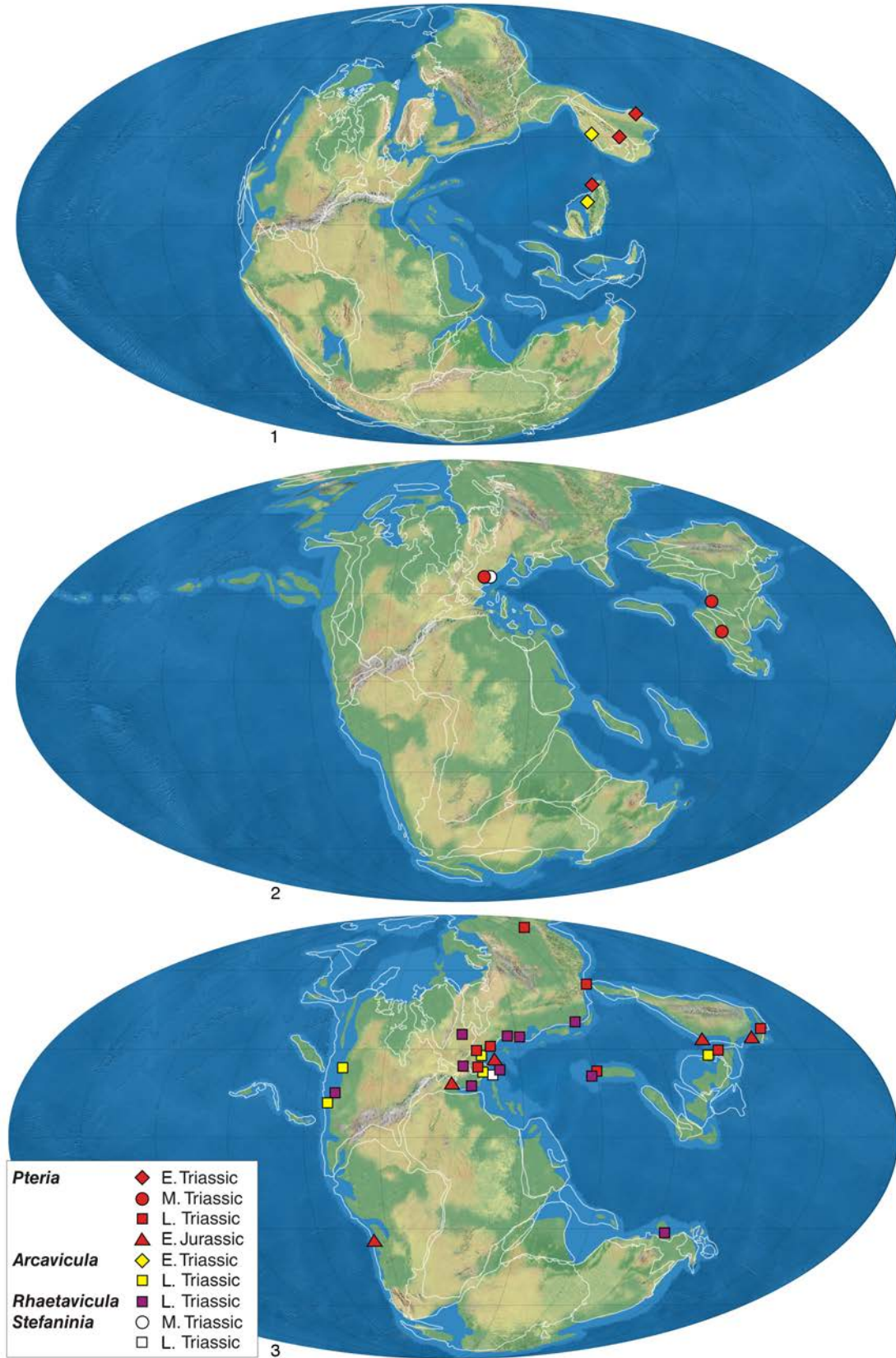


Figure 13. Paleogeographical distribution of Pteriidae (*Pteria*, *Arcavicula*, *Rhaetavicula*, *Stefania*). 1, Early Triassic; 2, Middle Triassic; 3, Late Triassic–Early Jurassic.

stages of development fixed by the byssus, but adults could have lived partially buried in the sediment. There is no information about the type of sediment in which it was found.

Mineralogy.—Bimineralic (Carter, 1990a, p. 206). There is no information about *Stefaninia* shell mineralogy or microstructure. We use data provided for the family Pteriidae. Outer shell layer: calcite (simple prismatic). Middle and inner shell layer: aragonite (nacreous).

Family BAKEVELLIIDAE King, 1850
Genus BAKEVELLIA King, 1848, p. 10

Neave (1939, p. 385) lists “Miller, 1877, p. 185, *pro Bakewellia* King, 1848” as author of the genus. Nevertheless, Miller (1877, p. 185) did not indicate he was proposing either an emendation or a replacement name, and already in 1850 King (p. 166–171, 255) spelled it consistently as *Bakevellia*, although he stated (p. 166, footnote) that the name was dedicated to Mr. Bakewell.

Type species.—*Avicula antiqua* Münster in Goldfuss, 1835 in 1833–1841, p. 126, *non* DeFrance, 1816.

Remarks.—Several subgenera were proposed within *Bakevellia* (see Damborenea, 1987b, p. 125–126), but Muster (1995) regarded almost all to be synonyms, considering only two of them to be valid, as also did Cox and others (1969): *B. (Bakevellia)* King, 1848, and *B. (Bakevellioides)* Tokuyama, 1959a. The subgenera described for our study interval were *Neobakevellia* Nakazawa, 1959, *Integribakevellia* Farsan, 1972, *Costibakevellia* Farsan, 1972, and *Spia* Skwarko, 1981 (see list of synonyms for both subgenera in Muster, 1995, p. 29, 42).

Stratigraphic range.—upper Permian–Upper Cretaceous. Cox and others (1969) assigned it a Permian–Upper Cretaceous range. Muster (1995) maintained this range, noting that the first record of the genus is dated as upper Permian. Sepkoski (2002) considered the oldest record to be Carboniferous, but we will not take this into account, since it is based on a personal communication by Yancey to Sepkoski (indicated in Sepkoski, 2002), which has not been published.

Paleogeographic distribution.—Cosmopolitan.

Paleoautoecology.—B, Se, S, Endo, Sed; By. The mode of life of bakevelliids is difficult to identify as that they do not have living representatives to compare with, and the study of the morphology alone does not always provide good results, because morphology traits are sometimes contradictory. It is also helpful to interpret the paleoecology of the environments in which the specimens are found. Most species assigned to *Bakevellia* are almost equivalve, they have a shallow byssal sinus and an anterior lobe, features that indicate an endobyssate way of life, living with the sagittal plane almost vertical (S. M. Stanley, 1972). This interpretation was proposed by Damborenea (1987b) for *Bakevellia (Neobakevellia?) pintadae* Damborenea, 1987b, and by Aberhan and Muster (1997) for *Bakevellia (Bakevellia) waltoni* (Lycett, 1863). However, Seilacher (1984) interpreted *Bakevellia subcostata* (Goldfuss, 1835 in 1833–1841) as reclined and partially buried in the sediment, resting on its left valve, with the commissure plane being almost horizontal.

Mineralogy.—Bimineralic (Márquez-Aliaga & Martínez, 1990a; Carter, 1990b). Outer shell layer: calcite (simple prismatic). Middle and inner shell layers: aragonite (nacreous).

Genus GERVILLELLA Waagen, 1907, p. 98

Type species.—*Perna aviculoides* J. Sowerby, 1814, p. 147.

Remarks.—Fürsich and Werner (1988, p. 112) argued that there are no substantial differences between *Gervillia* DeFrance, 1820, and *Gervillella* to consider them as independent taxa, and they included *Gervillella* as a subgenus of *Gervillia*. We follow Freneix (1965) and Muster (1995) in treating them as separated genera.

Stratigraphic range.—Lower Jurassic (Hettangian)–Upper Cretaceous (?) (Aberhan, 1998a; Muster, 1995). Several authors extended the range back to the Triassic (e.g., Gillet, 1924; Hayami, 1957a; Freneix 1965; Cox & others, 1969; Geyer, 1973; Lazo, 2003), but none of them justified this statement, and they did not figure any Triassic specimens. All except Geyer (1973) simply listed the stratigraphic range of several genera. Geyer mentioned the presence of *Gervillella* sp. from the Norian Payandé Formation in Colombia, but he did not figure it. It is possible that some Triassic species assigned to *Gervillia* should be referred to *Gervillella* instead, but there is no published reference of their presence in this period. The oldest confirmed record dates from the Hettangian (Aberhan, 1998a), and the youngest from the Upper Cretaceous (Muster, 1995). Sepkoski (2002) assigned the last appearance to the Maastrichtian, but it was not possible to see the original data source. Muster (1995) did not specify the stage, and there is no further information about this topic. However, it is not uncommon to find the genus mentioned from the Lower Cretaceous (Lazo, 2003, 2007a).

Paleogeographic distribution.—western Tethys, Austral, and Circumpacific (Fig. 14). The genus had a particularly wide distribution mainly during the Middle and Late Jurassic (Vörös, 1971; Fürsich & Werner, 1988; Liu, 1995; Muster, 1995; Sha & Grant-Mackie, 1996; Delvene, 2003; Sha, Johnson, & Fürsich, 2004).

Tethys domain: Early Jurassic: Hettangian–Sinemurian of England and Morocco (Liu, 1995).

Austral domain: Early Jurassic: Hettangian–Sinemurian of Southern Andes (Damborenea, 1996a; Damborenea & Lanés, 2007).

Circumpacific domain: Early Jurassic: Hettangian–Sinemurian of Canada (Aberhan & Muster, 1997; Aberhan, 1998a); Sinemurian of Chile (Aberhan, 1994a).

Paleoautoecology.—B, Se, S, Endo, Sed; By. Like most bakevelliids, *Gervillella* presents features that indicate a semi-infaunal endobyssate mode of life (S. M. Stanley, 1972; Aberhan & Muster, 1997) or so-called mud-sticker (Seilacher, 1984). All species assigned to this genus are almost equivalve, they possess an anterior auricle, and their external morphology is elongate spear-shaped. Thanks to its elongated shape, *Gervillella* could probably bury deeper than other bakevelliids (S. M. Stanley, 1972; Aberhan & Muster, 1997), similar to members of the family Pinnidae (S. M. Stanley, 1972). Although neither Damborenea (1987b) nor Aberhan and Muster (1997) found evidence in their specimens of a byssal notch, according to Cox (1940), one of the characters that defines the genus is that the anterior auricle extends anteroventrally and is limited in the left valve by a deep groove, which indicates the position of the byssus.

Mineralogy.—Bimineralic (Carter, 1990a, p. 207; Carter, 1990b, p. 336). Outer shell layer: calcite (simple prismatic). Middle and inner shell layers: aragonite (nacreous).

Genus GERVILLIA DeFrance, 1820, p. 502

Type species.—*Gervillia solenoidea* DeFrance, 1824a, p. 316.

Stratigraphic range.—Middle Triassic (Ladinian)—Upper Cretaceous (Maastrichtian) (Lerman, 1960; Abdel-Gawad, 1986). Both Cox and others (1969) and Muster (1995) indicated its range as beginning at the Upper Triassic, but there are Middle Triassic records of *Gervillia*, referred to the species *G. joleaudi* (Schmidt, 1935) from the Anisian of Israel (Lerman, 1960) and Ladinian of Spain (Márquez-Aliaga, 1985). These were not included in Muster's monograph (1995), but Waller and Stanley (2005) indicated that the generic assignation of this species requires revision. However, these authors based their opinion, exposed in the discussion of their new subgenus *Gervillaria* (*Baryvella*), in data from Schmidt (1935), who compared *G. joleaudi* with *Gervillia alberti* Credner, 1851. According to Márquez-Aliaga (1985), this last species is a true *Bakevella*; therefore, *Gervillia joleaudi* should be considered as a representative of *Gervillia* from the Sephardic province of the Tethys domain. With regard to the uppermost stratigraphic occurrence, all agreed that the genus disappeared in the Upper Cretaceous. Within our study interval, we will only consider the subgenus *Cultripsopsis* Cossmann, 1904. Boyd and Newell (1979) doubtfully assigned some of their specimens from the Permian of Tunisia to this subgenus.

Paleogeographic distribution.—Tethys and Circumpacific (Fig. 14). Although Escobar (1980) reported *Gervillia* from Hettangian–Sinemurian beds of Chile, only one of the specimens could be attributed with doubt to this genus (Damborenea, 1987b), so it will not be taken into account in the Austral domain in this temporal range. If the genus is present in this domain, it has occurred since the Pliensbachian.

Tethys domain: Middle Triassic: Anisian of Israel (Lerman, 1960); Ladinian of Spain (Márquez-Aliaga, 1983, 1985; Márquez-Aliaga, Hirsch, & López-Garrido, 1986; Márquez-Aliaga & Martínez, 1990a, 1996; Budurov & others, 1991; Márquez-Aliaga & Montoya, 1991; Martínez & Márquez-Aliaga, 1994; Niemeyer, 2002; Márquez-Aliaga & Ros, 2003); Late Triassic: China (Muster, 1995); Carnian of Italy (Fürsich & Wendt, 1977; Muster, 1995), Spain (Martín-Algarra & others, 1993), Slovenia (Jurkovsek, 1978), China (Wen & others, 1976); Norian–Rhaetian of Iran (Hautmann, 2001b); Rhaetian of Austria (Tanner, Lucas, & Chapman, 2004); Early Jurassic: early Hettangian of Tibet (China) (J. Yin & McRoberts, 2006); Hettangian–Sinemurian of Vietnam (Sato & Westermann, 1991).

Circumpacific domain: Late Triassic: Japan (Muster, 1995); Carnian of Japan (Tamura & others, 1978); Norian of Oregon (Newton, 1986; Newton & others, 1987); Early Jurassic: Hettangian of Japan (Hayami, 1957a, 1964, 1975; Muster, 1995).

Paleoautoecology.—B-Ps, Se-E, S, Endo-Epi, Sed; By. Some species of *Gervillia* are morphologically similar to species of *Gervillella* and *Gervillancea* (see discussion on their mode of life, p. 40, 44). These two genera are interpreted as having a semi-infaunal endobryssate mode of life (Waller & Stanley, 2005). Formerly, Muster (1995) regarded this mode of life to be unlikely for *Gervillia*, since it had a very short ligament area that would not be enough to maintain the shell stability. Seilacher (1984) suggested a pseudoplanktonic mode of life for some species of *Gervillia*, as epibryssate on ammonoids. He called these forms pendent forms. However, other species of *Gervillia* were interpreted as semi-infaunal endobryssate or mud-stickers (Seilacher, Matyja, & Wierzbowski, 1985). These interpretations are

based on the external shell morphology and on the ecological analysis of the depositional environment in which the specimens were found (see Seilacher, 1984; Seilacher, Matyja, & Wierzbowski, 1985). In the Muschelkalk of the Iberian Range (Spain), specimens recorded in marls are common, and they are usually found in semi-infaunal life position. Newton (in Newton & others, 1987) and Damborenea (1987b) interpreted their specimens as epibryssate, but they noted that the shells also had features indicative of a semi-infaunal habit. These are usually found associated with corals.

Mineralogy.—Bimineralic (De Renzi & Márquez-Aliaga, 1980; Carter, 1990a; Márquez-Aliaga & Martínez, 1990a; Martínez & Márquez-Aliaga, 1994). Outer shell layer: calcite (simple prismatic). Middle and inner shell layers: aragonite (nacreous).

Genus HOERNESIA Laube, 1866, p. 52

Type species.—*Mytulites socialis* Schlotheim, 1823 in 1822–1823, p. 112.

Stratigraphic range.—Lower Triassic (Olenekian)—Upper Triassic (Rhaetian) (Hallam, 1981; Dagys & Kurushin, 1985). Cox and others (1969) indicated a Triassic–Middle Jurassic range, although some authors believed *Hoernesia* disappeared in the Rhaetian (Hallam, 1981, 1990; Hallam & others, 2000). However, Muster (1995, p. 89) extended its range to the Middle Jurassic, because she included *Gervillia radians* Morris & Lycett, 1853 in 1851–1885, in the synonymy list of *Hoernesia socialis* (Schlotheim, 1823 in 1822–1823); besides, she did not consider *Hoernesia* to be present in the Early Triassic. The first record of *Hoernesia* dates from the Early Triassic (Dagys & Kurushin, 1985; Posenato, 2008a).

Paleogeographic distribution.—Tethys and Boreal (Fig. 14).

Tethys domain: Early Triassic: Italy (Neri & Posenato, 1985), Yunnan (China) (Guo, 1985); Middle Triassic: Bulgaria (Stefanov, 1942; Encheva, 1969), Spain (Via, Villalta, & Esteban, 1977; Márquez-Aliaga, 1983, 1985; Márquez-Aliaga & Martínez, 1996; Márquez-Aliaga & others, 2001, 2002, 2004; Márquez-Aliaga & Ros, 2002), Italy (Posenato, 2002; Posenato & others, 2002), Germany (Fuchs & Mader, 1980; Hagdorn, 1982; Hagdorn & Simon, 1983, 1991), Poland (Senkowiczowa, 1985; Kaim, 1997), Hungary (Szente, 1997); Anisian of China (Sha, Chen, & Qi, 1990); Anisian–Ladinian of northern Vietnam (Komatsu, Huyen, & Huu, 2010); Ladinian of the Alps (Austria and Italy) (Arthaber, 1908), Germany (Ürlichs, 1978); Late Triassic: China (Cowper-Reed, 1927), Malaysia (Tamura & others, 1975); Carnian of Italy (Laube, 1865), Slovenia (Jurkovsek, 1978); Norian of China (Lu, 1981); Norian–Rhaetian of Iran (Hautmann, 2001b); Rhaetian of Burma (Healey, 1908), Iran (Repin, 2001), Tibet (J. Yin & Enay, 2000).

Boreal domain: Early Triassic: Olenekian of northern Siberia (Dagys & Kurushin, 1985).

Paleoautoecology.—B, Se, S, Endo, Sed; By. *Hoernesia* is characterized by a strongly inequivalve shell and twisted valves, and thus it was interpreted as a so-called twisted recliner by Seilacher (1984). It also has an umbonal shell thickening, so its life position consisted of this area being introduced into the sediment, with the posterior part of the valves sticking out (Savazzi, 1984; Seilacher, 1990; Muster, 1995). The inferred life position is similar to that of *Gervillaria alaeformis* (J. Sowerby, 1819) (see discussion about the mode of life

of this species, below). Seilacher (1990) suggested chemosymbiosis as a functional explanation for this curious life position.

Mineralogy.—Bimineralic (Carter, 1990b, p. 337). Outer shell layer: calcite (simple prismatic). Middle and inner shell layers: aragonite (nacreous).

Genus LANGSONELLA Patte, 1926, p. 139

Type species.—*Gervilleia (Cultrioopsis) elongata* Mansuy, 1919, p. 7.

Stratigraphic range.—Middle Triassic (Anisian)—Upper Triassic (Carnian) (Diener, 1923; Komatsu, Huyen, & Huu, 2010). Cox and others (1969) referred this genus to the Triassic without further explanation and indicated it is monospecific. According to Diener (1923), the type species was described by Mansuy from the Carnian of Tonkin, which today covers most of Vietnamese northern regions. Later, Vu Khuc and Huyen (1998) mentioned *L. elongata* (Mansuy, 1919) as being typical from Ladinian beds in the same area, and, recently, Komatsu, Huyen, and Huu (2010) reported it from the Anisian and Ladinian of northern Vietnam.

Paleogeographic distribution.—Eastern Tethys (Fig. 14).

Tethys domain: Middle Triassic: Anisian–Ladinian of northern Vietnam (Komatsu, Huyen, & Huu, 2010); Ladinian of Tonkin (north of Vietnam) (Vu Khuc & Huyen, 1998); Late Triassic: Carnian of Tonkin (Vietnam) (Diener, 1923).

Paleoautoecology.—B, Se, S, Endo, Sed; By. We did not find any figures of the genus; therefore, it is difficult for us to refer it to a particular mode of life, but according to its description in Cox and others (1969), we consider it to be similar to *Hoernesia*.

Mineralogy.—Bimineralic (Carter, 1990a, p. 206–207). There are no data on *Langsonella* shell structure. We used data provided for the family Bakevelliidae. Outer shell layer: calcite (simple prismatic). Middle and inner shell layers: aragonite (nacreous).

Genus CUNEIGERVILLIA Cox, 1954, p. 48

Type species.—*Gervillia hagenowii* Dunker, 1846, p. 37.

Remarks.—Cox (1954) described *Cuneigervillia* and included *Edentula* Waagen, 1907, p. 96 (*non* Nitzsch, 1820, p. 189) as its synonym. Later, in Cox and others (1969), he regarded *Edentula* [= *Waagenoperna* Tokuyama, 1959a, p. 151] as a separate genus and included it into the Isognomonidae. In turn, Tokuyama (1959a) proposed the name *Waagenoperna* to replace *Edentula* Waagen, 1907. He pointed to significant differences between the *Cuneigervillia* type species designated by Cox (1954) (*Gervillia hagenowii* Dunker, 1846) and some species attributed to *Edentula* (*E. lateplanata* Waagen, 1907, and *E. triangularis* Kobayashi & Ichikawa, 1952). He designated *Edentula lateplanata* as the type species of *Waagenoperna*, maintaining the two genera as distinct taxa, relating *G. hagenowii* to the Bakevelliidae and *E. lateplanata* and *E. triangularis* to the Isognomonidae. Muster (1995) decided to include *Cuneigervillia* with the Isognomonidae, believing that although *Cuneigervillia* externally seems to be a bakevelliid, it possesses certain characteristics that are typical of the Isognomonidae, such as terminal or subterminal beaks and a toothless adult hinge. It is difficult to decide because both families share many characteristics, but the lack of teeth in the adult stage is not a critical feature because it also occurs in certain bakevelliids; for example, in some species of *Bakevella* (*Bakevella*) the dentition is obsolete in adults (Cox & others, 1969, p. 306). The *Treatise*

diagnosis states “hinge teeth present at least in lower growth stages” Regarding the beaks, they can either be subterminal (e.g., *Aguilerella*) or terminal (e.g., *Gervillia*). Furthermore, *Cuneigervillia* presents the typical teeth of *Bakevella* in juvenile stages. Therefore, according to Cox and others (1969), we include *Cuneigervillia* in the Bakevelliidae.

Stratigraphic range.—Lower Jurassic (Hettangian)—Lower Cretaceous (?) (Cox & others, 1969). Cox and others (1969) assigned it a lower Liassic to Lower Cretaceous range, since Tokuyama (1959a) referred several Carnian species to *Waagenoperna* that were initially assigned by Cox (1954) to *Cuneigervillia*.

Paleogeographic distribution.—western Tethys (Fig. 14).

Tethys domain: Early Jurassic: Europe and northern Africa (Cox & others, 1969); Hettangian of France (Freneix & Cubaynes, 1984), south of England (Warrington & Ivimey-Cook, 1990), Spain (Gómez, Goy, & Márquez-Aliaga, 2005; Márquez-Aliaga, Damborenea, & Goy, 2008a, 2008b; Márquez-Aliaga & others, 2010); Hettangian–Pliensbachian of northwestern Europe (Hallam, 1987); Sinemurian of Portugal (Liu, 1995).

Paleoautoecology.—B, Se, S, Endo, Sed; By. *Cuneigervillia* was interpreted as a semi-infaunal endobryssate bivalve (S. M. Stanley, 1972), as were most members of Bakevelliidae.

Mineralogy.—Bimineralic (Carter, 1990a, p. 206–207). There are no data on *Cuneigervillia* mineralogy and shell microstructure. Data provided for the family Bakevelliidae are used here. Outer shell layer: calcite (simple prismatic). Inner shell layer: aragonite (nacreous).

Genus GERVILLARIA Cox, 1954, p. 49

Type species.—*Modiola? alaeformis* J. Sowerby, 1819, p. 93.

Stratigraphic range.—Middle Triassic (Anisian)—Upper Cretaceous (Turonian) (Komatsu, Chen, & others, 2004; Muster, 1995). Cox and others (1969) assigned this genus a Jurassic–Cretaceous range in Europe, but, since then, new records have extended its stratigraphic range. The oldest record is Anisian (Komatsu, Chen, & others, 2004) and the youngest is Turonian (Muster, 1995).

Paleogeographic distribution.—Tethys, Austral, and Circumpacific (Fig. 14).

Tethys domain: Middle Triassic: Muschelkalk of Germany (Muster, 1995); Anisian of Qingyan (southern China) (Komatsu, Chen, & others, 2004); Late Triassic: southwestern China (Komatsu, Chen, & others, 2004); Rhaetian of Lombardy (Italy) (Muster, 1995), Italian Alps and Vietnam (Hautmann, 2001b), western Carpathians (Slovakia) (Tomašových, 2004), Tibet (China) (J. Yin & Grant-Mackie, 2005); Norian–Rhaetian of Iran (Hautmann, 2001b).

Austral domain: Early Jurassic: Sinemurian of the Andean Basin (Aberhan & Fürsich, 1997); Hettangian–Sinemurian of the Andean Basin (Damborenea & Manceñido, 2005b).

Circumpacific domain: Middle Triassic: Ladinian of western Nevada (Waller & Stanley, 2005); Late Triassic: Norian of southeastern Sonora (Mexico) (McRoberts, 1997a); Early Jurassic: Sinemurian of ?western Canada (Aberhan, 1998a), Chile (Aberhan, 1994a).

Paleoautoecology.—B, Se, S, Endo, Sed; By. Some species, such as *Gervillaria alaeformis* (J. Sowerby, 1819) (Muster, 1995, fig. 37) and *Gervillaria pallas* (A. F. Leanza, 1942) (Damborenea, 1987b, fig. 7; Muster, 1995, fig. 43), have a strongly inequivalve and inequilateral shell, with the left valve being more convex

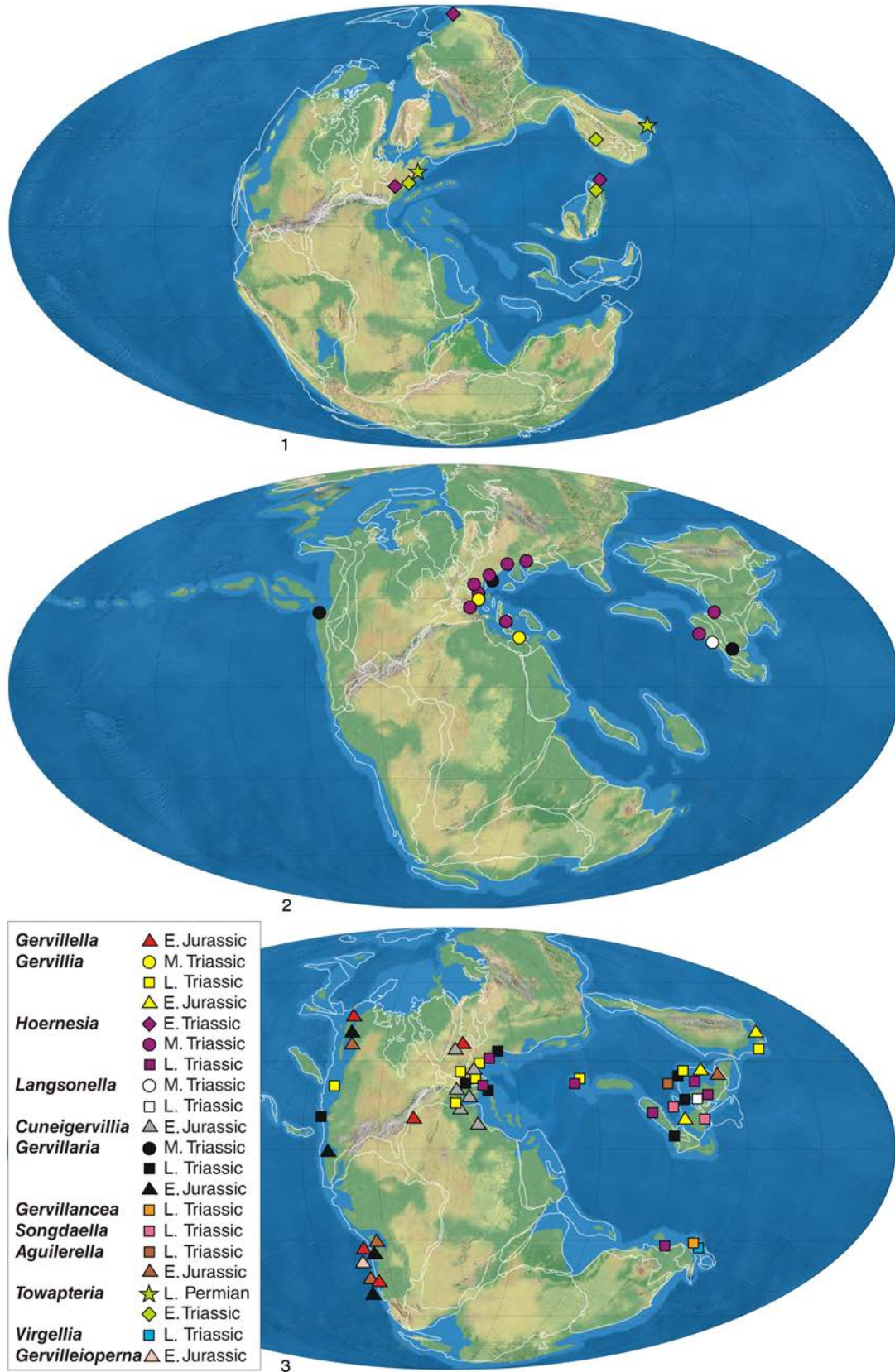


Figure 14. Paleogeographical distribution of Bakevelliidae (*Gervillella*, *Gervillia*, *Hoernesia*, *Langsonella*, *Cuneigervillia*, *Gervillaria*, *Gervillancea*, *Songdaella*, *Aguilerella*, *Towapteria*, *Virgellia*, *Gervilleioperna*). 1, Early Triassic; 2, Middle Triassic; 3, Late Triassic–Early Jurassic.

than the right, twisted valves, and an elongated posterior auricle. These species were interpreted as having a semi-infaunal endobysate mode of life, probably supplemented by byssal attachment (Damborenea, 1987b; Aberhan & Muster, 1997). Seilacher (1984, fig. 7) proposed an analogous interpretation for a similar species, *Hoernesia tortuosa*, including it as a twisted recliner. This category was also used by Aberhan and Muster (1997) for their specimens of *G. pallas*. *Gervillaria (Baryvella) ponderosa* Waller in Waller & Stanley, 2005, was also considered semi-infaunal endobysate, but this species had a peculiar external morphology, which probably means that its life position was also special (Waller & Stanley, 2005) (see discussion on *Gervillancea* mode of life, below). However, due to the mytiliform appearance of some species referred to *Gervillaria*, these were interpreted as epibyssate (S. M. Stanley, 1972). *Gervillaria ashcroftensis* (Crickmay, 1930a) (see Muster, 1995, fig. 39) was also thought to be epibyssate, according to its nearly equivalve shell, umbonal thickening, and flat anteroventral area, among other characteristics (see Aberhan & Muster, 1997).

Mineralogy.—Bimineralic (Carter, 1990a, p. 206–207). There are no data on *Gervillaria* mineralogy or shell microstructure. Data provided for family Bakevelliidae are used here. Outer shell layer: calcite (simple prismatic). Inner shell layer: aragonite (nacreous).

Genus GERVILLANCEA Skwarko, 1967, p. 54

Type species.—*Gervillancea coxiella* Skwarko, 1967, p. 54.

Stratigraphic range.—Upper Triassic (Carnian–Norian) (Skwarko, 1967). *Gervillancea* is a monospecific genus only known from Upper Triassic of New Guinea (Skwarko, 1967; Muster, 1995; Waller & Stanley, 2005). Although it was described before the publication of the *Treatise* (Cox & others, 1969), it was included neither there nor in Sepkoski (2002).

Paleogeographic distribution.—Southern Tethys (Fig. 14). *Gervillancea* was endemic in the Australian province (according to Damborenea, 2002b) of the Tethys domain. It was only reported from Papua New Guinea (Skwarko, 1967).

Paleoautoecology.—B, Se, S, Endo, Sed; By. One of the most striking features of this genus is its extremely long anterior auricle, which distinguishes it from almost all other genera of Bakevelliidae. According to Waller and Stanley (2005), there are two species, *Gervillaria (Baryvella) ponderosa* Waller in Waller & Stanley, 2005, and *Gervillia joleaudi* (Schmidt, 1935), that also have this feature. These two species, together with *Gervillancea coxiella*, may be a good example of evolutionary convergence, but, in fact, *Gervillia joleaudi* lacks an anterior auricle. The external shape of *Gervillancea* is very asymmetric and inequivalve. None of the specimens figured by Skwarko (1967) bears a byssal notch, but if the species was byssate, like other bakevelliids, the byssus probably emerged from the shell under the anterior auricle. Taking into account that it probably lived anchored to the substrate with the anterior auricle, a strong byssus was not necessarily needed to maintain stability inside the substrate. Pedal and byssal muscle scars indicate that these muscles were strong and able to aid the shell to penetrate up to a third of its dorsal line into the sediment, since the convexity of the shell increases at this point and thus limits the burial depth (see Waller & Stanley, 2005, p. 27–29). The bivalve most probably introduced

itself into the sediment during the juvenile stages, since the anterior auricle is comparatively thin and thus inadequate to penetrate the sediment in the adult stage.

Mineralogy.—Bimineralic (Carter, 1990a, p. 206–207). No data are available about the shell of *Gervillancea*, but it was probably bimineralic, as in other Bakevelliidae (J. D. Taylor, Kennedy, & Hall, 1969). Outer shell layer: calcite (simple prismatic). Inner shell layer: aragonite (nacreous).

Genus SONGDAELLA Vu Khuc, 1977b, p. 50 [180]

Type species.—*Songdaella graciosa* Vu Khuc, 1977b, p. 51 [182].

Remarks.—Vu Khuc (1977b) assigned *Songdaella* to the Bakevelliidae, but he indicated that the genus had intermediate characters between this family and the Isognomonidae. Muster (1995) did not include it in her monograph about the family Bakevelliidae and did not comment about its systematic position. In the absence of more information, we include *Songdaella* in Bakevelliidae.

Stratigraphic range.—Upper Triassic (Norian) (Vu Khuc, 1977b). *Songdaella* was only recorded from Norian beds (Vu Khuc, 1977b; J. Chen, 1982a; Vu Khuc & Huyen, 1998).

Paleogeographic distribution.—Eastern Tethys (Fig. 14). *Songdaella* was endemic to southern East Asia (Vu Khuc & Huyen, 1998).

Tethys domain: Norian of northern Vietnam (Vu Khuc, 1977b) and southern China (J. Chen, 1982a).

Paleoautoecology.—B, E, S, Epi, Sed; By. *Songdaella* is characterized by a mytiliform shell, and some of the specimens figured by Vu Khuc (1977b) are similar to *Mytilus*. The author related his new genus to *Aguilerella* according to its external morphology, which was interpreted as epibyssate by S. M. Stanley (1972), due to its external similarity with *Mytilus* and *Myalina*.

Mineralogy.—Bimineralic (Carter, 1990a, p. 206–207). There are no data about the shell of *Songdaella*. We use the data predominant in the family Bakevelliidae. Outer shell layer: calcite (simple prismatic). Inner shell layer: aragonite (nacreous).

Genus AGUILERELLA Chavan, 1951, p. 211

Type species.—*Perna kobyi* de Loriol, 1901, p. 99.

Stratigraphic range.—Upper Triassic (Rhaetian)—Lower Cretaceous (Hauterivian) (J. Yin & McRoberts, 2006; Kozai, Ishida, & Kondo, 2006).

Many authors restricted it to a Lower Jurassic–Upper Jurassic range (Cox & others, 1969; Muster, 1995; Sepkoski, 2002). This range was extended due to new records from the Rhaetian of Tibet (J. Yin & McRoberts, 2006) and from the Hauterivian (Kozai, Ishida, & Kondo, 2006).

Paleogeographic distribution.—Eastern Tethys and Circumpacific (Fig. 14). Although during the study interval it was only reported from eastern Tethys and Austral domains, from Toarcian times it extended also to western Tethys and Boreal regions (see Fürsich, 1982; Liu, 1995; Muster, 1995; J. Yin & Grant-Mackie, 2005; Zakharov & others, 2006).

Tethys domain: Late Triassic: Rhaetian of Tibet (China) (J. Yin, H. Yao, & Sha, 2004; J. Yin & McRoberts, 2006); Early Jurassic: Hettangian of China (J. Chen & Liu, 1981; J. Yin & McRoberts, 2006).

Circumpacific domain: Early Jurassic: Sinemurian of Chile (Aberhan, 1994a; Aberhan & Fürsich, 1997), Canada (Poulton, 1991); Hettangian–Sinemurian of South America (Damborenea, 1996a).

Paleoautoecology.—B, E, S, Epi, Sed; By. Due to its mytiliform aspect, it was thought to be epibyssate (S. M. Stanley, 1972). *Aguilerella* is one of the few bakevelliids, together with *Songdaella*, that are interpreted to be epibyssate due to their triangular form, without anterior lobe and with terminal beaks (Damborenea, 1987b). In some species, a gregarious behavior was observed (Fürsich, 1982; Damborenea, 1987b).

Mineralogy.—Bimineralic (Carter, 1990a, p. 206–207). There are no specific data about the shell of *Aguilerella*. Data provided for the family Bakevelliidae. Outer shell layer: calcite (simple prismatic). Inner shell layer: aragonite (nacreous).

Genus TOWAPTERIA Nakazawa & Newell, 1968, p. 59

Type species.—*Towapteria nipponica* Nakazawa & Newell, 1968, p. 59.

Stratigraphic range.—lower Permian (Sakmarian)–Lower Triassic (Induan) (Hayami & Kase, 1977; S. Yang, Wang, & Hao, 1986). Nakazawa and Newell (1968) proposed the genus *Towapteria* with material from the middle Permian of Japan. Cox and others (1969) did not take it into account in the *Treatise*, probably due to the proximity of publication. Hayami and Kase (1977) assigned it a Sakmarian–upper Permian range with some doubts. *Towapteria* was later reported from the Tethyan Early Triassic (see paleogeographic distribution below). Nevertheless, Muster (1995) assigned it an upper Permian, ?Upper Triassic, Middle Jurassic discontinuous range, due to the inclusion of some species previously assigned to *Gervillia* and *Costigervillia* (see synonymy list in Muster, 1995, p. 92). She did not see the material personally and the addition of most these species to the synonymy list was done doubtfully due to the lack of internal reliable characters for classification. Furthermore, Muster (1995) did not take into account some Tethyan, Early Triassic species, such as *T. scythica* (Wirth), among others.

Paleogeographic distribution.—Tethys and ?Circumpacific (Fig. 14).

Tethys domain: late Permian: Changhsingian of Italy (Farabegoli, Perri, & Posenato, 2007); Early Triassic: Induan of Italy (Broglio-Loriga, Neri, & Posenato, 1980, 1986; Broglio-Loriga, Masetti, & Neri, 1982; Neri, Pasini, & Posenato, 1986; Broglio-Loriga & others, 1988, 1990; Posenato, 1988, 2008a), China (S. Yang, Wang, & Hao, 1986; L. Li, 1995; Tong & Yin, 2002; Waller & Stanley, 2005; Komatsu, Huyen, & Chen, 2007).

Circumpacific domain: late Permian: ?Japan (Nakazawa & Newell, 1968; Hayami & Kase, 1977).

Paleoautoecology.—B, E, S, Epi, Sed; By. It is hard to assign a specific life habit to *Towapteria*, because there are some features indicative of an epibyssate and others of an endobyssate mode of life. Due to its external similarity to *Costigervillia* Cox & Arkell, 1948 in 1848–1850 (a genus not included here because it first appeared in the Middle Jurassic), we can assume that *Towapteria* was endobyssate, but its smooth and lobate anterior auricle and radially ribbed shell indicate otherwise. We suggest it was byssate and probably lived with the anterior part introduced in the sediment.

The ribs probably helped to stabilize the shell, as was postulated for *Costigervillia* by Seilacher (1984).

Mineralogy.—Bimineralic (Carter, 1990a, p. 206–207). No data are available about the shell of *Towapteria*. Data provided for family Bakevelliidae. Outer shell layer: calcite (simple prismatic). Inner shell layer: aragonite (nacreous).

Genus VIRGELLIA Freneix, 1965, p. 61

Type species.—*Virgellia coxi* Freneix, 1965, p. 64.

Remarks.—Fürsich & Werner (1988) considered *Virgellia* as subgenus of *Gervillia* Defrance, 1820, since, in their opinion, it had intermediate features between *Gervillia* and *Gervillella* (which they also regarded as subgenus of *Gervillia*). Following Freneix (1965) and Muster (1995), we regard *Virgellia* as a separate genus. Freneix (1965) proposed *Virgellia* and originally included in it three species: *V. coxi* Freneix, 1965, *V. fittoni* (Sharpe, 1850), and *V. sobralensis* (Sharpe, 1850). Later, Muster (1995) added *V. simbaiana* (Skwarko, 1967) to *V. coxi* and *V. sobralensis* (see synonymy list in Muster, 1995, p. 94–95).

Stratigraphic range.—Upper Triassic (Carnian)–Upper Jurassic (Kimmeridgian) (Muster, 1995). Cox and others (1969) and Sepkoski (2002) did not take *Virgellia* into account. The type species was originally described from Callovian sediments, and the original range assigned to the genus was Bajocian to Kimmeridgian (Freneix, 1965). Later, its range was extended by the inclusion of *V. simbaiana* by Muster (1995). The oldest record of *Virgellia* is from Carnian beds (Skwarko, 1967, 1981) and the youngest from Kimmeridgian beds (Freneix, 1965). It has not been recorded from the Lower Jurassic.

Paleogeographic distribution.—Southern Tethys (Fig. 14). Although during the interval of time under consideration it was only known from southern Tethys, during the Middle and Late Jurassic it was reported also from Tunisia (Freneix, 1965; Holzapel, 1998) and Portugal (Fürsich & Werner, 1988).

Tethys domain: Late Triassic: Carnian–Norian of Papua New Guinea (Skwarko, 1967, 1981; Muster, 1995).

Paleoautoecology.—B, Se, S, Endo, Sed; By. *Virgellia* was externally similar to *Gervillella* and probably had the same mode of life, though slightly less buried into the substrate, as it lacked the *Gervillella* spear shape but had a more developed anterior lobe (Muster, 1995).

Mineralogy.—Bimineralic (Carter, 1990a, p. 206–207). No data about *Virgellia* shell mineralogy or microstructure are available. Data provided for the family Bakevelliidae. Outer shell layer: calcite (simple prismatic). Inner shell layer: aragonite (nacreous).

Genus GERVILLEIOPERNA Krumbeck, 1923b, p. 76

Type species.—*Gervilleioperna timoriensis* Krumbeck, 1923b, p. 76.

Remarks.—Although Cox and others (1969) and other authors included *Gervilleioperna* in the Isognomonidae, we assign it to the Bakevelliidae following Damborenea (1987b), noting that it had a periferom shell and a strong radial carina.

Stratigraphic range.—Lower Jurassic (Sinemurian)–Middle Jurassic (Aalenian) (Aberhan, 1994a; Aberhan & Hillebrandt, 1996). The oldest record of *Gervilleioperna* is from Sinemurian beds (Aberhan, 1994a). During the Toarcian, its distribution became restricted to the Circumpacific domain (in Chile) (Aberhan & Hillebrandt, 1996).

Paleogeographic distribution.—Circumpacific (Fig. 14). Although *Gervilleioerna* was present beginning in Sinemurian times, it reached a diversity peak in the Pliensbachian and became extinct during the Aalenian. It is especially abundant in the Tethys domain during the Pliensbachian (Accorsi-Benini & Broglio-Loriga, 1975; Buser & Debeljak, 1994; Liu, 1995; Aberhan & Fürsich, 1997; Fraser & Bottjer, 2001a, 2001b; Fraser, Bottjer, & Fischer, 2004), while during the Sinemurian, it was only found in the Circumpacific domain. It was also reported from the northern part of the Austral domain during the Pliensbachian (Damborenea, 1987b). *Gervilleioerna* was not recorded in high paleolatitudes, and it was therefore restricted to warm waters (Damborenea, 1996a). It had a pan-Tethyan distribution, ranging from the Pacific coast (South America) through southern Europe and northern Africa to the eastern Tethys (Timor).

Circumpacific domain: Early Jurassic: Sinemurian of Chile (Aberhan, 1994a; Aberhan & Muster, 1997).

Paleoautoecology.—B, Se, S, Endo, R, Sed; By. Along with *Lithiotis*, *Lithioerna*, *Cochlearites*, and *Mytiloerna*, *Gervilleioerna* was a reef builder, especially during Pliensbachian times, replacing the coral reefs of the Late Triassic (Fraser, Bottjer, & Fischer, 2004). *Gervilleioerna* was interpreted as being reclined, lying on its left valve (Seilacher, 1984; Damborenea 1987b; Fraser, Bottjer, & Fischer, 2004). Buser and Debeljak (1994) interpreted it as epifaunal epibyssate similarly to Recent *Isognomon* species, but we believe the semi-infaunal endobyssate option is more reasonable, because its left valve is much heavier than the right and it would have easily sunk into the soft sediment (Damborenea, 1987b). Seilacher (1984) interpreted it as a cup-shaped recliner in soft sediments, similar to *Gryphaea*. Fraser, Bottjer, and Fischer (2004, fig. 10A) agreed, but they classified it as epifaunal. Aberhan and Hillebrandt (1996) suggested that *Gervilleioerna* (*Gervilleioerna aurita*) Aberhan & Hillebrandt was semi-infaunal endobyssate, lying on the umbonal region and the anterior part of its left valve, and with its commissural plane oblique to the substrate surface. Since a byssal notch is observed (Cox & others, 1969, p. 325), it most likely was endobyssate.

Mineralogy.—Aragonitic (Accorsi-Benini & Broglio-Loriga, 1975; Carter, 1990a; Carter, Barrera, & Tevesz, 1998). Accorsi-Benini and Broglio-Loriga (1975) studied the shell of their specimens of *Gervilleioerna*, but they did not check the mineralogical composition (aragonite or calcite) of the shell layers. Carter (1990a) noted that further analysis is needed to determine whether the outer layer contains prismatic calcite. Outer shell layer: aragonite-calcite (?). Inner shell layer: aragonite (?).

Family CASSIANELLIDAE Ichikawa, 1958

Genus CASSIANELLA Beyrich, 1862, p. 9

Type species.—*Avicula gryphaeata* Münster in Goldfuss, 1835 in 1833–1841, p. 127.

Stratigraphic range.—?Permian, Middle Triassic (Anisian)–Upper Triassic (Rhaetian). Cox and others (1969) assigned *Cassianella* a Triassic and probably Permian range. Ciriacks (1963) and Waterhouse (1987) mentioned *Cassianella* from the lower and middle Permian (up to Guadalupian), but specimens in both papers were referred to the genus by external morphology only, and in neither reference were internal characters described. Although Ciriacks (1963, p. 31) mentioned *Cassianella* from the Lower Triassic, we did not find

any information about this, and he did not figure any specimens. *Cassianella* was common from the Anisian to Rhaetian (see paleogeographic distribution).

Paleogeographic distribution.—Cosmopolitan (Fig. 15).

Tethys domain: Middle Triassic: Anisian of southern China (Komatsu, Chen, & others, 2004); Anisian–Ladinian of Bulgaria (Stefanov, 1942), Italy (Posenato, 2008a); Ladinian of Spain (Márquez-Aliaga, 1983, 1985; Márquez-Aliaga, García-Fórner, & Plasencia, 2002), Slovakia (Kochanová, Mello, & Siblík, 1975), Israel (Lerman, 1960), Italy (Rossi Ronchetti, 1959); Late Triassic: Sumatra (Krumbeck, 1914), Alps (Austria) (Tomašových, 2006a, 2006b), China (Cowper-Reed, 1927; J. Chen, 1982a; Gou, 1993); Carnian of the Italian Alps (Bittner, 1895; Leonardi, 1943; Fürsich & Wendt, 1977), Carpathians (Bittner, 1901a), Turkey (Bittner, 1891), Spain (Márquez-Aliaga & Martínez, 1996), Israel (Lerman, 1960); Norian of western Caucasus (Ruban, 2006a), China (Wen & others, 1976; J. Chen & Yang, 1983), Singapore (Kobayashi & Tamura, 1968a; Norian–Rhaetian of Iran (Hautmann, 2001b); late Rhaetian of Tibet (J. Yin & McRoberts, 2006), Pamira (Polubotko, Payevskaya, & Repin, 2001), Alps (Italy) (Desio, 1929; McRoberts, Newton, & Allasinaz, 1995), India (Healey, 1908).

Circumpacific domain: Late Triassic: Peru (Körner, 1937), Japan (Kobayashi & Ichikawa, 1949a; Tamura, 1990); Norian of Oregon (United States) (Newton, 1986, 1989; Newton & others, 1987), southwestern Alaska (McRoberts & Blodgett, 2000), Canada (Tozer, 1962, 1970); Rhaetian of Nevada (United States) (Silberling, 1961; Laws, 1982); Norian–Rhaetian of Chile (Chong & Hillebrandt, 1985).

Austral domain: Late Triassic: Carnian of New Zealand (Trechmann, 1918; Marwick, 1953); Norian–Rhaetian of Argentina (Riccardi & others, 1997, 2004; Damborenea & Manceñido, 2012).

Boreal domain: Late Triassic: northern Siberia (Kurushin, 1990; Polubotko & Repin, 1990); Carnian of Primorie (Kiparisova, 1972); Norian–Rhaetian of northeastern Russia (Kiparisova, Bychkov, & Polubotko, 1966).

Paleoautoecology.—B, E, S, Un, Sed; R. Cassianellids are generally interpreted as being reclining bivalves, lying on their left valve on the sediment (Fürsich & Wendt, 1977; Laws, 1982; Newton & others, 1987; Hautmann, 2001b). Some species, such as *C. lingulata* Gabb, 1870, and *C. angusta* Bittner, 1891, were thought by Laws (1982) and Newton (in Newton & others, 1987), respectively, to be byssate, although there is no byssal notch.

Mineralogy.—Aragonitic (Carter, 1990b, p. 338–339; Carter, Barrera, & Tevesz, 1998). Carter, Barrera, and Tevesz (1998) assigned an aragonitic mineralogy for all shell layers to the family Cassianellidae. Previously, Carter (1990b) noted that some species of *Cassianella* [e.g., *C. beyrichi* Bittner, 1895, or *C. inaequiradiata* (Schafhäütl, 1852)] have calcite in the outer shell layer. *Cassianella* is the only genus of this family for which there are studies of the mineralogy and shell microstructure. Outer shell layer: calcite or aragonite (prismatic). Inner shell layer: aragonite (prismatic).

Genus BURCKHARDTIA Frech, 1907, p. 334

Type species.—*Cassianella* (*Burckhardtia*) *boesei* Frech, 1907, p. 334.

Remarks.—According to Alencaster de Cserna (1961), the type species was first referred to *?Pterinea* by Burckhardt and Scalia (1905).

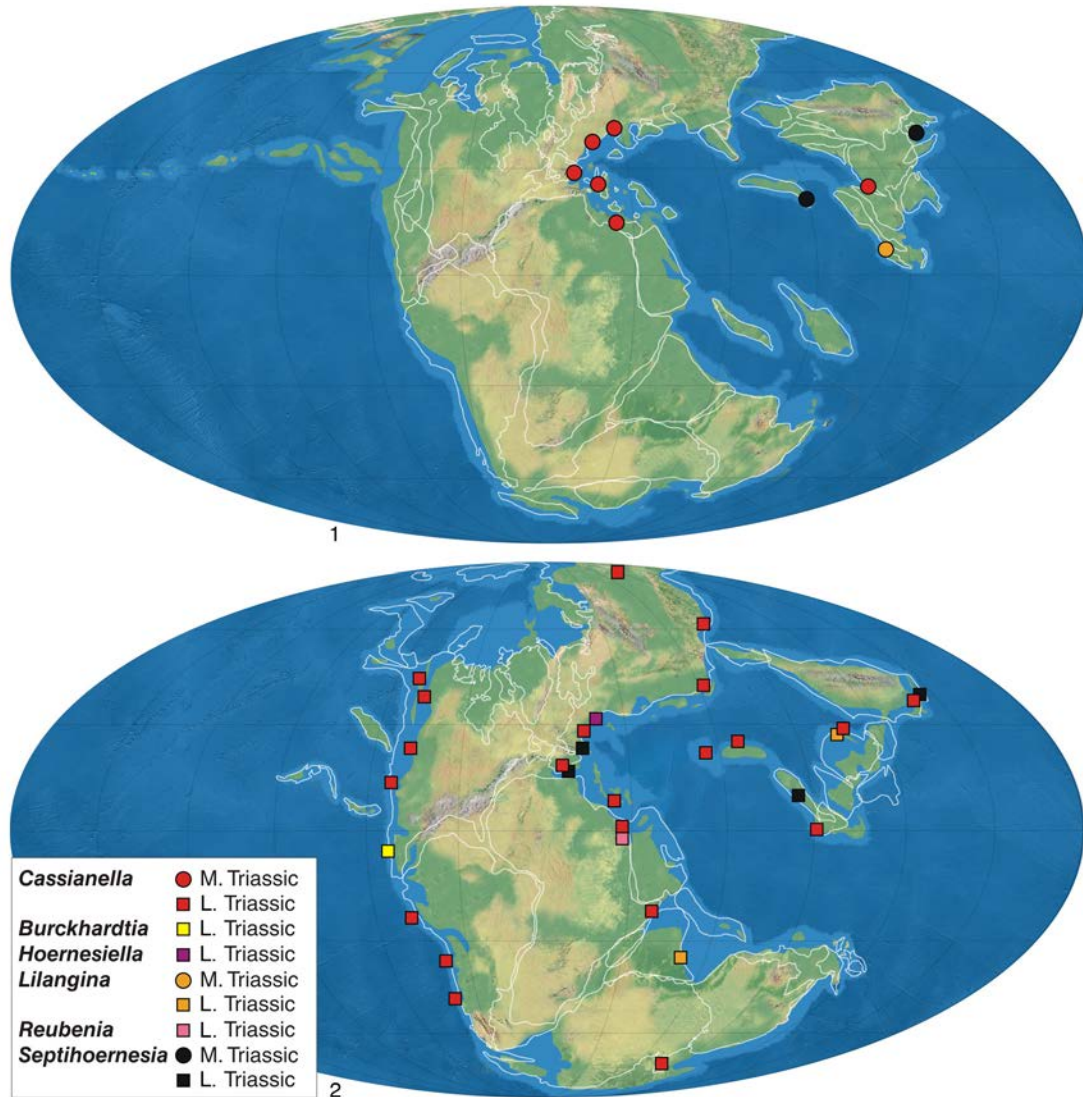


Figure 15. Paleogeographical distribution of Cassianellidae (*Cassianella*, *Burckhardtia*, *Hoernesella*, *Lilangina*, *Reubenia*, *Septihoernesia*). 1, Middle Triassic; 2, Late Triassic.

Frech (1907) argued that this species was better included in *Cassianella* on the basis of its characteristics, and he named the subgenus *Burckhardtia*. But Alencaster de Cserna (1961) suggested that this species is more related to *Myophoria* Bronn, 1835 in 1834–1838, than to *Cassianella* Beyrich, 1862, and she included it in the first genus. Following Cox and others (1969), we regard it as a separate genus within the family Cassianellidae due to the presence of obtuse wings, a feature not known among myophorids.

Stratigraphic range.—Upper Triassic (Carnian) (Frech, 1907). Frech (1907) described the genus from Carnian beds of Zacatecas (Mexico), and it appears to be endemic in this area and restricted to this age (Burckhardt & Scalia, 1905; Diener, 1923; Alencaster de Cserna, 1961; Cox & others, 1969; Hallam, 1981; Kobayashi & Tamura, 1983a; Barboza-Gudino, Tristán-González, & Torres-Hernández, 1990; Sepkoski, 2002).

Paleogeographic distribution.—Circumpacific (Fig. 15).

Circumpacific domain: Late Triassic: Carnian of Mexico (Burckhardt & Scalia, 1905; Frech, 1907; Alencaster de Cserna, 1961; Barboza-Gudino, Tristán-González, & Torres-Hernández, 1990).

Paleoautoecology.—B, E, S, Un, Sed; R. *Burckhardtia* probably had a mode of life similar to *Cassianella*, but considering that it is almost subequivalve, a semi-infaunal mode of life, similar to *Hoernesia*, would perhaps be more likely.

Mineralogy.—Aragonitic (Carter, 1990a, p. 207; Carter, Barrera, & Tevesz, 1998). Data provided for family Cassianellidae. There are no studies on the shell of *Burckhardtia* (see *Cassianella* mineralogy, p. 46). Outer shell layer: calcite or aragonite (prismatic). Inner shell layer: aragonite (prismatic).

Genus HOERNESIELLA Ichikawa, 1958, p. 195

ex Gugenberger, 1935, p. 250

Type species.—*Hoernesella horrida* Gugenberger, 1935, p. 250.

Remarks.—Gugenberger did not designate a type species for his genus *Hoernesiella*. Ichikawa (1958, p. 195) designated *Hoernesiella horrida* as type species, and he claimed the generic authorship under Article 25 c 3 of ICZN (1999). Years later, Cox in Cox and others (1969, p. 312), surely without knowledge of Ichikawa's (1958) paper, noticed the lack of type species, and designated another type species for *Hoernesiella*: *H. carinthiaca* Gugenberger, 1935, p. 250, also claiming the generic name authorship (see Stenzel, 1971, p. 1215). Vokes (1980) attributed the authorship to Ichikawa (1958) by priority of type species designation, and this approach is followed here.

Stratigraphic range.—Upper Triassic (Carnian) (Cox & others, 1969). Cox and others (1969), Stenzel (1971), Hallam (1981), and Sepkoski (2002) assigned it a Carnian range. It was not possible to find more information about this genus.

Paleogeographic distribution.—western Tethys (Fig. 15).

Tethys domain: Late Triassic: Carnian of Carinthia (Austria) (Ichikawa, 1958; Cox & others, 1969).

Paleoautoecology.—B, E, S, Un, Sed; R. Similar to *Cassianella*.

Mineralogy.—Aragonitic (Carter, 1990a, p. 207; Carter, Barrera, & Tevesz, 1998). Data provided for family Cassianellidae. There are no specific studies on the shell of *Hoernesiella* (see *Cassianella* mineralogy, p. 46). Outer shell layer: calcite or aragonite (prismatic). Inner shell layer: aragonite (prismatic).

Genus LILANGINA Diener, 1908, p. 62

Type species.—*Lilangina nobilis* Diener, 1908, p. 62.

Stratigraphic range.—Middle Triassic (Anisian)—Upper Triassic (Carnian) (Cox & others, 1969; Komatsu, Huyen, & Huu, 2010). All sources checked assigned *Lilangina* to the Carnian (Diener, 1923; Cox & others, 1969; Hallam, 1981; Kobayashi & Tamura, 1983a). However, recently, Komatsu, Huyen, and Huu (2010) reported it from the Anisian and Ladinian.

Paleogeographic distribution.—Eastern Tethys (Fig. 15).

Tethys domain: Middle Triassic: Anisian–Ladinian of northern Vietnam (Komatsu, Huyen, & Huu, 2010); Late Triassic: Carnian of Kashmir (Diener, 1923; Cox & others, 1969; Kobayashi & Tamura, 1983a), China (Wen & others, 1976; Kobayashi & Tamura, 1983a; Sha, Chen, & Qi, 1990).

Paleoautoecology.—B, E, S, Un, Sed; R. Similar to *Cassianella*.

Mineralogy.—Aragonitic (Carter, 1990a, p. 207; Carter, Barrera, & Tevesz, 1998). Data provided for family Cassianellidae. There are no specific studies on the shell of *Lilangina* (see *Cassianella* mineralogy, p. 46). Outer shell layer: calcite or aragonite (prismatic). Inner shell layer: aragonite (prismatic).

Genus REUBENIA Cox, 1924, p. 61

Type species.—*Reubenia hesbanensis* Cox, 1924, p. 63.

Stratigraphic range.—Upper Triassic (Carnian) (Cox, 1924). Cox (1924) described *Reubenia* from the Carnian beds of Jordan, including two species, the type species and *Reubenia attenuata* Cox, 1924. All reviewed literature (Kutassy, 1931; Cox & others, 1969; Hallam, 1981; Sepkoski, 2002) assigned it the same stratigraphic range.

Paleogeographic distribution.—western Tethys (Fig. 15).

Tethys domain: Late Triassic: Carnian of Jordan (Cox, 1924).

Paleoautoecology.—B, E, S, Un, Sed; R. Similar to *Cassianella*.

Mineralogy.—Aragonitic (Carter, 1990a, p. 207; Carter, Barrera, & Tevesz, 1998). Data provided for family Cassianellidae. There are no specific studies on the shell of *Reubenia* (see *Cassianella* mineralogy, p. 46). Outer shell layer: calcite or aragonite (prismatic). Middle shell layer: aragonite (nacreous). Inner shell layer: aragonite (prismatic).

Genus SEPTIHOERNESIA Cox, 1964, p. 40

Type species.—*Gervillia johannisaustriacae* Klipstein, 1845 in 1843–1845, p. 249.

Stratigraphic range.—Middle Triassic (Ladinian)—Upper Triassic (Carnian) (Allasinaz, 1966; Tamura, 1990). Cox and others (1969) assigned it a Triassic range, without further comments. Sepkoski (2002) assigned it a Triassic (lower Anisian–Carnian) range, allegedly using Hallam (1981) as data source, but Hallam only mentioned it from Ladinian and Carnian times. The published records indicate that the genus was only present in these two Triassic stages.

Paleogeographic distribution.—Tethys and Circumpacific (Fig. 15).

Tethys domain: Middle Triassic: Ladinian of Malaysia (Tamura & others, 1975); Late Triassic: Carnian of Italy (Allasinaz, 1966; Fürsich & Wendt, 1977), Spain (Martín-Algarra, Solé de Porta, & Márquez-Aliaga, 1995), Malaysia (Tamura & others, 1975).

Circumpacific domain: Middle Triassic: Ladinian of Japan (Tamura, 1990); Late Triassic: Carnian of Japan (Tamura, 1990).

Paleoautoecology.—B, E, S, Un, Sed; R. Similar to *Cassianella*.

Mineralogy.—Aragonitic (Carter, 1990a, p. 207; Carter, Barrera, & Tevesz, 1998). There are no studies on the shell of *Septihoernesia* (see *Cassianella* mineralogy, p. 46). Outer shell layer: calcite or aragonite (prismatic). Inner shell layer: aragonite (prismatic).

Family DATTIDAE Healey, 1908

Genus DATTA Healey, 1908, p. 63

Type species.—*Datta oscillaris* Healey, 1908, p. 63.

Stratigraphic range.—Upper Triassic (Rhaetian) (Healey, 1908). Healey (1908) described the genus from Rhaetian beds of Burma, and Cox and others (1969) repeated these data. Kobayashi and Tamura (1983a) recorded *Datta* from several Upper Triassic localities but did not mention stages or the original data source. The statement in Damborenea (2002b, p. 56): “. . . During the Jurassic and Lower Cretaceous, most genera of Anomiidae, Burmesidae, Ceratomyoposidae, Cuspidariidae [Dattidae] Diceratidae . . .” is an error, and there are no records of *Datta* from the Jurassic.

Paleogeographic distribution.—Southern Tethys (Fig. 16). The original material is from Burma (Healey, 1908). Later, Kobayashi and Tamura (1983a) also reported the genus from the Late Triassic of Kashmir and Yunnan (China), but they did not indicate the original source, and no information related to these records was found.

Paleoautoecology.—B, E, S, ?, ?. It is difficult to assign a mode of life to this genus since the only information available is from a left valve mold with a possible chondrophore. The shell morphological features suggest it was probably epifaunal.

Mineralogy.—Bimineralic (Carter, 1990a, p. 205). Data provided for superfamily Pterioidea. There are no specific studies on *Datta* shell. Outer shell layer: calcite (prismatic). Inner shell layer: aragonite (nacreous).

Family ISOGNOMONIDAE Woodring, 1925

It is often difficult to distinguish between Isognomonidae and Bakevelliidae; good examples are the genera *Isognomon* (*Mytiloperna*) von Ihering, 1903, and *Gervilleopera* Krumbek, 1923b, about which there is no agreement among different authors (see discussions for these taxa, below and p. 45). It is quite evident that these two families are phylogenetically related, and consequently setting limits is complicated. A revision of their diagnostic features is needed to establish a consensus. There are also certain difficulties in distinguishing between Inoceramidae and Isognomonidae (see Crampton, 1988).

Genus ISOGNOMON [Lightfoot, 1786], p. 41, 52

Lightfoot proposed the name in an anonymous catalogue (1786, authorship determined by Dance, 1962, see also Kay, 1965) spelling the name both as *Isognoma* and *Isognomon*, and later Dall, Bartsch, and Rehder (1938, p. 61–62) regarded *Isognomon* as the original spelling and *Isognoma* as a misspelling (first revisers action according to Coan, Valentich Scott, & Bernard, 2000, p. 196).

Type species.—*Ostrea isognomon* Linnaeus, 1764, p. 533 (= *Ostrea isognomum* in Linné, 1758), by absolute tautonymy (see discussion in Rehder, 1967, p. 6, and Coan, Valentich Scott, & Bernard, 2000, p. 196). This differs from the interpretation by Cox (in Cox and others, 1969, p. 322), which was followed by most authors.

Remarks.—According to Cox and others (1969), there are two subgenera of *Isognomon* within our interval of study, *I. (Isognomon)* (but see below) and *I. (Mytiloperna)*. However, some authors noted that probably the latter is more related to bakevelliids than to isognomonids. *Mytiloperna* was described by H. von Ihering (1903) as a genus based in *Perna americana* Forbes; Cox (1940) demoted it to a subgenus of *Isognomon* Lightfoot, 1786, a position maintained in Cox and others (1969) (see Accorsi-Benini & Broglio-Loriga, 1975, for details). There are several reasons to consider that *Mytiloperna* does not fit into the Isognomonidae. One is the shell microstructure (Broglio-Loriga & Posenato, 1996). Another is that adults had a hinge with teeth, a feature of Bakevelliidae and not of Isognomonidae, which were toothless in the adult stage (Seilacher, 1984; Aberhan, 1998a). However, while pending a good revision of the family, it is advisable to treat *Mytiloperna* as an isognomonid (Jaitly, Fürsich, & Heinze, 1995). Additionally, due to a misinterpretation about the correct way of fixation of the type species of *Isognomon* (see above, and IZCN, 1999, Art. 68.1 and 68.4), most Mesozoic species should be referred to *Isognomon (Melina)* Retzius, 1788, p. 22, and not to *Isognomon (Isognomon)*, a fact overlooked by most authors, even by those who accepted *I. isognomon* as type of the genus.

Stratigraphic range.—Upper Triassic (Carnian)–Holocene (Cox & others, 1969). Cox and others (1969) assigned an Upper Triassic to Holocene range to *Isognomon (Isognomon)* and an Lower Jurassic to Upper Jurassic range to *Isognomon (Mytiloperna)*. Linck (1972) reported the last subgenus from the Carnian, but he included in *Mytiloperna* (considered at genus level) some modioliform specimens somewhat different from the typical ones. Today there are numerous species living in tropical seas (Beesley, Ross, & Wells, 1998).

Paleogeographic distribution.—Tethys (Fig. 16). During other intervals of geological time, the genus also lived in Circumpacific and Austral regions, especially during the Pliensbachian (see e.g., Damborenea, 1987b; Broglio-Loriga & Posenato, 1996; Aberhan & Fürsich, 1997; Aberhan 1994a, 1998a; Liu, 1999; Fraser, Bottjer, & Fischer, 2004). However, during the temporal interval under consideration, it was only known from the Tethys domain. Holocene species of *Isognomon* are mainly distributed in tropical seas.

Tethys domain: Late Triassic: Carnian of China (Sha, Chen, & Qi, 1990), Germany (Linck, 1972), southern Italian Alps (Fürsich & Wendt, 1977), Italy (Gelati & Allasinaz, 1964); Norian of Austria (Tichy, 1975), Italy (Terranini, 1958); late Norian of southern China (J. Chen, 1982a); Norian–Rhaetian of Iran, Burma, and Vietnam (Hautmann, 2001b; Fürsich & Hautmann, 2005); Rhaetian of Alps (Italy) (Pozzi, Gelati, & Allasinaz, 1962); Early Jurassic: Hettangian of Japan (Kondo & others, 2006), Europe and northeastern Asia (Hallam, 1977); Hettangian–Toarcian of Japan (Hayami, 1957a, 1975); Sinemurian of Morocco (Liu, 1995), northwestern Europe (Hallam, 1987).

Paleoautoecology.—B, Se, S, Endo, Sed; By. A semi-infaunal endobryssate mode of life seems likely for most Mesozoic species, although some Recent species live epifaunally (S. M. Stanley, 1970, 1972). This disparity in mode of life can be recognized by differences in shell morphology. Living species are often very inequivalve, unlike Mesozoic species, which were equivalve or subequivalve (Hayami, 1957a); there are also differences in shell thickness, the umbonal part being thicker than the ventral part in Mesozoic species (see Fürsich, 1980; Seilacher, 1984; Broglio-Loriga & Posenato, 1996; Fraser, Bottjer, & Fischer, 2004).

Fürsich (1980) analyzed some of the fossil species and observed that, if only shell characters were taken into account, his interpretations were wrong and not viable when he could contrast these results with direct observation of individuals found in life position in the field. All fossil species studied in his work of 1980 seem to support a semi-infaunal endobryssate mode of life. Furthermore, fossil species are often found forming groups, and thus they were interpreted as gregarious (Fürsich, 1982; Damborenea, 1987b).

With regard to *I. (Mytiloperna)*, several authors studied its morphology in relation to its mode of life (e.g., Seilacher, 1984; Broglio-Loriga & Posenato, 1996; Fraser, Bottjer, & Fischer, 2004). These last two papers distinguished several *Mytiloperna* morphotypes with different life habit interpretations, ranging from epifaunal to semi-infaunal.

Mineralogy.—Bimineralic (Carter, 1990b, p. 339). Accorsi-Benini and Broglio-Loriga (1975) and Broglio-Loriga and Posenato (1996) described a fibrous microstructure in the inner shell layer of *Mytiloperna* sp. specimens. Outer shell layer: calcite (simple prismatic). Inner shell layer: aragonite (nacreous).

Genus LEPROCONCHA Giebel, 1856, p. 67

Type species.—*Leproconcha paradoxa* Giebel, 1856, p. 67.

Remarks.—When Giebel (1856) described the genus, he did not mention its systematic relations, although he indicated that it was intermediate between Ostreacea and Malleacea. Nevertheless, Cox and others (1969) decided to include it with doubts into the Isog-

nomonidae. Looking at the drawings in Giebel (1856, pl. 2, 10, 13), we can understand why this assignation was more than doubtful. We assume that the ligament pits were the key feature to include *Leproconcha* in this family, but, unlike the rest of isognomonids, it shows an almost equivalve shell and an ostreid external appearance. Lacking any better solution, we follow Cox and others (1969), even knowing it is very unlikely that this genus belongs to this family.

Stratigraphic range.—Middle Triassic (Giebel, 1856). Giebel (1856) described *Leproconcha* from Muschelkalk of the Germanic Basin. Diener (1923), Kutassy (1931), Cox and others (1969), and Kobayashi and Tamura (1983a) repeated these data, and no further information was found.

Paleogeographic distribution.—western Tethys (Fig. 16).

Tethys domain: Middle Triassic: Muschelkalk of Germany (Giebel, 1856).

Paleoautoecology.—B, E, S, ?, ?. Probably epifaunal.

Mineralogy.—Unknown. There is no information about mineralogy or microstructure of *Leproconcha* shell. We cannot assign it the mineralogy predominant in the family because we have serious doubts about the family assignation of this genus.

Genus WAAGENOPERNA Tokuyama, 1959a, p. 151

Type species.—*Edentula lateplanata* Waagen, 1907, p. 97.

Remarks.—*Waagenoperna* Tokuyama, 1959a was proposed to replace *Edentula* Waagen, 1907 (*non* Nitzsch, 1820), and *Edentula lateplanata* Waagen, 1907, was designated as type species by Tokuyama (1959a). Some years earlier, Cox (1954) had proposed the name *Cuneigervillia* also to replace *Edentula*, choosing *Gervillia hagenowii* Dunker, 1846, as the type species. When Tokuyama (1959a) compared the two type species, he noticed that while *Gervillia hagenowii* is a bakevelliid (in fact, Cox, 1954, included *Cuneigervillia* in the family Bakevelliidae), *Edentula lateplanata* is an isognomonid, like other species attributed to *Edentula* (*E. triangularis* Kobayashi & Ichikawa, 1952). Lower Jurassic species also referred to *Cuneigervillia* by Cox clearly showed that this genus was not objectively the same as *Edentula* (in fact, they have different type species), and he decided to maintain both names, *Cuneigervillia* and *Waagenoperna* (= *Edentula*), which was followed by Cox and others (1969).

Nakazawa and Newell (1968) proposed a new subgenus within *Waagenoperna*, *W. (Permoperna)*, and although some authors (Z. Fang, 1982) treated *Permoperna* at generic level, the original rank is here retained because it does not present substantial differences from *Waagenoperna s.s.*

Tëmkin (2006, p. 270) erroneously indicated that *Waagenoperna* was based on *W. triangularis* (Kobayashi & Ichikawa, 1952).

Stratigraphic range.—lower Permian (Sakmarian)—Upper Triassic (upper Norian) (Hayami & Kase, 1977; J. Chen, 1982a). Cox and others (1969) assigned it a middle Permian—Upper Triassic range. The stratigraphic range should be extended back, since Nakazawa and Newell (1968) reported *Waagenoperna (Permoperna)* from the lower Permian (Sakmarian). Sepkoski's (2002) range starts from the Guadalupian, which is odd considering that he took his data from Hayami and Kase (1977) and Skelton and Benton (1993), who indicated Sakmarian as the first record. Regarding the upper extension of this genus, J. Chen (1982a, p. 303) quoted *Waagenoperna* from

the upper Norian of southern China, indicating that the association to which it belonged is “the uppermost Triassic bivalve zone in this region.” There are several reports from Hettangian brackish environments of southern China (Sha & Jiang, 2004; Jiang, Sha, & Pan, 2008), although none was corroborated by illustrations or descriptions of the material.

Paleogeographic distribution.—Tethys and Circumpacific (Fig. 16).

Tethys domain: Late Triassic: Carnian of southern Alps (Broili, 1904; Tokuyama, 1959a), southern China (Gu & others, 1980); late Norian of China (J. Chen, 1982a).

Circumpacific domain: **late** Permian: Japan (Nakazawa & Newell, 1968; Hayami, 1975); Middle Triassic: Ladinian of Japan (Tokuyama, 1959a; Hayami, 1975); Late Triassic: Carnian—Norian of Japan (Tokuyama, 1959a; Hayami, 1975).

Paleoautoecology.—B, Se, S, Endo, Sed; By. Although *Waagenoperna* had a mytiliform shell and most isognomonids were interpreted as epifaunal bivalves, *Waagenoperna* was thought to be a semi-infaunal endobysate bivalve, similar to *Pinna* and some pterineids (S. M. Stanley, 1972). This author relied on morphological evidence, such as the strongly prosocline, slightly inflated, subequivalve shell and the presence of an anterior lobe, features not shared with any other member of the family Isognomonidae.

Mineralogy.—Biminerale (Carter, 1990a, p. 209). There are no data about the *Waagenoperna* shell. Information provided for family Isognomonidae. Outer shell layer: calcite (simple prismatic). Middle and inner shell layers: aragonite (nacreous).

Family POSIDONIIDAE Neumayr, 1891

The Posidoniidae family members are hardly distinguishable from each other because one of the main diagnostic features is the ligament area, and this is only preserved in exceptional cases. Due to the usually very thin shell, all internal shell characters are frequently destroyed during diagenesis. Waller (in Waller & Stanley, 2005) gathered the families Posidoniidae and Halobiidae Kittl, 1912, in the superfamily Posidonioidea Frech, 1909. This arrangement is probably more appropriate than the one followed here, but according to Amler (1999), we consider the first family in the superfamily to be Pterioidea Gray 1847, and the second one to be Halobioidea H. J. Campbell, 1994.

Genus BOSITRA De Gregorio, 1886, p. 11

Type species.—*Posidonia ornati* Quenstedt, 1851 in 1851–1852, p. 501.

Remarks.—Following Waller (in Waller & Stanley, 2005), we regard *Posidonia* Bronn, 1828, as a Paleozoic genus, referring described species from Lower and Middle Triassic to *Bositra*. We consider *Peribositria* Kurushin & Trushchelev, 1989, to be a synonym of *Bositra* (see discussion for *Peribositria* in Genera not Included, p. 167).

Stratigraphic range.—Lower Triassic (lower Olenekian)—Middle Jurassic (lower Oxfordian) (Waller & Stanley, 2005). Cox and others (1969) assigned it a Jurassic range, but after Waller and Stanley (2005) emended the genus and they transferred species traditionally included in *Posidonia* from Lower and Middle Triassic, the range was extended back to the Triassic. The problem in the

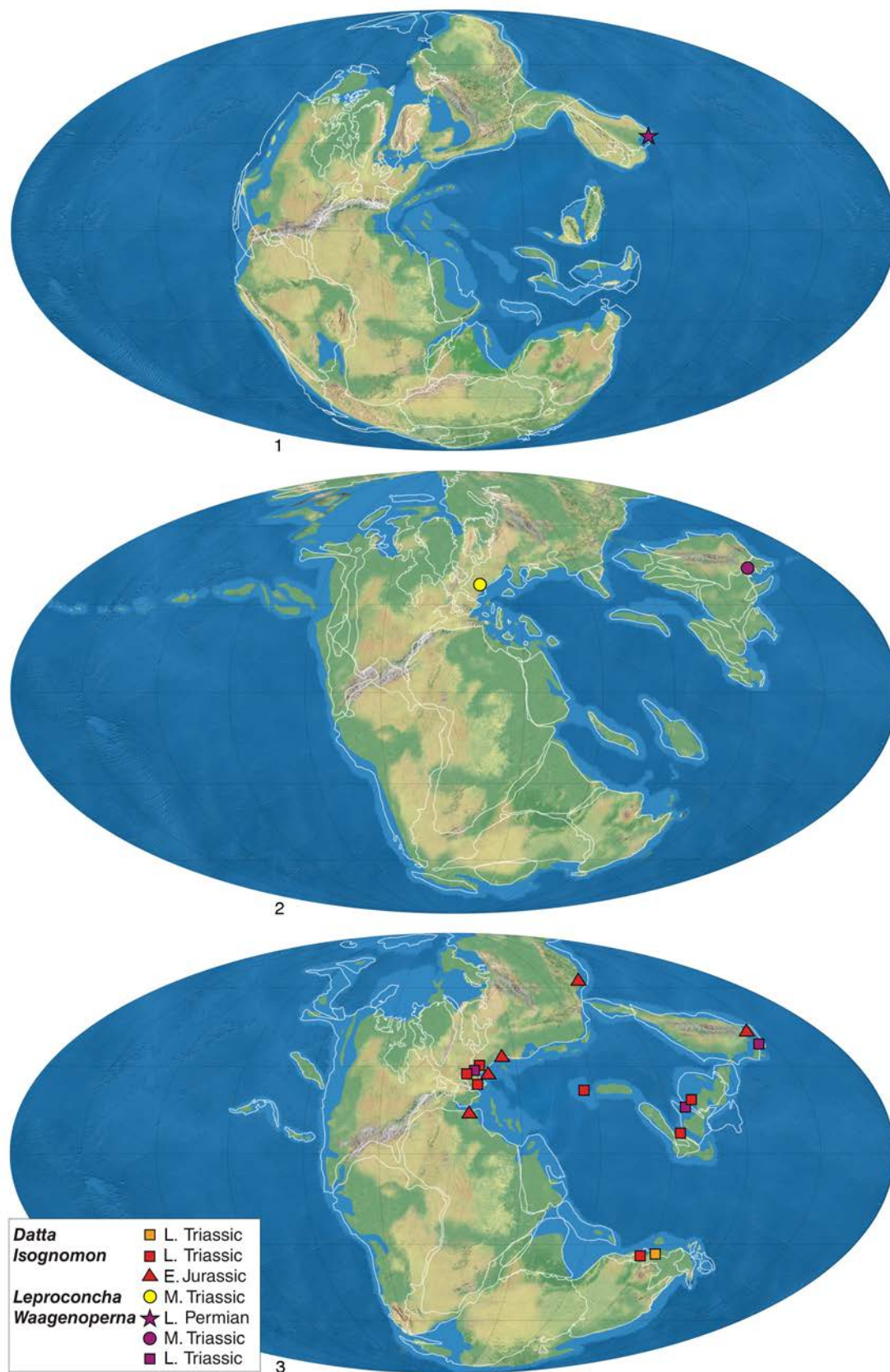


Figure 16. Paleogeographical distribution of Isognomonidae (*Isognomon*, *Leproconcha*, *Waagenoperna*) and Dattidae (*Datta*). 1, late Permian; 2, Middle Triassic; 3, Late Triassic–Early Jurassic.

differentiation of both genera is that the main diagnostic characters are in the ligament area, as well as other internal structures, which are often destroyed during diagenesis (Waller in Waller & Stanley, 2005). Fürsich and Werner (1988) reported *Bositra* from the Upper Jurassic (Kimmeridgian) of Portugal, but their specimens were referred to this genus with some hesitation since the ligament area is not preserved.

Paleogeographic distribution.—Tethys, Circumpacific, and Boreal (Fig. 17). During the Early Triassic, *Bositra* was distributed mainly in the Boreal domain, extending over the Tethys and Circumpacific domains during the Middle Triassic, to become virtually cosmopolitan during the Early Jurassic (Waller & Stanley, 2005), especially during the Toarcian (Damborenea, 1987b; Aberhan, 1994a, 1998a; Monari, 1994; Liu, 1995; Harries & Little, 1999; Gahr, 2002), coinciding with the peak of early Toarcian extinction. We did not take into account the mention in Waterhouse (2000), because Waller and Stanley (2005) affirm the specimens are more clariids than posidoniids.

Tethys domain: Middle Triassic: Slovenia (Jurkovsek, 1984); Anisian of China (Wen & others, 1976; Ling, 1988; Komatsu, Akasaki, & others, 2004a; J. Chen & Stiller, 2007), western Carpathians (Slovakia) (Kochanová, 1985); Anisian–Ladinian of Vietnam (Vu Khuc & Huyen, 1998); Ladinian of Spain (Márquez-Aliaga, 1983, 1985; Márquez-Aliaga & Ros, 2003); Late Triassic: Carnian of China (Wen & others, 1976), Italy (Fürsich & Wendt, 1977); Norian of China (Sha, Chen, & Qi, 1990).

Circumpacific domain: Middle Triassic: Anisian of Japan (Hayami, 1975), of Nevada (United States) (Waller & Stanley, 2005).

Boreal domain: Early Triassic: Siberia (Kiparisova, 1938; Dagens & Kurushin, 1985), Arctic Archipelago (Canada) (Tozer, 1961, 1962, 1970).

Paleoautoecology.—B, E, S, Un, Sed; R. *Bositra* was interpreted as a pseudoplanktonic bivalve (S. M. Stanley, 1972) or as nekto-planktonic (Jefferies & Minton, 1965; Hayami, 1969a; Duff, 1975), according to its distribution and morphological characteristics. Other authors rejected these interpretations considering the habit of species assigned to *Bositra* as benthic (M. A. Conti & Monari, 1992; Etter, 1996).

Etter (1996) did a comprehensive study reviewing all possible modes of life ever attributed to *Bositra*, demonstrating that a benthic mode of life is entirely plausible and providing arguments to reject the other two options. Since a byssal notch is not observed, a reclined mode of life would have been the most likely (Waller & Stanley, 2005). The reason for its frequent presence in oxygen-poor sedimentary environments should more probably be related to an opportunistic behavior than to a pseudoplanktonic mode of life (Etter, 1996). An updated discussion on the mode of life for *Bositra* was provided by Caswell, Coe, and Cohen (2009, and see references therein).

Mineralogy.—Bimineralic (Carter, 1990b, p. 340; Waller & Stanley, 2005). Outer shell layer: calcite (homogeneous-prismatic). Inner shell layer: aragonite (nacreous).

Genus AMONOTIS Kittl, 1904, p. 736

Type species.—*Amonotis cancellaria* Kittl, 1904, p. 736.

Stratigraphic range.—Upper Triassic (Carnian). *Amonotis* was reported from Carnian beds (Cox & others, 1969; C. Chen & Yu, 1976; Sha, Chen, & Qi, 1990) and apparently also from the Norian, although Norian records lack illustrations or they were dubiously assigned to the genus (Niu, Xu, & Ma, 2003; Tang & others, 2007).

Paleogeographic distribution.—Tethys (Fig. 17). *Amonotis* was found both in western and eastern Tethys, although some authors (Hallam, 1981; Metwally, 1993) only included European occurrences in their compilations.

Tethys domain: Late Triassic: Carnian of Yugoslavia (Cox & others, 1969), China (C. Chen & Yu, 1976; Sha, Chen, & Qi, 1990).

Paleoautoecology.—B, E, S, Epi, Sed; By. According to S. M. Stanley (1972), almost all posidoniids were epibyssate bivalves, though almost none of the genera shows a sinus or byssal notch, and some of them could be pseudoplanktonic, although there is no evidence that *Amonotis* was one of them. Therefore, we consider *Amonotis* as to be an epibyssate bivalve in agreement with Sha, Chen, and Qi (1990), but the possibility of a reclined habit similar to *Bositra* cannot be ruled out.

Mineralogy.—Bimineralic (Carter, 1990a, p. 211). Data provided for family Posidoniidae. We lack information about the shell of *Amonotis*. Outer shell layer: calcite (prismatic-homogeneous). Inner shell layer: aragonite (nacreous).

Genus VELDIDENELLA Alma, 1925, p. 118

Type species.—*Veldidenella dieneri* Alma, 1925, p. 118.

Stratigraphic range.—Middle Triassic (upper Anisian–upper Ladinian) (Kochanová, 1985). Cox and others (1969) assigned it a Upper Triassic range, and both Sepkoski (2002) and other compilation papers (e.g., Metwally, 1993) repeated this information. But according to the information published on this monospecific genus, these data appear to be wrong. According to Kutassy (1931), Alma in 1925 described the type species of this genus from Anisian beds of the northern Alps. Tichy (1970), in his catalog of type specimens housed at the Museum of Natural History in Vienna, also indicated Anisian as the age of the type species. Subsequently, Kochanová (1985) reported *Veldidenella dieneri* from Anisian beds of the western Carpathians and from upper Ladinian beds of the southern Austrian Alps.

Paleogeographic distribution.—western Tethys (Fig. 17).

Tethys domain: Middle Triassic: Anisian of northern Alps (Austria) (Kutassy, 1931), Carpathians (Slovakia) (Kochanová, 1985); Ladinian of northern Alps (Austria) (Kochanová, 1985).

Paleoautoecology.—B, E, S, Epi, Sed; By. Similar to *Amonotis*.

Mineralogy.—Bimineralic (Carter, 1990a, p. 211). There are no data about *Veldidenella* mineralogy or shell microstructure. Data provided for the family Posidoniidae. Outer shell layer: calcite (prismatic-homogeneous). Inner shell layer: aragonite (nacreous).

Genus CAENODIOTIS Monari, 1994, p. 171

nom. nov. pro Diotis Simonelli, 1884, p. 125, *non* Schmarda, 1859, p. 5

Type species.—*Posidonomya janus* Meneghini, 1853, p. 27

Remarks.—Damborenea (1987b, p. 191) noticed that the name *Diotis* was used previously for a group of worms (*Diotis* Schmarida, 1859). Years later, Monari (1994) proposed the name *Caenodiotis* to replace *Diotis* Simonelli, 1884, in accordance with Article 52 of ICZN (1999). Following Cox and others (1969) and Monari (1994), we include *Caenodiotis* in Posidoniidae, although given its probable relations to *Posidonotis* (Damborenea, 1987b), it could perhaps be included in Entoliidae.

Stratigraphic range.—Lower Jurassic (Sinemurian–Pliensbachian) (Monari, personal communication, 2007). According to Cox and others (1969), *Diotis* was distributed during the early and middle Early Jurassic, but we could not check exactly which stages. Monari (1994) noted its presence from the Pliensbachian in several Italian localities. He also found it in the Sinemurian of the Umbria-Marche region (Monari, personal communication, 2007). We assign the range Sinemurian–Pliensbachian to this genus, until we can determine the age of the units widely referred to as lower Liassic by Cox and others (1969).

Paleogeographic distribution.—western Tethys (Fig. 17). During the Early Jurassic, especially during the Pliensbachian, the genus was distributed in Italy (Monari, 1994), Hungary (Szente, 1990), and Spain (Jiménez de Cisneros, 1923). During the time interval here analyzed, we only consider the Sinemurian records.

Tethys domain: Early Jurassic: Sinemurian of Italy (Monari, personal communication, 2007).

Paleoautoecology.—B, E, S, Epi, Sed; By. Similar to *Amonotis*.

Mineralogy.—Bimineralic (Carter, 1990a, p. 211). There are no data about the *Caenodiotis* shell. Data provided for family Posidoniidae. Outer shell layer: calcite (prismatic-homogeneous). Inner shell layer: aragonite (nacreous).

Genus STEINMANNIA Fischer, 1886 in 1880–1887, p. 960

nom. nov. pro Aulacomya Steinmann, 1881, p. 259, *non* Mörch, 1853, p. 53

Type species.—*Posidonia bronni* Voltz in Zieten, 1833 in 1830–1833, p. 72.

Remarks.—*Steinmannia* is very similar morphologically to *Bositra* De Gregorio, 1886, and *Posidonia* Bronn, 1828, and the observation of the ligament type is key to discriminating between these genera (multivincular in *Steinmannia*, alivincular in *Bositra*, and duplivincular in *Posidonia*), but its preservation is not common (Waller in Waller & Stanley, 2005). Although Guillaume (1928) and later authors (e.g., Cox & others, 1969; Milova, 1988) included *Steinmannia* in the Inoceramidae due to the ligament type, Waller (in Waller & Stanley, 2005) thought the ligament of *Steinmannia* was not of the inoceramid type: “the relatively few ligament pits on the ligament area of *Steinmannia bronni* (three or four according to Guillaume, 1928, p. 221; three to five according to Milova, 1988, p. 63, pl. 2, 1–3) may be a phylogenetically independent multiplication of the simple alivincular ligament of *Bositra* possibly functionally associated with increase in size and convexity.” Following Waller (in Waller & Stanley, 2005), we consider *Steinmannia* more related to Posidoniidae than Inoceramidae. Some authors included the type species of *Steinmannia* in *Bositra* (e.g., Hallam, 1976, 1987; Caswell,

Coe, & Cohen, 2009). *Multisidonia* Polubotko, 1992, p. 60 (type species *M. omolonensis* Polubotko, 1992, p. 60), distinguished by a greater number of ligamental pits, is a possible synonym.

Stratigraphic range.—Lower Jurassic (upper Sinemurian–lower Toarcian) (Guillaume, 1928; Milova, 1988). Cox and others (1969) assigned it a Toarcian range, but Milova (1988) reported a new species, *Steinmannia viligaensis* Milova, from upper Sinemurian beds (also another from the Pliensbachian, *Steinmannia alikiensis* Milova, 1988), and the type of *Multisidonia* is also late Sinemurian in age (Polubotko, 1992). Sepkoski (2002) did not consider this genus.

Paleogeographic distribution.—Boreal (Fig. 17). During the Early Jurassic, especially in the Toarcian, the genus was distributed in the Tethys domain (France, England, Germany, Switzerland) (Guillaume, 1928).

Boreal domain: Early Jurassic: Sinemurian of northeastern Russia (Milova, 1988).

Paleoautoecology.—B, E, S, Un, Sed; R. See mode of life for *Bositra* (p. 50).

Mineralogy.—Bimineralic (Carter, 1990a, p. 211). There are no data about the shell of *Steinmannia*. Data provided for family Posidoniidae. Outer shell layer: calcite (prismatic-homogeneous). Inner shell layer: aragonite (nacreous).

Genus ELLESMERELLA Waterhouse, 2008, p. 172

Type species.—*Posidonia aranea* Tozer, 1961, p. 102.

Remarks.—Waterhouse (2008) proposed *Ellesmerella* based on *P. aranea*, included it in the family Aulacomyellidae Ichikawa, 1958, and considered it to be related to *Bositra*. McRoberts (2010) suggested it could be better placed into Posidoniidae or Halobiidae. Provisionally, we include *Ellesmerella* in the Posidoniidae.

Stratigraphic range.—Lower Triassic (upper Olenekian) (Tozer, 1961). The monospecific genus *Ellesmerella* was only reported from the Olenekian stage (Tozer, 1961, 1962, 1970; Vozin & Tikhomirova, 1964; Tozer & Parker, 1968; Waterhouse, 2008; McRoberts, 2010). It has a very short stratigraphical range (uppermost Olenekian) (McRoberts, 2010).

Paleogeographic distribution.—Boreal (Fig. 17).

Boreal domain: Early Triassic: late Olenekian of Arctic Archipelago (Canada) (Tozer, 1961), Svalbard (Norway) (Tozer & Parker, 1968), British Columbia (Tozer, 1962, 1970), northeastern Siberia (Vozin & Tikhomirova, 1964).

Paleoautoecology.—B, E, S, Un, Sed; R. Similar to *Bositra*.

Mineralogy.—Bimineralic (Carter, 1990a). There are no data about the shell of *Ellesmerella*. Data provided for family Posidoniidae and/or Halobiidae.

Superfamily PINNOIDEA Leach, 1819

Family PINNIDAE Leach, 1819

In our study interval, there are two genera belonging to Pinnidae: *Pinna* Linnaeus, 1758, and *Atrina* Gray, 1842, p. 83 [1840, p. 151, *nom. nud.*]. These two genera are morphologically very similar in their juvenile stages, but adults are differentiated mainly by the presence of a median shell carina, which is associated with the separation of the internal nacreous layer into two lobes in *Pinna* and is absent in *Atrina* (Cox & others, 1969; Waller & Stanley, 2005). Cox and others

(1969) assigned a Carboniferous–Holocene range to *Pinna* (*Pinna*) and a Middle Jurassic–Holocene range to *Atrina*. However, many specimens assigned to *Pinna* (*Pinna*) from beds older than Middle Jurassic do not have this median carina, and thus they should probably be referred to *Atrina* or some Paleozoic genera (*Pteronites* McCoy, 1844, *Aviculopinna* Meek, 1864, or *Meekopinna* Yancey, 1978) (see Waller & Stanley, 2005, p. 29). In the absence of a review on this subject, we assign provisional stratigraphic ranges for both genera.

Genus PINNA Linnaeus, 1758, p. 707

Type species.—*Pinna rudis* Linnaeus, 1758, p. 707.

Stratigraphic range.—Lower Triassic–Holocene (Nakazawa, 1961). Although, as already mentioned, Cox and others (1969) assigned it a range from the Carboniferous, we could not locate any record of specimens attributed to this age except in the *Treatise*. A specimen of *Pinna* (*Pinna*) *costata* Phillips from the Carboniferous of Belgium was figured in Cox and others (1969, p. 282), but this specimen does not show the typical carina, and therefore it is not supposed to belong to *Pinna* (Waller & Stanley, 2005). R. Zhang and Yan (1993) reported the genus from the Carboniferous, but they did not illustrate or describe the material. The oldest positive records are from the Lower Triassic. Nakazawa (1961) figured *Pinna muikadaniensis* Nakazawa, 1961 (p. 267; plate 13, 14), and, although in the description he did not mention the median carina, he said: “. . . parting mediate distinct but weak in the umbonal half and obsolete in the rear part, deviating towards the antero-ventral side . . .” and the figure shows evidence of a true carina. Seguí (1999, p. 21, fig. 1), in the description of his specimen of *Pinna bascoi* Seguí, 1999, from Ladinian of Spain, said: “There is an edge signal that starting from the apex disappears at about 2/3 of the height. This edge divides the shell into two parts.” This edge can be seen in his figures and seems to correspond with the carina. We doubtfully consider Nakazawa’s (1961) Lower Triassic record as valid, since the material is not well preserved and we cannot be sure that it actually belongs to *Pinna*.

Paleogeographic distribution.—Tethys, Circumpacific, and Austral (Fig. 18). Although *Pinna* had a cosmopolitan distribution during our study interval, recent species are restricted to tropical and subtropical seas (Cox & others, 1969). No records were located from the Boreal domain.

Tethys domain: Early Triassic: China (F. Wu, 1985); Middle Triassic: Ladinian of Spain (Seguí, 1999); Late Triassic: southern China (Gou, 1993); Carnian of Slovenia (Jelen, 1988), southern Alps (Italy) (Fürsich & Wendt, 1977), Lombardy (Italy) (Allasinaz, 1964, 1966), Germany (Linck, 1972); Norian of Australia (Grant-Mackie, 1994); Norian–Rhaetian of Iran (Hautmann, 2001b); Rhaetian of Burma (Healey, 1908), Alps (Austria) (Winkler, 1861), Tibet (China) (J. Yin & McRoberts, 2006), Pamir (Afghanistan) (Polubotko, Payevskaya, & Repin, 2001), Hungary (Vörös, 1981), Italy (Allasinaz, 1962; Sirna, 1968); Early Jurassic: Hettangian of Tibet (China) (J. Yin & McRoberts, 2006), England and Morocco (Liu, 1995), Italy (Sirna, 1968), France (Martin, 1860); Sinemurian of Portugal, Spain, England, France, and Morocco (Liu, 1995).

Austral domain: Late Triassic: Carnian of New Zealand (Trechmann, 1918; Marwick, 1953); Early Jurassic: Hettangian–Sinemurian

of Argentina (Damborenea, 1996a; Damborenea & Manceñido, 2005b); Sinemurian of Argentina (Damborenea & Lanés, 2007).

Circumpacific domain: Early Triassic: Japan (Nakazawa, 1961; Hayami, 1975); Late Triassic: Norian of Chile (Hayami, Maeda, & Ruiz-Fuller, 1977); Early Jurassic: Sinemurian of Canada (Aberhan, 1998a).

Paleoautoecology.—B, Se, S, Endo, Sed; By. Depending on the species, *Pinna* currently lives more or less with the anterior half of the shell buried in the sediment as endobysate, with a strong byssus attached to fragments of rocks or other objects, such as sea grass roots (García-March, 2005), although some were found epibysate on hard substrates (S. M. Stanley, 1970). Regarding fossil species, there are many examples of *Pinna* in upright position, similar to living species (e.g., Fürsich, 1980, 1982; Damborenea, 1987a). It is rare to find complete fossil specimens; only the anterior parts, which are buried in life, are usually found. More detailed information about its mode of life can be found in Yonge (1953) and Seilacher (1984), among many others.

Mineralogy.—Biminerale (Yonge, 1953; Carter, 1990a; García-March, 2005; García-March, Márquez-Aliaga, & Carter, 2008). Outer shell layer: calcite (prismatic simple). Inner shell layer: aragonite (nacreous).

Genus ATRINA Gray, 1842, p. 83

Gray, 1840, p. 151, *nom. nud.*

Type species.—*Pinna nigra* Dillwyn, 1817, p. 325.

Stratigraphic range.—Middle Triassic (Anisian)–Holocene (Stiller, personal communication, 2008). Although Cox and others (1969) assigned it a range from the Middle Jurassic, Waller (in Waller & Stanley, 2005) reported *Atrina* from the Ladinian. Also Stiller, in his doctoral thesis (Stiller, personal communication, 2008), reported it from the Anisian. Although, as noted, it may have appeared before, we will take this well-documented record as its first appearance. In addition, Waller and Stanley (2005, p. 29–30) noted that Carboniferous Pinnidae could possibly be referable to *Atrina* and not to *Pinna*.

Paleogeographic distribution.—Tethys and Circumpacific (Fig. 18). Although in the past *Atrina* was regarded as a cosmopolitan genus, this is not the case for the time interval here considered. Its distribution was surely greater than the one mentioned below, because many species attributed to *Pinna* may belong to *Atrina* instead, but there are no specific data for the study interval.

Circumpacific domain: Middle Triassic: late Ladinian of Nevada (United States) (Waller & Stanley, 2005).

Tethys domain: Middle Triassic: Anisian of China (Stiller, 2001, personal communication, 2008).

Paleoautoecology.—B, Se, S, Endo, Sed; By. *Atrina* living species are semi-infaunal bivalves that live endobysate, attached by a strong byssus to rock fragments or other materials embedded in the sediment, with the commissure plane being almost vertical, similar to *Pinna*. Unlike *Pinna*, which lives with two-thirds of its shell into the sediment, *Atrina* lives almost completely buried (García-March, Márquez-Aliaga, & Carter, 2008). The same mode of life is assumed for Mesozoic specimens. The external shell spines were interpreted by S. M. Stanley (1970) as protection against breakage of the exposed portion of the shell, rather than a defensive device as in other bivalves.

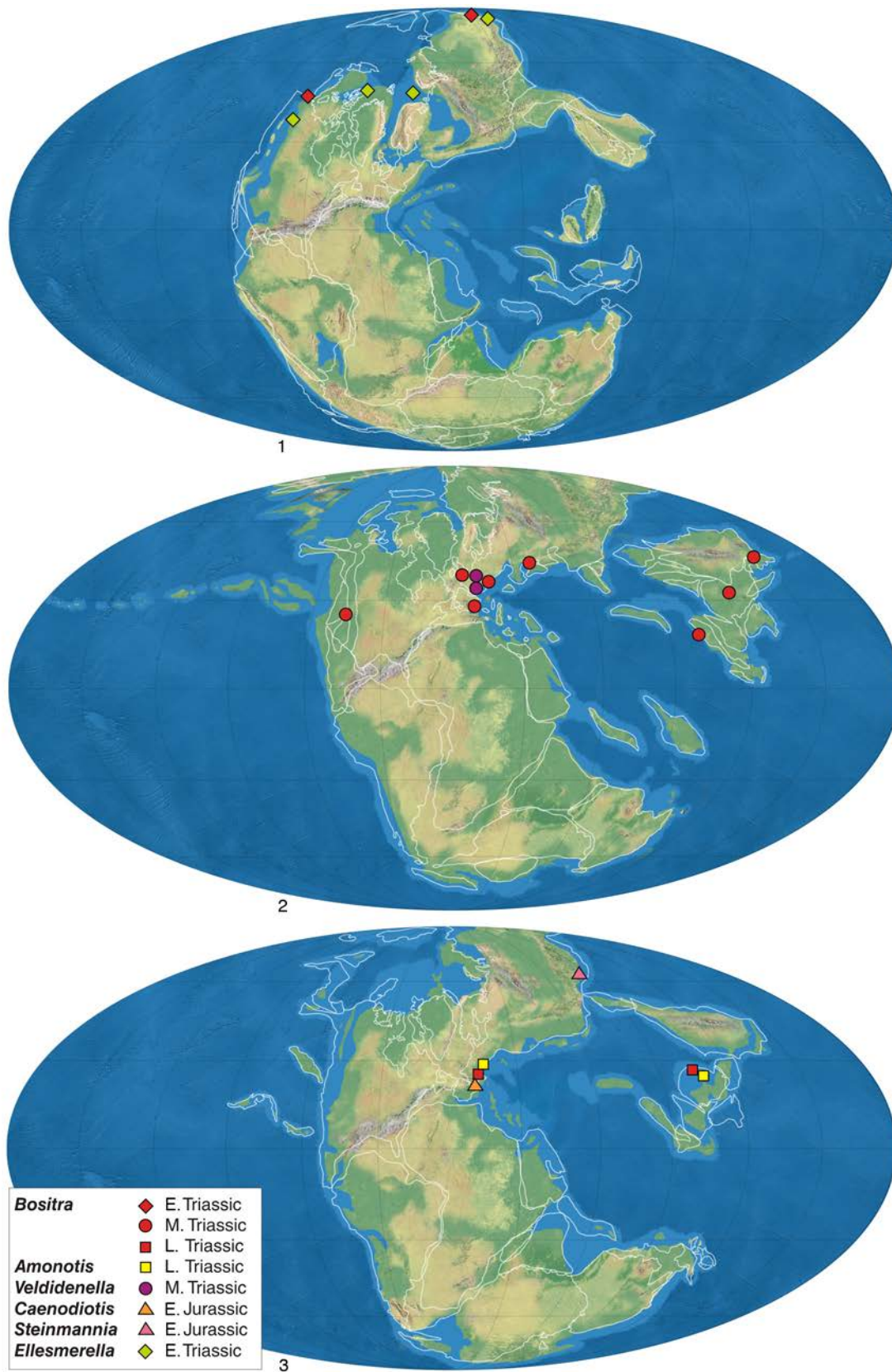


Figure 17. Paleogeographical distribution of Posidoniidae (*Bositra*, *Amonotis*, *Veldidenella*, *Caenodiotis*, *Steinmannia*, *Ellesmerella*). 1, Early Triassic; 2, Middle Triassic; 3, Late Triassic–Early Jurassic.

Mineralogy.—Bimineralic (Carter, 1990a; García-March, 2005). Outer shell layer: calcite (simple prismatic). Inner shell layer: aragonite (nacreous).

Superfamily LIMOIDEA Rafinesque, 1815

Family LIMIDAE Rafinesque, 1815

Genus PALAEOLIMA Hind, 1903 in 1896–1905, p. 38

Type species.—*Pecten simplex* Phillips, 1836, p. 212.

Remarks.—Newell (1999, p. 4) rejected *Palaeolima* because the material of the type species was lost and topotypes were not available. On the other hand, Waller and Stanley (2005, p. 32) stated that “Dickins (1963, p. 91), however, had earlier addressed this problem and designated a neotype of Phillips’s species, specifically the specimen figured by Hind (1903 in 1896–1905, p. 19, fig. 26) from Little Island, County Cork, Ireland.” According to these authors, *Palaeolima* remains valid.

Stratigraphic range.—Upper Devonian (?Famennian)–Upper Triassic (Norian) (Lu, 1981; Waller & Stanley, 2005). Cox and others (1969) assigned it a Carboniferous–Late Triassic range. Following Waller and Stanley (2005), the range is extended back to the Upper Devonian. The youngest records are from the Upper Triassic of China (Lu, 1981; J. Chen, 1982a; Lu & Chen, 1986).

Paleogeographic distribution.—Tethys and Circumpacific (Fig. 19). *Palaeolima* had an almost cosmopolitan distribution during the Paleozoic, especially during the Carboniferous–Permian (until the Guadalupian) interval (Yancey, 1985; González, 1992; Hoare, 1993; Nakazawa, 1999, 2002; Sterren, 2000, 2004; Cisterna & Sterren, 2003; Waller & Stanley, 2005). During the Triassic, it is found only from the Tethys and Circumpacific domains.

Tethys domain: late Permian: Kashmir (India) (Brookfield, Twitchett, & Goodings, 2003), China (Y. Zhang, 1981; M. Wang, 1993; L. Li, 1995); Early Triassic: China (Ling, 1988); Middle Triassic: Anisian of southern China (Komatsu, Akasaki, & others, 2004); Late Triassic: China (J. Chen, 1982a; Lu & Chen, 1986; Gou, 1993); Carnian of Italy (Corazzari & Lucchi-Garavello, 1980); Norian of China (Lu, 1981).

Circumpacific domain: Middle Triassic: Ladinian of Nevada (United States) (Waller & Stanley, 2005).

Paleoautoecology.—B, E, S, Epi, Sed; By. Living members of the family Limidae live epibyssate or reclined on the substrate or fixed by a slender byssus that may break, allowing occasional swimming (S. M. Stanley, 1970). From his observations of living species, S. M. Stanley (1970) concluded that good swimmers are often equivalent with symmetrical, equally sized auricles, and they have a large umbonal angle. In terms of external shell morphology, *Palaeolima* can be compared to the species *Lima lima* (Linnaeus, 1758), which lives epibyssate with a strong byssus. But the species assigned to *Palaeolima* lack a byssal notch. Other species, such as *Lima scabra* (Born, 1778) and *Lima hians* (Gmelin, 1791), are fairly symmetrical, live epibyssate with a weak byssus that can break, and swim occasionally (S. M. Stanley, 1970). *Palaeolima* has a rather symmetrical shell, and the auricles are of equal size, but the umbonal angle does not normally exceed 80° (from illustrations in the literature). We assume that *Palaeolima* lived epibyssate, as did *P. scabra*, although it is very unlikely that it could swim.

Mineralogy.—Bimineralic (Carter, 1990b, p. 345). Outer shell layer: calcite (simple prismatic). Middle and inner shell layers: aragonite (cross-lamellar).

Genus AVICULOLIMA E. Philippi, 1900, p. 622

Type species.—*Aviculolima jaekeli* E. Philippi, 1900, p. 622.

Remarks.—Although *Aviculolima* is externally similar to *Pteria*, Cox and others (1969) included it in the Limidae with doubts. Having no further information, we follow these authors in their allocation.

Stratigraphic range.—Middle Triassic (Anisian) (Diener, 1923). The only information we have about *Aviculolima* was given by Diener (1923) and Cox and others (1969). In both papers, the authors limit themselves to transcribing data from the original paper in which the genus was proposed. The genus was reported from the Lower Muschelkalk of northern Germany (probably Anisian).

Paleogeographic distribution.—western Tethys (Fig. 19). According to available information, the genus appears to be endemic to northern Germany.

Tethys domain: Middle Triassic: Lower Muschelkalk of northern Germany (Diener, 1923).

Paleoautoecology.—B, E, S, Epi, Sed; By. Given its external resemblance to *Pteria*, probably it was an epifaunal and byssate bivalve, although the generic diagnosis does not mention byssal structures.

Mineralogy.—Bimineralic (Cox & others, 1969; Carter, 1990a, p. 215). There is no information about *Aviculolima* shell. Data provided for family Limidae. Outer shell layer: calcite (prismatic). Inner shell layer: aragonite (non-nacreous).

Genus BADIOTELLA Bittner, 1890, p. 94

Type species.—*Badiotella schaurothiana* Bittner, 1895, p. 201. (See notes in Bittner, 1895, p. 200, and Cox & others, 1969, p. 386, related to the nomenclatural status of this genus and its type species).

Stratigraphic range.—Middle Triassic (Ladinian)–Upper Triassic (Carnian) (Diener, 1923). Although Cox and others (1969) assigned it a Ladinian range, there is evidence that the genus was also present in the Upper Triassic (see Bittner, 1895; Broili, 1904; Diener, 1923). Sepkoski (2002) assigned it a Ladinian–Carnian range, following the compilation made by Hallam (1981). The youngest records are from Carnian beds (see paleogeographic distribution).

Paleogeographic distribution.—Tethys (Fig. 19).

Tethys domain: Middle Triassic: China (Lu & Chen, 1986); Ladinian of the Alps (Broili, 1904; Cox & others, 1969); Late Triassic: Carnian of the Alps (Bittner, 1895; Broili, 1904; Diener 1923), China (Gou, 1993).

Paleoautoecology.—B, E, S, Epi–Un, Sed; By–R. Like all members of this family, *Badiotella* was an epifaunal bivalve. Byssal structures are not reported in published literature, so it possibly lived slightly reclined or fixed by a weak byssus.

Mineralogy.—Bimineralic (Cox & others, 1969; Carter, 1990a, p. 215). There are no data about *Badiotella* mineralogy or shell microstructure. Information provided for family Limidae. Outer shell layer: calcite (prismatic). Inner shell layer: aragonite (non-nacreous).

Genus LIMATULA Wood, 1839, p. 235

Type species.—*Pecten subauriculata* Montagu, 1808, p. 63.

Remarks.—*Limatula* and *Limea* Bronn, 1831, are genera with living representatives and conservative morphology. Even in Recent species, there is some confusion about which taxa should be referred to one genus or the other (Allen, 2004), and this distinction is much more complicated with fossil specimens.

Stratigraphic range.—Middle Triassic (Ladinian)—Recent. Cox and others (1969) assigned it a Triassic–Holocene range. The oldest record is Ladinian (Tamura, 1973); we did not find any records from the Lower Triassic, or from the Lower Jurassic, although from Toarcian times onward, it was fairly common throughout the Jurassic (Hallam, 1976, 1977, 1981; Fürsich, 1982; Pugaczewska, 1986; Komatsu, Saito, & Fürsich, 1993; Liu, 1995; Sha and others, 1998; J. Yin & Grant-Mackie, 2005).

Paleogeographic distribution.—Tethys, Circumpacific, and Austral (Fig. 19).

Tethys domain: Middle Triassic: Ladinian of Malaysia (Tamura, 1973); Late Triassic: Rhaetian of Italy (Chiesa, 1949), Hungary (Vörös, 1981).

Circumpacific domain: Late Triassic: Norian of Japan (Tokuyama, 1959b; doubtful record also in Nakazawa, 1963).

Austral domain: Late Triassic: Carnian of New Zealand (Trechmann, 1918).

Paleoautoecology.—B, E, S, Epi, FaM; By-Sw. Some living species, such as *Limatula strangei* (G. B. Sowerby, 1872), live among rocks and corals, and they are able to swim (Beesley, Ross, & Wells, 1998). They have equivalve and slightly inequilateral shells and subequal auricles. The shell morphology remained practically unchanged from the Triassic to the present (Allen, 2004); we assume that Mesozoic species had similar modes of life. *Limatula* probably lived byssate most of the time and reclined on the substrate, with the anterior part down (Fürsich, 1982).

Mineralogy.—Bimineralic (Carter, 1990b, p. 345). Outer shell layer: calcite (prismatic). Inner shell layer: aragonite (?).

Genus LIMEA Bronn, 1831, p. 115

Type species.—*Ostrea strigilata* Brocchi, 1814, p. 571.

Remarks.—The only subgenus considered by Cox and others (1969) in our study interval is *Limea* (*Eolimea*) Cox in Cox and others, 1969, p. 389, with a Middle Triassic range. From the Middle Triassic to the Miocene, when *Limea* (*Limea*) appears, there is a long time interval without records of this genus. This was noticed by Dhondt (1989), who also noted that *Pseudolimea* Arkell in Douglas & Arkell, 1932, which ranges from Triassic to Cretaceous, was distinguished from *Limea* mainly by the shape of the ribs. Moreover, other subgenera of *Limea*, such as *Isolimea* or *Eolimea*, are differentiated by their strong ornamentation. Dhondt noted that *Pseudolimea* was very similar to *Limea* and it could fill this time gap, and she included it as a subgenus of *Limea*. This arrangement is followed here.

Stratigraphic range.—Middle Triassic (Anisian)—Holocene (Cox & others, 1969). The stratigraphic range of *Limea* recognized here is the same as in Cox and others (1969). The oldest record is from Anisian times (Kaim, 1997).

Paleogeographic distribution.—Cosmopolitan (Fig. 19).

Tethys domain: Middle Triassic: Poland (Kaim, 1997); Anisian western Caucasus (Russia) (Ruban, 2006a); Ladinian of Spain (Márquez-Aliaga, 1983; Pérez-López, 1991; Pérez-López & others, 1991; López-Gómez & others, 1994; Márquez-Aliaga & Martínez, 1996; Márquez-Aliaga, García-Forner, & Plasencia, 2002), Italy (Rossi Ronchetti, 1959); Late Triassic: Norian of southern China (J. Chen & Yang, 1983); Early Jurassic: Hettangian of northern Alps (Austria) (Golebiowski, 1990); Hettangian–Sinemurian of England (Liu, 1995), Spain (Calzada, 1982); Sinemurian of France, Portugal, and Morocco (Liu, 1995), Turkey (M. A. Conti & Monari, 1991).

Circumpacific domain: Late Triassic: Carnian of Japan (Nakazawa, 1952; Hayami, 1975); Norian of Oregon (United States) (Newton in Newton & others, 1987), Nevada (United States) (Laws, 1982); Norian of Chile (Hayami, Maeda, & Ruiz-Fuller, 1977); Rhaetian of Chile (Chong & Hillebrandt, 1985); Early Jurassic: Hettangian–Sinemurian of western Canada (Aberhan, 1998a; Aberhan, Hrudka, & Poulton, 1998), Chile (Aberhan, 1994a).

Austral domain: Late Triassic: Carnian of New Zealand (Grant-Mackie, 1960); Rhaetian of New Zealand (MacFarlan, 1998) and Argentina (Damborenea & Manceñido, 2012); Early Jurassic: Hettangian–Sinemurian of Neuquén Basin (Argentina) (Damborenea, 1996a; Damborenea & Manceñido, 2005b), New Zealand (MacFarlan, 1998).

Boreal domain: Early Jurassic: Hettangian–Sinemurian of?Greenland (Liu, 1995).

Paleoautoecology.—B, E, S, Epi, Sed; By. *Limea* is a long-ranging genus that exhibits a conservative morphology throughout its history (Allen, 2004). The Recent species of this genus live mainly in deep water, and it was proposed that the extinct species also lived mostly in this type of environment (Dhondt, 1989). *Limea* species probably lived as epibyssate and reclined on one of the valves (Fürsich, 1982), similar to living species.

Mineralogy.—Bimineralic (Cox & others, 1969; Carter, 1990a, p. 215). There are no data about *Limea* shell. Data provided for family Limidae. Outer shell layer: calcite (prismatic). Inner shell layer: aragonite (non-nacreous).

Genus MYSIDIOPTERA Salomon, 1895, p. 117

Type species.—*Mysidioptera ornata* Salomon, 1895, p. 117.

Remarks.—Two subgenera are considered in the study interval, *M.* (*Mysidioptera*) and *M.* (*Pseudacesta*) Waagen, 1907, p. 113.

Stratigraphic range.—Lower Triassic (Olenekian)—Upper Triassic (Rhaetian). Cox and others (1969) assigned it a Lower Triassic–Upper Triassic range, and this is maintained here. *Mysidioptera* was not abundant in the Triassic, but it had a climax during Ladinian and Carnian; and although it was scarce during the Rhaetian, it lived to the end of the stage, when it became extinct.

Paleogeographic distribution.—Cosmopolitan (Fig. 19).

Tethys domain: Middle Triassic: Anisian of China (Wen & others, 1976; Lu & Chen, 1986; Sha, Chen, & Qi, 1990; Komatsu, Chen, & others, 2004; Komatsu, Akasaki, & others, 2004), Malaysia (Tamura & others, 1975), Swiss Dolomites (Zorn, 1971), Italian Dolomites (Posenato, 2008b), Israel (Lerman, 1960), northern Vietnam (Kom-

atsu, Huyen, & Huu, 2010); Ladinian of Alps (Austria) (Salomon, 1895), north of Vietnam and Thailand (Vu Khuc & Huyen, 1998), Malaysia (Tamura, 1973), Lombardy (Italy) (Rossi Ronchetti, 1959), northern Vietnam (Komatsu, Huyen, & Huu, 2010); Late Triassic: China (Gou, 1993); Carnian of southern Alps (Bittner, 1895, 1900; Salomon, 1895; Broili, 1904; Allasinaz, 1966; Fürsich & Wendt, 1977; Posenato, 2008a, 2008b), Carpathians (Slovakia) (Bujnovsky, Kochanová, & Pevny, 1975; Kochanová, Mello, & Siblík, 1975), Jordan (Cox, 1924); Rhaetian of Tibet (China) (Hallam & others, 2000), East of the Alps (Austria) (Tomašových, 2006a, 2006b).

Circumpacific domain: Early Triassic: Olenekian of Japan (Nakazawa, 1961; Hayami, 1975); Late Triassic: Japan (Hayami, 1975), Norian of Oregon (Newton in Newton & others, 1987), Norian of Sonora (Mexico) (Damborenea in Damborenea & González-León, 1997).

Austral domain: Late Triassic: Carnian of New Zealand (Waterhouse, 1960).

Boreal domain: Late Triassic: Carnian of Arctic area of British Columbia (Canada) (Tozer, 1962, 1970).

Paleoautoecology.—B, E, S, Epi, Sed; By. The external shell morphology of different species attributed to *Mysidiopora* indicates an epibyssate habit, since most show a byssal notch. It could live on both hard and soft substrates (Newton in Newton & others, 1987). They were reported from a variety of facies, as they are thought to have colonized different environments (Damborenea in Damborenea & González-León, 1997).

Mineralogy.—Bimineralic (Cox & others, 1969; Carter, 1990a, p. 215). There are no data about *Mysidiopora* shell mineralogy. Data provided for family Limidae. Outer shell layer: calcite (prismatic). Inner shell layer: aragonite (non-nacreous).

Genus PLAGIOSTOMA J. Sowerby, 1814, p. 175

Type species.—*Plagiostoma gigantea* J. Sowerby, 1814, p. 176.

Stratigraphic range.—Middle Triassic (Anisian)—Upper Cretaceous (Maastrichtian) (Abdel-Gawad, 1986; Komatsu, Chen, & others, 2004). Cox and others (1969) assigned it a Middle Triassic–Cretaceous range. However, Sepkoski (2002) considered it to be from the Lower Triassic (Induan), indicating that data were taken from Abdel-Gawad (1986), but this author only mentioned *Plagiostoma* from the Cretaceous. This datum is wrong, since *Plagiostoma* was not present before the Middle Triassic (see Paleogeographic distribution, below), and it may have derived from Lower Triassic *Mysidiopora* (Bittner, 1895; Waller & Stanley, 2005). Dagens and Kurushin (1985) reported *Plagiostoma aurita* (Popov) and *Plagiostoma popovi* Kurushin in Dagens & Kurushin, 1985, from the Lower Triassic, but the figured specimens have little in common with the diagnosis of the genus *Plagiostoma*.

Paleogeographic distribution.—Cosmopolitan (Fig. 19).

Tethys domain: Middle Triassic: Hungary (Sente, 1997), Poland (Kaim, 1997); Anisian of Germany (Hautmann, 2006a), southern China (Sha, Chen, & Qi, 1990; Komatsu, Chen, & others, 2004), Switzerland (Zorn, 1971); Ladinian of Sardinia (Italy) (Posenato, 2002; Posenato & others, 2002), Malaysia (Tamura, 1973; Tamura & others, 1975); Late Triassic: China (J. Chen, 1982a; Gou, 1993), Oman (R. Hudson & Jefferies, 1961); Carnian of Malaysia (Tamura & others, 1975), Lombardy (Italy) (Allasinaz, 1966); Norian of

Himalaya (Tibet, China) (J. Yin, Enay, & Wan, 1999), southern China (Wen & others, 1976; Sha, Chen, & Qi, 1990), northwestern China (Lu, 1981); Norian–Rhaetian of Iran and the Alps (Hautmann, 2001b); Rhaetian of eastern Alps (Austria) (Tomašových, 2006a, 2006b), Tibet (China) (Hautmann & others, 2005; J. Yin & McRoberts, 2006), Hungary (Vörös, 1981), Lombardy (Italy) (Allasinaz, 1962); Early Jurassic: Hettangian of southern England (Ivimey-Cook & others, 1999), Tibet (China) (Hautmann & others, 2005; J. Yin & McRoberts, 2006), Italy (Gaetani, 1970); Hettangian–Sinemurian of England and France (Liu, 1995), Lombardy (Italy) (Allasinaz, 1962); Sinemurian of Caucasus (southwestern Russia) (Ruban, 2006b), Portugal and Morocco (Liu, 1995).

Circumpacific domain: Middle Triassic: Ladinian of Nevada (United States) (Waller & Stanley, 2005); Late Triassic: Japan (Kobayashi & Ichikawa, 1949a; Tokuyama, 1959a); Carnian of Japan (Hayami, 1975); Norian of Oregon (United States) (Newton in Newton & others, 1987; but see Waller & Stanley, 2005); Early Jurassic: ?Mexico (Damborenea in Damborenea & González-León, 1997); Hettangian–Sinemurian of western Canada (Aberhan, 1998a), Mexico and Texas (Liu, 1995), northern Chile (Aberhan, 1994a); Sinemurian of Japan (Hayami, 1975; Hayami in Sato & Westermann, 1991).

Austral domain: Early Jurassic: Sinemurian of Neuquén Basin (Argentina) (Damborenea, 1996a; Damborenea & Manceñido, 2005b).

Boreal domain: Late Triassic: Carnian of Primorie (Kiparisova, 1972).

Paleoautoecology.—B, E, S, Epi, Sed; By. Like most limids, *Plagiostoma* was probably an epibyssate bivalve. Although no description pointing to a byssal notch was found, we assume that the byssus would have emerged below the anterior auricle. We cannot rule out that it could eventually swim, but this is unlikely due to the shell thickness (Seilacher, 1984); a reclining habit on its broad anterior base is more likely.

Mineralogy.—Bimineralic (Carter, 1990a, p. 215; Carter, 1990b, p. 345). Outer shell layer: calcite (prismatic). Inner shell layer: aragonite (non-nacreous).

Genus SERANIA Krumbeck, 1923a, p. 218

Type species.—*Serania seranensis* Krumbeck, 1923a, p. 218.

Stratigraphic range.—Upper Triassic (Norian–Rhaetian) (Hautmann, 2001b). According to Kutassy (1931), *Serania* was proposed by Krumbeck (1923a) on the basis of material from Norian beds of Indonesia and Persia. Cox and others (1969) assigned it a Norian age, as did also Sepkoski (2002), based on Hallam's (1981) data. It was subsequently reported also from Rhaetian beds (Hautmann, 2001b).

Paleogeographic distribution.—Eastern Tethys (Fig. 19). *Serania* was a monospecific genus endemic for the eastern Tethys.

Tethys domain: Late Triassic: Norian of Indonesia and Persia (Kutassy, 1931); Norian–Rhaetian of Iran (Hautmann, 2001b).

Paleoautoecology.—B, E, S, Epi, Sed; By. Like most members of family Limidae, *Serania* was probably an epibyssate bivalve, similar to *Plagiostoma* (Hautmann, 2001b). *Serania seranensis* shows a deep byssal notch (see Cox & others, 1969, p. 392), which implied a strong byssus.

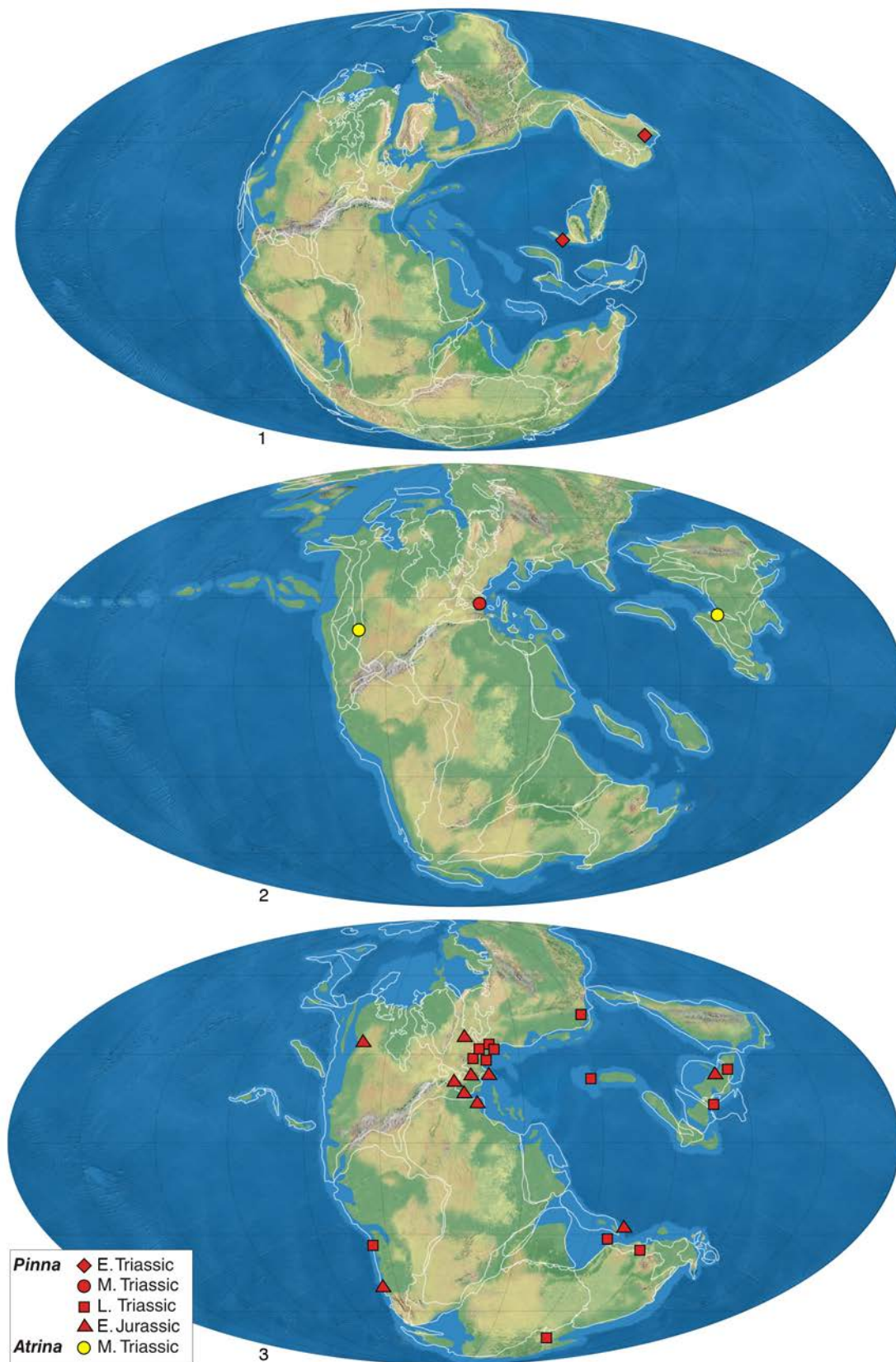


Figure 18. Paleogeographical distribution of Pinnidae (*Pinna*, *Atrina*). 1, Early Triassic; 2, Middle Triassic; 3, Late Triassic–Early Jurassic.

Mineralogy.—Bimineralic (Cox & others, 1969; Carter, 1990a, p. 215). There are no data about the shell of *Serania*. Data provided for family Limidae. Outer shell layer: calcite (prismatic). Inner shell layer: aragonite (non-nacreous).

Genus TIROLIDIA Bittner, 1895, p. 202

Type species.—*Lima (Tirolidia) haueriana* Bittner, 1895, p. 202.

Stratigraphic range.—Middle Triassic (Ladinian)—Upper Triassic (Carnian) (Diener, 1923). Cox and others (1969) assigned a Middle Triassic–Upper Triassic range. Bittner (1895) proposed *Tirolidia* from Ladinian and Carnian beds of the southern Alps. Diener (1923) and Kutassy (1931) provided the same data. Little else could be found, except that Hallam (1981) assigned it a Ladinian–Carnian range in western Tethys, and thus this genus seems to be endemic to the southern Alps.

Paleogeographic distribution.—western Tethys (Fig. 19).

Tethys domain: Middle Triassic: Ladinian of Southern Alps (Bittner, 1895); Late Triassic: Carnian of Southern Alps (Bittner, 1895).

Paleoautoecology.—B, E, S, Epi, Sed; By. *Tirolidia* is slightly inequilateral and has unequal auricles, so it is not a good candidate to be a swimmer. We assign it an epibyssate mode of life, similar to other members of this family.

Mineralogy.—Bimineralic (Cox & others, 1969; Carter, 1990a, p. 215). No specific data about *Tirolidia* mineralogy and shell microstructure are known. Data provided for family Limidae. Outer shell layer: calcite (prismatic). Inner shell layer: aragonite (non-nacreous).

Genus ANTIQUILIMA Cox, 1943, p. 179

Type species.—*Lima antiquata* J. Sowerby, 1818, p. 25.

Stratigraphic range.—Middle Triassic (Ladinian)—Lower Cretaceous (Aptian) (Hayami, 1965; Waller & Stanley, 2005). Cox and others (1969) considered it to be a Jurassic genus (Liassic–Bajocian), but, since then, new records have expanded its range. The oldest record of *Antiquilima* is from Ladinian beds of Nevada (Waller & Stanley, 2005) and the youngest from Lower Cretaceous beds (Aptian) (Hayami, 1965).

Paleogeographic distribution.—Cosmopolitan (Fig. 19). According to Damborenea (2000), *Antiquilima* probably originated in the Eastern Pacific and subsequently it spread to the Tethys, which agrees with the data found about the genus.

Tethys domain: Late Triassic: Norian–Rhaetian of Iran (Hautmann, 2001b); Rhaetian of the Alps (Austria) (Tomašových, 2006a, 2006b), Tibet (China) (J. Yin & McRoberts, 2006), western Carpathians (Slovakia) (Tomašových, 2004); Early Jurassic: Hettangian–Sinemurian of England (Liu, 1995); Sinemurian of France (Vörös, 1971; Liu, 1995), Apennines (Italy) (Monari, 1994).

Circumpacific domain: Middle Triassic: Ladinian of Nevada (United States) (Waller & Stanley, 2005); Late Triassic: Norian of northern Chile (Hayami, Maeda, & Ruiz-Fuller, 1977), Oregon (United States) (Newton, 1986; Newton in Newton & others, 1987); Early Jurassic: Hettangian–Sinemurian of northern Chile (Aberhan, 1994a); Sinemurian of Canada (Aberhan, 1998a), Japan (Hayami, 1975).

Austral domain: Early Jurassic: Sinemurian of Argentina (Damborenea, 1996a; Damborenea & Manceñido, 2005b; Damborenea & Lanés, 2007).

Boreal domain: Late Triassic: Carnian of Primorie (Kiparisova, 1972); Norian of northeastern of Asia (Kurushin, 1990; Polubotko & Repin, 1990); Norian–Rhaetian of eastern Siberia (Kiparisova, Bychkov, & Polubotko, 1966), northeastern Russia (Milova, 1976); Early Jurassic: Hettangian of northeastern Asia (Kurushin, 1990; Polubotko & Repin, 1990), northeastern Russia (Milova, 1976).

Paleoautoecology.—B, E, S, Epi, Sed; By. In most species, a byssal notch is present (e.g., specimens described in Hayami, Maeda, & Ruiz-Fuller, 1977; Newton in Newton & others, 1987; Hautmann, 2001b), and most likely it was an epibyssate bivalve as in the rest of the limids. According to Newton (in Newton & others, 1987), *Antiquilima* could sever the byssus and swim for short distances, as do some modern species of the family Limidae. However, due to its external morphology, it was probably not a good swimmer.

Mineralogy.—Bimineralic (Cox & others, 1969; Carter, 1990a, p. 215; Waller & Stanley, 2005). Outer shell layer: calcite (prismatic). Inner shell layer: aragonite (non-nacreous).

Genus CTENOSTREON Eichwald, 1862, p. 374

Type species.—*Ostracites pectiniformis* von Schlotheim, 1820, p. 231.

Stratigraphic range.—Upper Triassic (upper Rhaetian)—Lower Cretaceous (?Valanginian). Cox and others (1969) assigned it a Jurassic (Liassic)—Lower Cretaceous (Neocomian) range. Sepkoski (2002) considered that it originated in the lower Hettangian following Hallam (1977, 1987). The origin of this genus was regarded as Hettangian for a long time (Hallam, 1977, 1987, 1990), but recently J. Yin, H. Yao, and Sha (2004) and J. Yin and McRoberts (2006) found *Ctenostreon* in layers transitional between the Rhaetian and Hettangian. These Himalayan records were dated as Rhaetian, because they were associated with the ammonoid *Choristoceras* (J. Yin, H. Yao, & Sha, 2004). We ignore to what part of the Neocomian Cox and others (1969) referred for the last record. The youngest record of the genus dates from Valanginian times (Császár & Turnšek, 1996), but specimens were neither figured nor described, so we tentatively consider this as the last appearance.

Paleogeographic distribution.—Tethys, Austral, and Circumpacific (Fig. 19).

Tethys domain: Late Triassic: Rhaetian of southern China (J. Yin, H. Yao, & Sha, 2004; J. Yin & McRoberts, 2006); Early Jurassic: Hettangian of Tibet (China) (J. Yin & McRoberts, 2006; J. Yin & others, 2007).

Austral domain: Early Jurassic: Hettangian–Sinemurian of the Neuquén Basin (Argentina) (Damborenea, 1996a; Damborenea & Manceñido, 2005b).

Circumpacific domain: Early Jurassic: Sinemurian of Japan (Hayami, 1975), Chile (Aberhan, 1994a).

Paleoautoecology.—B, E, S, Epi, Sed; By. *Ctenostreon* is regarded as an epibyssate bivalve, although the byssal notch is not always evident and sometimes it is even absent. Its shell is thick compared with other members of this family; we assume that it would not need a very strong byssus. Seilacher (1984) suggested that it is one of those limids for which a swimming mode of life is excluded, due to its

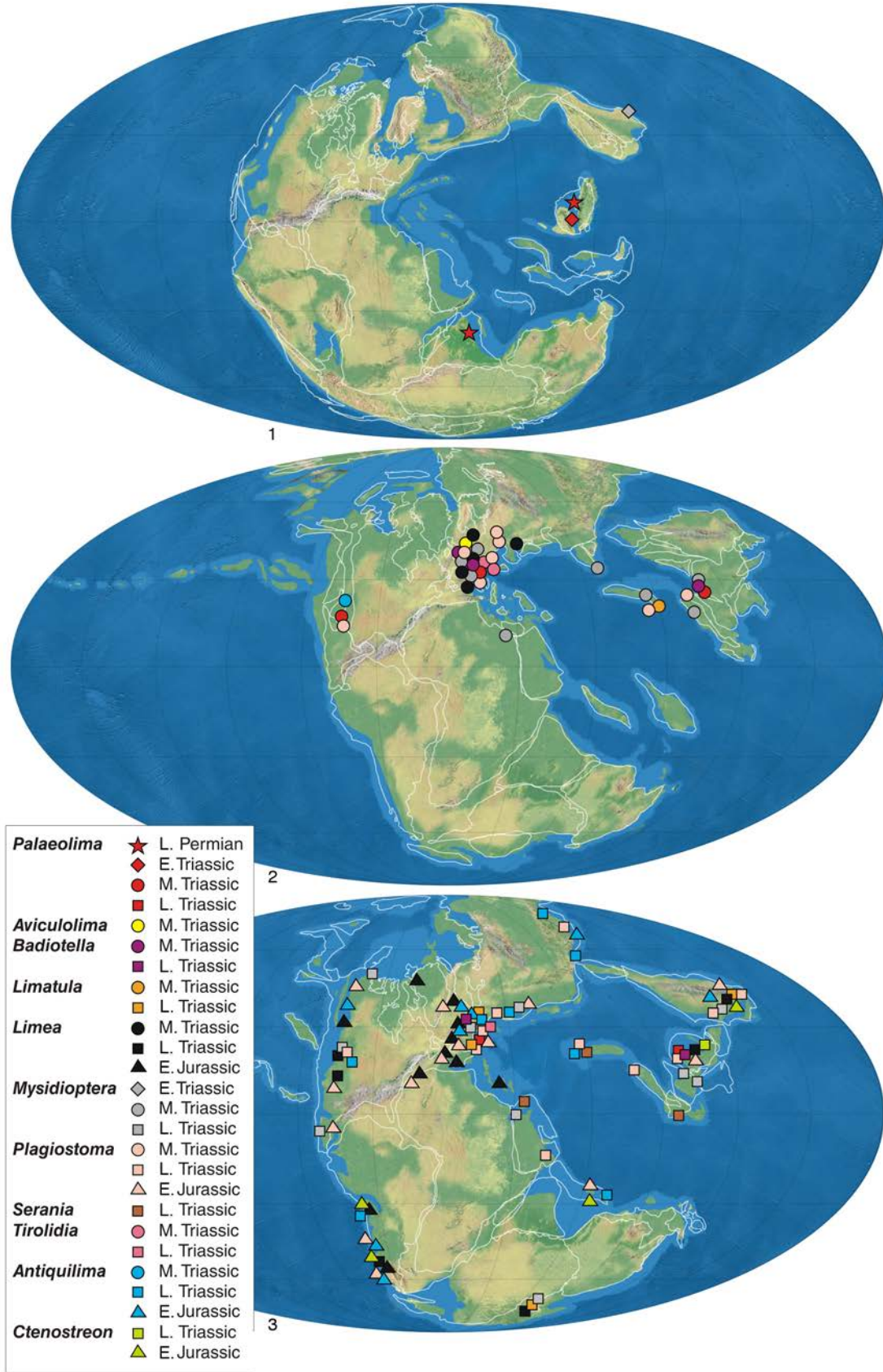


Figure 19. Paleogeographical distribution of Limidae (*Palaeolima*, *Aviculolima*, *Badiotella*, *Limatula*, *Limea*, *Mysidioptera*, *Plagiostoma*, *Serania*, *Tirolidia*, *Antiquilima*, *Ctenostreon*). 1, late Permian–Early Triassic; 2, Middle Triassic; 3, Late Triassic–Early Jurassic.

thick shell and presence of spines; it was probably a pleurothetic reclined bivalve.

Mineralogy.—Bimineralic (Cox & others, 1969; Carter, 1990a, p. 215). No specific data about *Ctenostreon* mineralogy and shell microstructure is known. Information provided for family Limidae. Outer shell layer: calcite (prismatic). Inner shell layer: aragonite (non-nacreous).

Superfamily OSTREOIDEA Wilkes, 1810

Family GRYPHAEIDAE Vialov, 1936

Genus GRYPHAEA Lamarck, 1801, p. 398

Type species.—*Gryphaea arcuata* Lamarck, 1801, p. 398.

Remarks.—Newell and Boyd (1970, 1989, 1995) discussed the external morphological similarity between *Pseudomonotis* and *Gryphaea* (see fig. 47 in Newell & Boyd, 1995). Frequently, these genera can only be distinguished by the shell microstructure and which valve is attached to the substrate (right and left respectively) (Newell & Boyd, 1995). Many of the *Pseudomonotis* records from Triassic and Jurassic could actually belong to *Gryphaea*, since *Pseudomonotis* is now regarded as a strictly Paleozoic genus, and it is not an ostreoid.

Stratigraphic range.—Upper Triassic (Carnian)—Upper Cretaceous (Campanian) (McRoberts, 1992; Newell & Boyd, 1989). Stenzel (1971) considered that *Gryphaea* was present in the Upper Triassic of the Boreal domain and had a worldwide distribution for most of the Jurassic (Hettangian–Oxfordian). New records changed the observed stratigraphic range of this genus: *Gryphaea* was reported from Upper Triassic beds, from the Carnian (McRoberts, 1992) in the Paleopacific eastern margin, in addition to the Boreal regions. It had not been found anywhere in upper Norian and Rhaetian beds, so McRoberts (1992) interpreted it as a Lazarus taxon that reappeared in the Hettangian stage, but Rubilar (1998) reported *Gryphaea* from the Norian–Rhaetian of Chile.

The youngest record is from the Upper Cretaceous (Newell & Boyd, 1989). Although there are some papers that mentioned *Gryphaea* up until the Pleistocene, they are not taken into account as they are biostratigraphic studies and they do not describe or figure the listed material.

Paleogeographic distribution.—Cosmopolitan (Fig. 20).

Tethys domain: Early Jurassic: Tibet (China) (Gou, 2003); Hettangian of Italy (Gaetani, 1970); Hettangian–Sinemurian of France (Liu, 1995; Nori & Lathuilière, 2003), England, Spain, Portugal, and Morocco (Liu, 1995).

Circumpacific domain: Late Triassic: Carnian–Norian of Canada, Oregon, and Nevada (United States) (McRoberts, 1992), northern and southern Alaska (McRoberts, 1992; McRoberts & Blodgett, 2000); Norian of Chile (Hayami, Maeda, & Ruiz-Fuller, 1977); Norian–Rhaetian of Chile (Rubilar, 1998); Early Jurassic: Hettangian of Chile (Aberhan, 1994a); Sinemurian of Chile (Steinmann, 1929; Chong & Hillebrandt, 1985; Hillebrandt, 1990; Aberhan, 1994a; Malchus & Aberhan, 1998; Rubilar, 1998), Canada (Poulton, 1991).

Austral domain: Early Jurassic: Sinemurian of Argentina (Damborenea & Manceñido, 2005b; Damborenea & Lanés, 2007).

Boreal domain: Late Triassic: Arctic area of Siberia (Kiparisova, 1954), northeastern Russia (Milova, 1976); Carnian of Arctic Island (Canada) (Tozer, 1970); Carnian–Norian of Primorie (Kiparisova, 1972); Early Jurassic: Hettangian of northeastern Russia (Milova, 1988).

Paleoautoecology.—B, E, S, Un, Sed; R. Some species of *Gryphaea* lived cemented to the substrate during the juvenile stages, but they often changed to a reclined life habit in the adult stage (Fürsich & others, 2001). Seilacher (1984) interpreted certain *Gryphaea* species as being cup-shaped recliners, living on soft substrates: they probably rested on their left valve, which is strongly convex and thick, unlike the flat and smooth right valve. The left valve was used to anchor the shell to soft sediments. *Gryphaea* would thus live epifaunally or partially buried. The specimens are usually found in fine-grained sediments (clay, marl) that are characteristic of low-energy marine environments (Lewy, 1976). The shell morphology of *Gryphaea*, as in other ostreids, is strongly influenced by the environment. Nori and Lathuilière (2003) proved that several factors (temperature, oxygen level, and humidity) were responsible for the different morphologies.

Mineralogy.—Bimineralic (Carter, 1990a, p. 232). Although the shell microstructure of Triassic specimens is not known, Jurassic specimens have a prismatic outer shell layer and a foliated inner shell layer, both being calcitic (Carter, 1990a). However, McRoberts and Carter (1994) found that middle and inner layers of *G. nevadensis* were originally of nacreous microstructure (aragonite).

Family OSTREIDAE Wilkes, 1810

Genus UMBROSTREA Hautmann, 2001a, p. 359

Type species.—*Umbrostrea emamii* Hautmann, 2001a, p. 361.

Remarks.—Hautmann (2001a) proposed *Umbrostrea* to include some specimens from the Upper Triassic of Iran that attached by the left valve (consensual basis for defining the true oysters), built reefs, and possessed an inner foliated shell microstructure and aragonitic inner shell layer (data considered as preliminary by the author). He proposed two new species, *Umbrostrea emamii* and *Umbrostrea iranica*, and tentatively considered *Umbrostrea?* aff. *parasitica* (Krumbeck, 1913) within the genus. Subsequently, Márquez-Aliaga and others (2005) examined a sample of hundreds of specimens attributed to *Enantiostreon difforme* (Goldfuss, 1833 in 1833–1841) [= *Ostracites cristadiformis* Schlotheim, 1820] and *Enantiostreon spondyloides* (Schlotheim, 1820) from the Lower and Upper Muschelkalk (Middle Triassic, Anisian–Ladinian) of the Germanic Basin, from levels equivalent to those from where the *Enantiostreon* species were described, attributed by these authors to real oysters. The authors accepted that the first record of ostreids from those levels was by Seilacher (1954), who classified some specimens attached by their left valve to *Plagiostoma* shells as *Alectryonia* (= *Lopha*), but with *Enantiostreon* morphology. Seilacher (1954) relied on the kind of so-called twisting of the valves and on the antimarginal pattern of the shell folds. This last criterion was developed by Checa and Jiménez-Jiménez (2003b) for cemented bivalves, and it is characteristic of ostreids. In the same paper, Márquez-Aliaga and others (2005) studied the Hispanic Muschelkalk (Ladinian) specimens attributed to *E. difforme* by Márquez-Aliaga (1985), on which microstructural studies were performed (De Renzi & Márquez-Aliaga, 1980; Márquez-Aliaga & Martínez, 1990b; Márquez-Aliaga & Márquez, 2000). In these studies, the authors verified the presence of foliated and calcitic outer shell layer and an inner shell layer replaced by sparite of possible aragonitic origin; this type of microstructure is characteristic of ostreids. However, the absence of internal features in all the studied

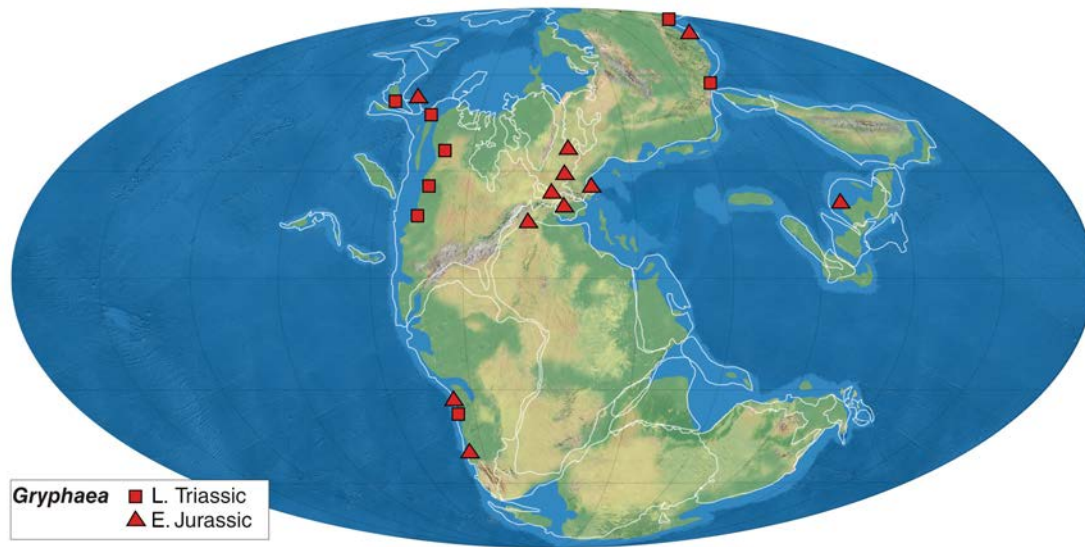


Figure 20. Paleogeographical distribution of Gryphaeidae (*Gryphaea*). Late Triassic–Early Jurassic.

specimens did not solve the controversial problem of the origin of the oysters. Thus, several replies to this proposal were generated, including other evolutionary aspects (see discussion in Márquez-Aliaga & others, 2005; Hautmann, 2006b; Checa & others, 2006; and Malchus, 2008). Other authors, like Ivimey-Cook and others (1999) and J. Yin and McRoberts (2006), preferred to include the species *Enantiostreon difforme* within *Terquemia* Cox, 1964. Here we provisionally accept the criteria of Márquez-Aliaga and others (2005).

Stratigraphic range.—Middle Triassic (Anisian)—Upper Triassic (Rhaetian) (Hautmann, 2001a; Márquez-Aliaga & others, 2005). Hautmann (2001a, 2001b) assigned it a Norian–Rhaetian range. Accepting the species assigned by Márquez-Aliaga and others (2005) into *Umbrostrea*, the range extends from the Middle Triassic, with the origin of *U. cristadiformis* and *U. spondyloides* being in Anisian times.

Paleogeographic distribution.—Tethys (Fig. 21).

Tethys domain: Middle Triassic: Anisian of Poland (Kaim, 1997), Bulgaria (Budurov & others, 1993), Hungary (Szente, 1997); Ladinian of Sardinia (Márquez-Aliaga & others, 2000; Posenato, 2002), Spain (Márquez-Aliaga, 1985; Márquez-Aliaga & Martínez, 1996); Late Triassic: Norian of Indonesia (Diener, 1923); Norian–Rhaetian of Iran (Hautmann, 2001a, 2001b; Fürsich & Hautmann, 2005), Rhaetian of England (Ivimey-Cook & others, 1999), ?Rhaetian of Tibet (China) (J. Yin & McRoberts, 2006).

Paleoautoecology.—B, E, S, C, Sed; C. Although Hautmann (2001a, 2001b) considered that *Umbrostrea* lived cemented to the substrate by the left valve, the species *U. cristadiformis* and *U. spondyloides* could attach by either valve (Márquez-Aliaga & others, 2005). It lived forming small reefs in fully marine environments and was associated with corals, brachiopods, and other bivalves (Hautmann, 2001a).

Mineralogy.—Bimineralic (De Renzi & Márquez-Aliaga, 1980; Carter, Barrera, & Tevesz, 1998; Hautmann, 2001a). In the diagnosis of *Umbrostrea*, Hautmann (2001a) indicated that the species attrib-

uted to this genus are characterized by a regular simple prismatic outer shell layer of calcite, a middle shell layer of foliated calcite, and an aragonitic inner shell layer of unknown microstructure. *Umbrostrea cristadiformis* had a foliated calcitic outer shell layer and an aragonitic inner shell layer (De Renzi & Márquez-Aliaga, 1980). According to Carter, Barrera, and Tevesz (1998), *U. spondyloides* (upper Muschelkalk, Ladinian, southwestern Germany) had an aragonitic inner shell layer and calcitic middle and upper shell layers, the last with regular to homogeneous and irregular prismatic microstructures. Outer shell layer: calcite (simple prismatic–foliated). Middle shell layer: calcite (?foliated). Inner shell layer: aragonite (?nacreous).

Genus ACTINOSTREON Bayle, 1878, expl. pl. 132

Type species.—*Ostrea solitaria* J. de C. Sowerby, 1824, p. 105.

Remarks.—*Palaeolopha* Malchus, 1990, is regarded a junior synonym of *Actinostreon* (see discussion under *Palaeolopha*, Genera not Included, p. 166).

Stenzel (1971) considered *Actinostreon* as a subgenus of *Lopha*, and this was followed by most authors. However, Malchus (1990) included *Actinostreon*, together with his new genus *Palaeolopha*, in his new family Palaeolophidae, and he regarded *Actinostreon* as an independent genus different from *Lopha*. Checa and Jiménez-Jiménez (2003b) included the species *Enantiostreon difforme* (Goldfuss, 1833 in 1833–1841) [= *Ostracites cristadiformis* Schlotheim, 1823 in 1822–1823] in *Actinostreon*, since Malchus (1990) included this species in *Palaeolopha*, and they followed the synonymy proposed by Hautmann (2001a, p. 359), i.e. *Actinostreon* = *Palaeolopha* Malchus, 1990). Subsequently, Márquez-Aliaga and others (2005) included the species *cristadiformis* in *Umbrostrea* Hautmann, 2001a.

Stratigraphic range.—Upper Triassic (Rhaetian)—Upper Cretaceous (Maastrichtian) (Chiplonkar & Badve, 1977; Hautmann, 2001a). Stenzel (1971) assigned it a Jurassic–Cretaceous range; these data were incorporated by Sepkoski (2002), who added Maastrichtian

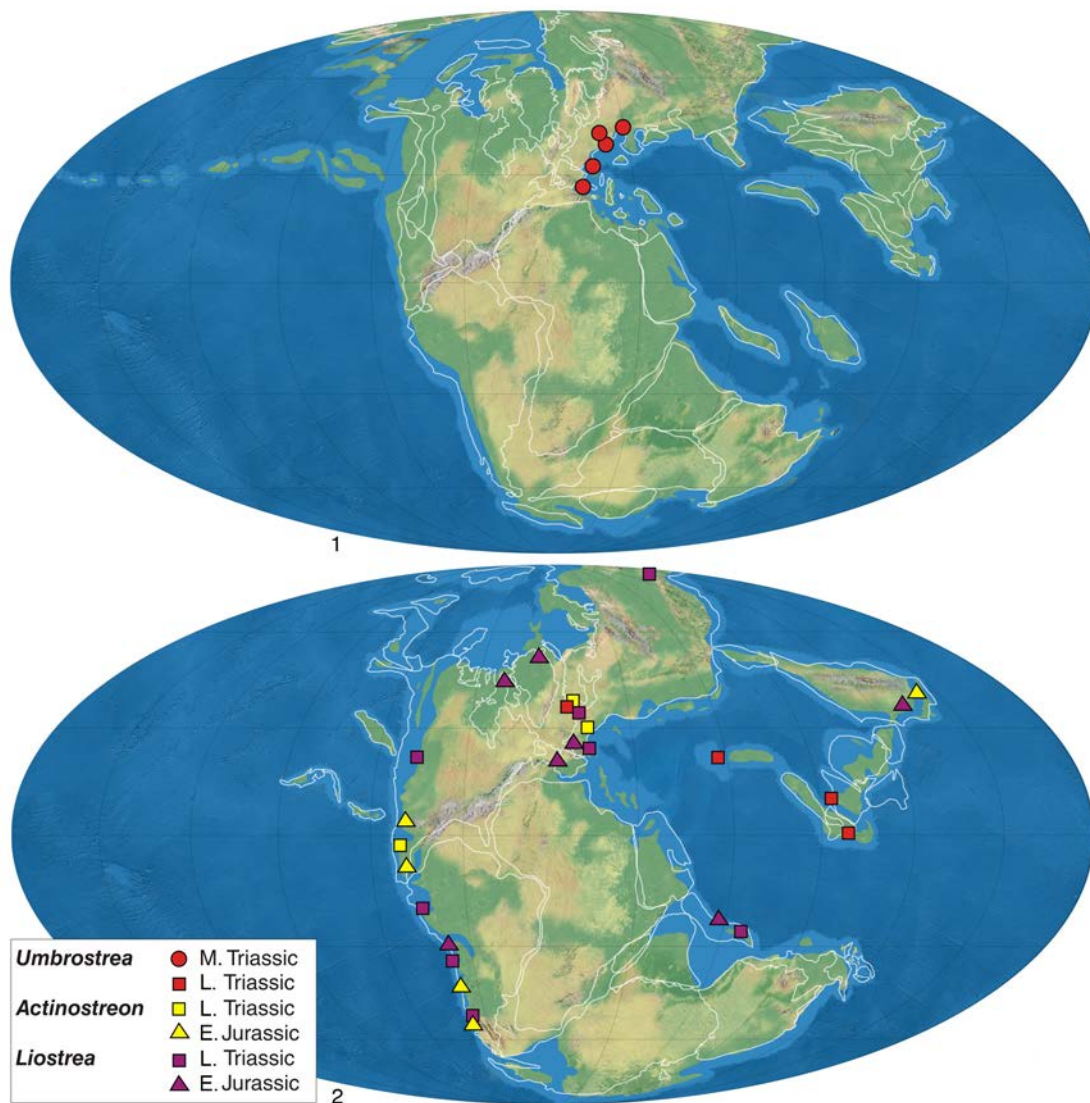


Figure 21. Paleogeographical distribution of Ostreidae (*Umbrostrea*, *Actinostreon*, *Liostrea*). 1, Middle Triassic; 2, Late Triassic–Early Jurassic.

as the last appearance, but he did not indicate the original source. The oldest records are from Rhaetian (Ivimey-Cook & others, 1999; Hautmann, 2001a). *Actinostreon* was very well represented throughout the Jurassic, and there are very few records from the Cretaceous. The youngest record is the species *Lopha* (*Actinostreon*) *diluvian* (Linnaeus) from Maastrichtian beds (Chiplonkar & Badve, 1977), quoted also by Ayyasami (2006) from the Turonian, both in southern India, although the latter is a biostratigraphic paper. However, this species is frequently assigned to *Lopha*, although according to Malchus (1990), *Lopha* had a Tertiary origin.

Paleogeographic distribution.—Tethys, Circumpacific, and Austral (Fig. 21).

Tethys domain: Late Triassic: Rhaetian of England (Penarth Group) (Ivimey-Cook & others, 1999), Austria (Hautmann, 2001a).

Circumpacific domain: Late Triassic: Norian of Mexico (Damborenea in Damborenea & González-León, 1997); Early Jurassic:

Hettangian–Sinemurian of Mexico and Texas (United States) (Liu, 1995), Andes (Chile and Argentina) (Damborenea, 1996a, 2000); Sinemurian of Chile (Aberhan, 1994a; Sha, Smith, & Fürsich, 2002), Japan (Toyora Group) (Hayami, 1975).

Austral domain: Early Jurassic: Hettangian–Toarcian of the Andes (Chile and Argentina) (Damborenea, 1996a, 2000).

Paleoautoecology.—B, E, S, C, Sed; C. *Actinostreon* was a cemented bivalve that attached itself to the substrate by the left valve. Usually it formed clusters in high-energy marine environments (Sha, Smith, & Fürsich, 2002). It could attach to inorganic substrates and also to the shells of other organisms. Most often it attached by cementation to individuals of the previous generation, but it was also found on other bivalves (e.g., *Modiolus* in Ivimey-Cook & others, 1999) or solitary (Machalski, 1998). According to Sha (2002), ostreids have planktotrophic larvae that are responsible for their wide dispersion.

Mineralogy.—Calcitic (Carter, 1990a; Hautmann, 2001a). According to Carter (1990a), *Lophahaidingeriana* (Emmrich, 1853) had predominantly foliated middle and inner shell layers, but a thin prismatic outer shell layer may also be present. Hautmann (2001a) found no trace of an aragonitic inner shell layer in one of his *Actinostreon haidingerianum* (Emmrich, 1853) specimens, and in a tangential section, he observed thin layers of foliated structure. The aragonite is limited to the miostracum and ligostracum (Hautmann, 2001a). The shells show a typical structure with biconvex chambers (Malchus, 1998). Outer shell layer: calcite (?prismatic). Middle and inner shell layers: calcite (regular foliated).

Genus LIOSTREA Douvillé, 1904, p. 273

Type species.—*Ostrea sublamellosa* Dunker, 1846, p. 41.

Stratigraphic range.—Upper Triassic (Carnian)—Upper Cretaceous (Cenomanian) (Hayami, 1975; Carter, 1990a). Stenzel (1971) reported *Liostrea* as being present in the Norian of Siberia and from the Rhaetian to the Jurassic of Europe. Subsequently, the genus was reported from Carnian beds of Japan (Hayami, 1975). The oldest record is from the Ladinian (Waller in Waller & Stanley, 2005), but, in these specimens, some diagnostic characters are not seen, and thus a definite identification is not possible. This record is regarded as dubious *Liostrea* until more material is found in the area. If confirmed, the origin of *Liostrea* goes back to the Middle Triassic. According to Carter (1990a), the youngest record is *Liostrea oxiana* Romer from the Cretaceous (Cenomanian) (Seeling & Bengtson, 1999).

Paleogeographic distribution.—Cosmopolitan (Fig. 21).

Tethys domain: Late Triassic: Carnian of China (J. Chen, 1982a), ?Italy (Gaetani, 1970); Rhaetian of Tibet (China) (?Hautmann & others, 2005; J. Yin & McRoberts, 2006), England (Ivimey-Cook & others, 1999), Italy (Gaetani, 1970); Early Jurassic: Hettangian of Tibet (China) (?Hautmann & others, 2005; J. Yin & McRoberts, 2006), England (Liu, 1995; Ivimey-Cook & others, 1999), Italy (Gaetani, 1970); Sinemurian of England and Portugal (Liu, 1995).

Circumpacific domain: Late Triassic: Carnian of ?Peru (Cox, 1949); Norian of Oregon (United States) (Newton, 1986; Newton in Newton & others, 1987); Norian–Rhaetian of Chile (Rubilar, 1998); Early Jurassic: Sinemurian of Japan (Hayami, 1975), Chile (Rubilar, 1998).

Austral domain: Late Triassic: Rhaetian of Argentina (Riccardi & others, 2004; Damborenea & Manceñido, 2012).

Boreal domain: Late Triassic: Norian of Siberia (Stenzel, 1971); Early Jurassic: Hettangian–Sinemurian of Greenland (Liu, 1995).

Paleoautoecology.—B-Ps, E, S, C, Sed-FaM; C. *Liostrea* cemented to the substrate by the left valve, like the other ostreids. Unlike *Gryphaea*, it has a large cementation area. *Liostrea* cemented itself to hard substrates, bivalve shells, or other organisms (Newton in Newton & others, 1987). It was usually found forming reefs during the Jurassic (Fürsich, Palmer, & Goodyear, 1994). However, the species *Liostrea erina* (d'Orbigny) was found cemented to ammonoids (*Leioceras*) in the Middle Jurassic Opalinum Clay (Switzerland), so it is supposed to have been pseudoplanktonic (Etter, 1996). This author found evidence indicating that the cementation was achieved when the ammonoids were still alive (see fig. 4 in Etter, 1996). Other species, such as *L. plastica* (Trautschold) from the Upper Jurassic of Greenland,

were also found cemented to ammonoids, but it was not possible to determine whether the cementation was pre- or postmortem for the ammonites (Fürsich, 1982).

Mineralogy.—?Calcitic (Carter, Barrera, & Tevesz, 1998). There are no conclusive studies on *Liostrea* mineralogy or shell microstructure. According to Carter, Barrera, and Tevesz (1998), the mineralogy of the different shell layers of members of family Ostreidae is calcitic.

Superfamily DIMYOIDEA Fischer, 1886 in 1880–1887

Family DIMYIDAE Fischer, 1886 in 1880–1887

Genus ATRETA Etallon, 1862, p. 191

Type species.—*Ostrea blandina* d'Orbigny, 1850, p. 375 (designated by Cox, 1964, p. 45).

Remarks.—*Dimyodon* Munier-Chalmas in Fischer, 1886 in 1880–1887, p. 937, is considered to be a junior synonym of *Atreta* (see discussion for *Dimyodon*, Genera not Included, p. 160). Although for a long time it was regarded as a plicatulid, both Fürsich and Werner (1988) and Hodges (1991), analyzing specimens of *Atreta unguis* (Loriol ex Merian, 1900) and *Atreta intusstriata* (Emmrich, 1853), respectively, demonstrated the presence of dimyarian structures typical of family Dimyidae.

Stratigraphic range.—Upper Triassic (Carnian)—Upper Cretaceous (Maastrichtian) (Bittner, 1895; Abdel-Gawad, 1986). Cox and others (1969) assigned it an Upper Triassic (Carnian)—Upper Cretaceous (Campanian) range. Sepkoski (2002) referred its origin to the Rhaetian, based on data provided by Skelton and Benton (1993). The oldest records of *Atreta* are from Carnian beds, with the species *A. richthofeni* (Bittner, 1895) and *A. subrichthofeni* (Krumbeck, 1924). H. Yin (1985) reported *Dimyodon* from Anisian and Ladinian beds. J. Chen, Stiller, and Komatsu (2006) believed that Anisian specimens of *Dimyodon* (*D. qingyanensis* Yin in Gan & Yin, 1978) were actually juvenile stages of *Protostrea sinensis* Hsu in Hsu & Chen, 1943 (type of *Protostrea* Chen, 1976). *Atreta nilssoni* (von Hagenow, 1842) is the latest species of the genus, reported from the Maastrichtian (Abdel-Gawad, 1986).

Paleogeographic distribution.—Tethys (Fig. 22). Over the study interval, this genus was only known from the Tethys domain, but in the upper Pliensbachian, it is recorded from Argentina (Damborenea, 2002a). *Atreta* showed dispersal patterns from the western Tethys to Eastern Circumpacific domain across the Hispanic corridor during the Early Jurassic (Damborenea, 2000).

Tethys domain: Late Triassic: Carnian of southern Alps (Bittner, 1895; Fürsich & Wendt, 1977), Timor (Krumbeck, 1924); Norian of Oman (Hautmann, 2001a); Norian–Rhaetian of Austria (Tanner, Lucas, & Chapman, 2004), Iran (Hautmann, 2001a, 2001b); Rhaetian of the Alps (Austria) (Tomašových, 2006a, 2006b), western Carpathians (Slovakia) (Tomašových, 2004), Austria and Germany (Hodges, 1991), England (Penarth Group) (Ivimey-Cook & others, 1999), Italy (Allasinaz, 1962); Early Jurassic: Hettangian of northwestern Europe (Hallam, 1987); early Liassic of South Wales (Hodges, 1991), Italy (Allasinaz, 1962).

Paleoautoecology.—B, E, S, C, Sed; C. *Atreta* was a cemented bivalve (fixed by its right valve) on other live invertebrates, such as sponges (Delvene, 2003; P. D. Taylor & Wilson, 2003), echinoids (Saint-Seine, 1951; Jagt, Neumann, & Schulp, 2007), other bivalves

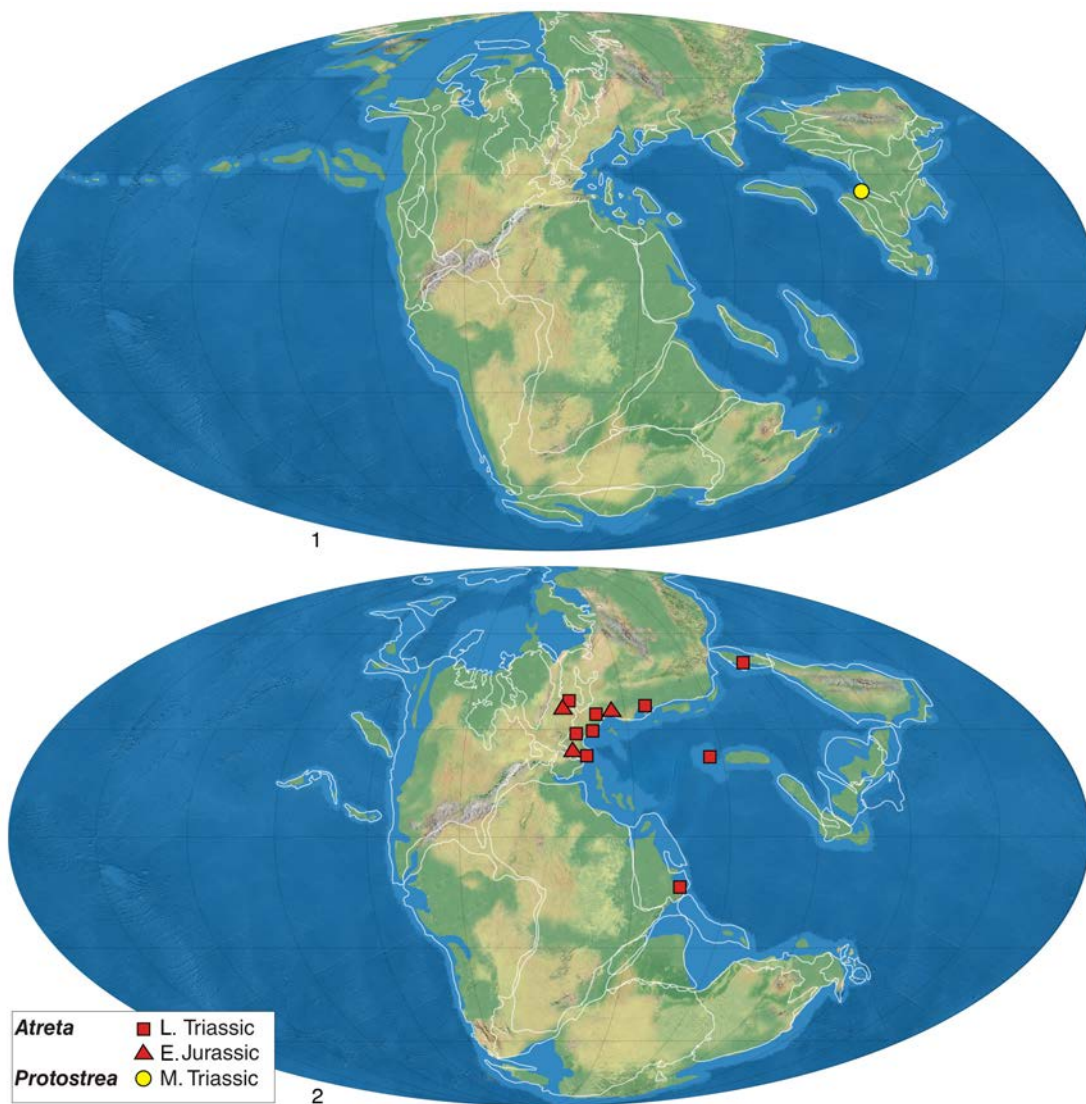


Figure 22. Paleogeographical distribution of Dimyidae (*Atreta*, *Protostrea*). 1, Middle Triassic; 2, Late Triassic–Early Jurassic.

such as *Plagiostoma*, *Gryphaea*, *Pinna*, *Antiquilima* (Hodges, 1991), *Indopecten* (Hautmann, 2006a), *Lopha*, *Cardinia*, *Myoconcha*, and corals (Damborenea, 2002a). It is usually associated with other encrusting bivalves such as *Liostrea* (Hodges, 1991) or *Lopha* (Damborenea, 2002a). It was a gregarious bivalve, although it is rare to find it encrusting other individuals of the same species, and specimens are usually oriented with their dorsal part upward on sloping surfaces (Damborenea, 2002a).

Mineralogy.—Bimineralic (Malchus, 2000). Hodges (1991) did not find any shell preserved, and he believed it was likely that it was originally aragonitic. Malchus (2000) studied the microstructure of lower stages of excellently preserved *Atreta* specimens and found a foliated calcitic in outer shell layer and a well-developed cross-lamellar microstructure in the inner shell layer. Hautmann (2001a, 2006a) indicated that his specimens have a foliated calcite microstructure in the outer shell layer, and they did not have the

inner one preserved. Outer shell layer: calcite (foliated). Inner shell layer: aragonite (cross-lamellar).

Genus PROTOSTREA Chen in Gu & others, 1976, p. 243

Type species.—*Ostrea sinensis* Hsu in Hsu & Chen, 1943, p. 136.

Remarks.—This genus was also called *Proostrea* (e.g., Skelton & Benton, 1993; Sepkoski, 2002) or *Prostrea* (e.g., Kobayashi & Tamura, 1983a) by mistake. Although its type species was originally included in Ostreoidea, following Morris in Skelton and Benton (1993), Komatsu, Akasaki, and others (2004), and J. Chen, Stiller, and Komatsu (2006), we include *Protostrea* in the Dimyidae (see J. Chen, Stiller, & Komatsu, 2006, for review and emendation of the genus). These authors interpreted *Dimyodon qingyanensis* Yin in Gan & Yin, 1978, as a juvenile stage of *Protostrea sinensis* and considered it the oldest member of the family Dimyidae.

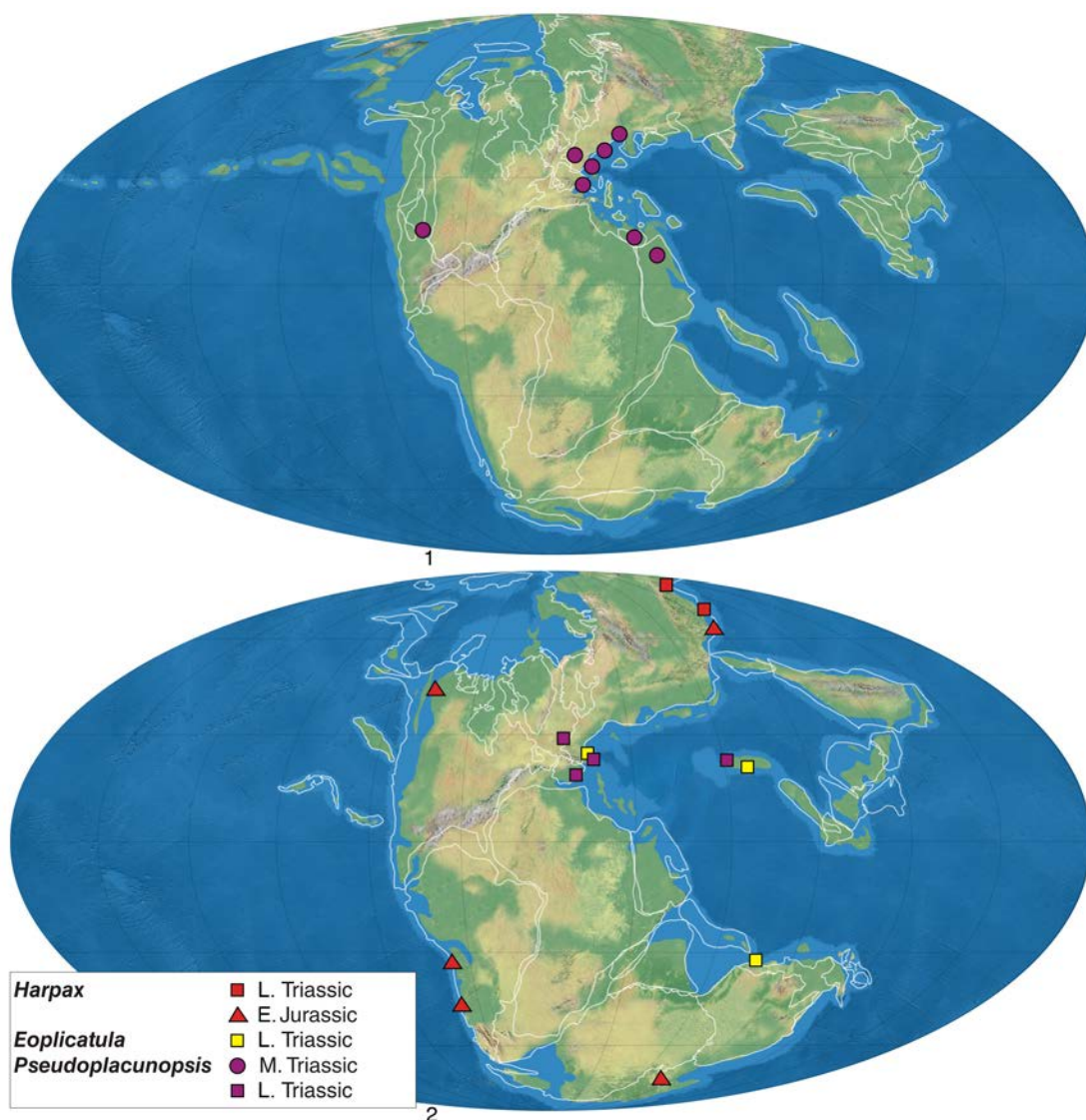


Figure 23. Paleogeographical distribution of Plicatulidae (*Harpax*, *Eoplicatula*, *Pseudoplicatunopsis*). 1, Middle Triassic; 2, Late Triassic–Early Jurassic.

Stratigraphic range.—Middle Triassic (Anisian) (J. Chen, Stiller, & Komatsu, 2006). *Protostrea* is a monospecific genus only known from the upper Anisian in the Qingyan formation (Stiller, 2000; Komatsu, Chen, & others, 2004; J. Chen, Stiller, & Komatsu, 2006).

Paleogeographic distribution.—Eastern Tethys (Fig. 22).

Tethys domain: Middle Triassic: Anisian of southern China (Guizhou province) (Stiller, 2000; Komatsu, Akasaki, & others, 2004; J. Chen, Stiller, & Komatsu, 2006).

Paleoautoecology.—B, E, S, C, Sed; *C. Protostrea sinensis* probably lived cemented to the substrate by their right valve by a large cementation area (J. Chen, Stiller, & Komatsu, 2006). Often it is found cemented to other shells and corals (Komatsu, Chen, & others, 2004). *Protostrea* was also a substrate for other organisms, such as crinoids (Stiller, 2000).

Mineralogy.—Bimineralic. Not much is known about the shell mineralogy and microstructure of members of the family Dimyidae.

Waller (1978) indicated that they may have had an inner shell layer of aragonite and cross-lamellar microstructure and that they do not have a simple prismatic calcitic layer. J. Chen, Stiller, and Komatsu (2006, p. 160) studied thin sections of their specimens, which, although recrystallized into calcite, “. . . the shells originally probably had a mainly crossed-lamellar microstructure (originally aragonitic); in parts (at least of right valves) there are relics of (an) irregular simple-prismatic outer layer (s) (originally calcitic).”

Superfamily PLICATULOIDEA Watson, 1930
Family PLICATULIDAE Watson, 1930
Genus HARPAX Parkinson, 1811, p. 221

Type species.—*Harpax parkinsoni* Bronn, 1824, p. 52.

Remarks.—Although *Harpax* was considered a junior synonym of *Plicatula* Lamarck, 1801, by Cox and others (1969), some authors still regarded it as a valid subgenus of *Plicatula* (Okuneva, 1985; Dam-

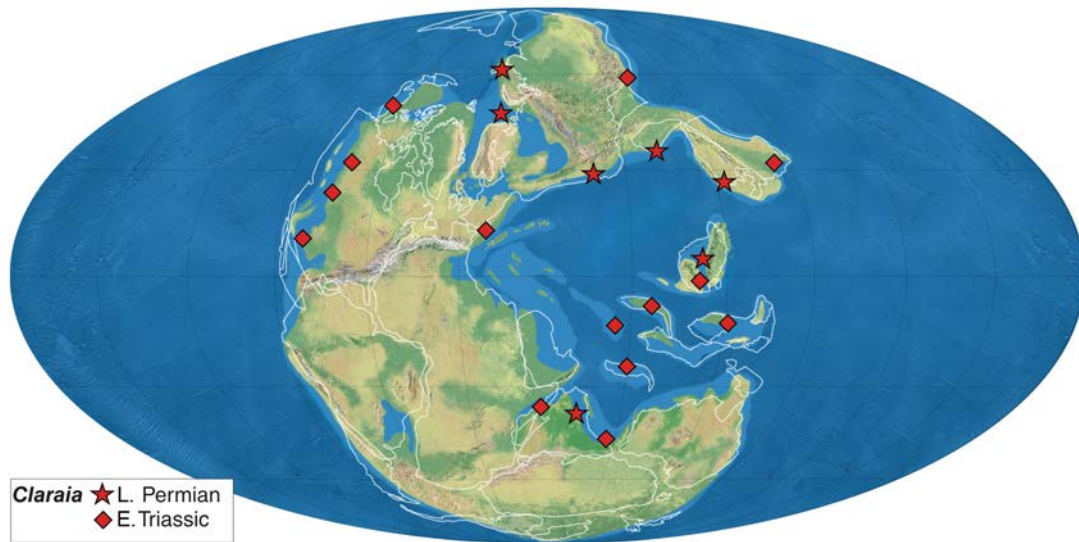


Figure 24. Paleogeographical distribution of Pterinopectinidae (*Claraia*), late Permian–Early Triassic.

borenea, 1993; Aberhan, 1994a, 1998a; Gahr, 2002, among others). Recently, Damborenea (2002a) validated the genus, distinguishing it from *Plicatula* due to its hinge details, relative convexity of the valves, ornamentation, and ligament (see discussion in Damborenea, 2002a, p. 86–89). The hinge of many species attributed to *Plicatula* is unknown, and so species undoubtedly included in *Harpax* are: *Harpax parkinsoni* Bronn, 1824, *Harpax rapa* (Bayle & Coquand, 1851), *Harpax kolymica* (Polubotko in Kiparisova, Bychkov, & Polubotko, 1966), *Harpax simplex* Milova, 1976, *Harpax spinosa* (J. Sowerby, 1819), and *Harpax auricula* (Eudes-Deslongchamps, 1860), among others.

Stratigraphic range.—Upper Triassic (Norian)—Lower Jurassic (Toarcian) (Damborenea, 1993; Gahr, 2002). It is difficult to assign a specific range to this genus, since diagnostic characters (for example, the hinge) of many species are not known (Damborenea, 2002a). The oldest solid records are from the Norian (Okuneva, 1985; Damborenea, 1993), with the youngest being from the lower Toarcian of Spain and Portugal (Gahr, 2002). Hautmann (2001a, 2001b) considered the genus to be only present in the Lower Jurassic.

Paleogeographic distribution.—Boreal and Austral, ?Tethys (Fig. 23). *Harpax* had a bipolar distribution, at least during the Early Jurassic (Damborenea, 1993, 1996a, 2001). It originated in the Boreal domain during the Late Triassic. Later, during the Pliensbachian–Toarcian, it was also reported from the Tethys domain (Gahr, 2002). With some doubt, it was also reported from the Rhaetian–Hettangian boundary in Tibet (J. Yin & McRoberts, 2006) and from Sinemurian beds of Morocco (Tomašových, 2006c).

Boreal domain: Late Triassic: Norian of Siberia (Okuneva, 1985), northeastern Asia (Polubotko & Repin, 1990); Norian–Rhaetian of Siberia (Kiparisova, Bychkov, & Polubotko, 1966; Polubotko, 1968a; Bychkov & others, 1976); Early Jurassic: northeastern Russia (Milova, 1976); Hettangian of northeastern Asia (Polubotko & Repin, 1990); Hettangian–Sinemurian of Canada (Aberhan, 1998a; Aberhan, Hrudka, & Poulton, 1998).

Austral domain: Early Jurassic: Argentina (Damborenea, 1993, 2002a, 2002b); Hettangian–Sinemurian of Chile and Argentina (Damborenea, 1996a), ?New Zealand (Damborenea, 1993); Sinemurian of Chile (Aberhan, 1994a).

Paleoautoecology.—B, E, S, C, Sed; C. The distribution of bipolar (or antitropical) organisms is determined by temperature and substrate availability (Sha, 1996). They are abundant in shallow water areas at high latitudes and in deep water areas at low-latitude seas (Sha & Fürsich, 1994). According to several studies (see Damborenea, 2002a, p. 93), juvenile stages of *Harpax* were often cemented by the right valve to hard substrates (other shells, pebbles, rocks). However, in adult stages, they were often found loose in the sediment, so they had a free mode of life (Damborenea, 2002a). Sha (1996), based on various characters, such as the presence of byssal notch and sinus and pseudoctenolium, believed that in its juvenile stages, it also remained byssate, and he suggested that perhaps it had a pseudoplanktonic mode of life, attaching to floating objects (e.g., wood) or other swimming or nektonic organisms.

Mineralogy.—Bimineralic (Carter, 1990a, p. 226; Carter, Barrera, & Tevesz, 1998, p. 1003). Outer shell layer: calcite (foliated). Middle shell layer: calcite. Inner shell layer: aragonite.

Genus EOPLICATULA Carter, 1990a, p. 221

Type species.—*Plicatula imago* Bittner, 1895, p. 213.

Stratigraphic range.—Upper Triassic (Carnian–Rhaetian) (Bittner, 1895; Hautmann, 2001a, 2001b). Carter (1990a) proposed *Eoplicatula* as a subgenus of *Plicatula* and only included the type species from the Carnian of Italy. Subsequently, Hautmann (2001a) included the species *Plicatula difficilis* Healey, 1908, from Rhaetian beds of Burma and *Eoplicatula parvadehensis* Hautmann, 2001a, from the Norian of Iran. Hautmann and others (2005) reported *Eoplicatula* from Rhaetian beds of southern Tibet but did not figure or describe the specimens.

Paleogeographic distribution.—Tethys (Fig. 23).

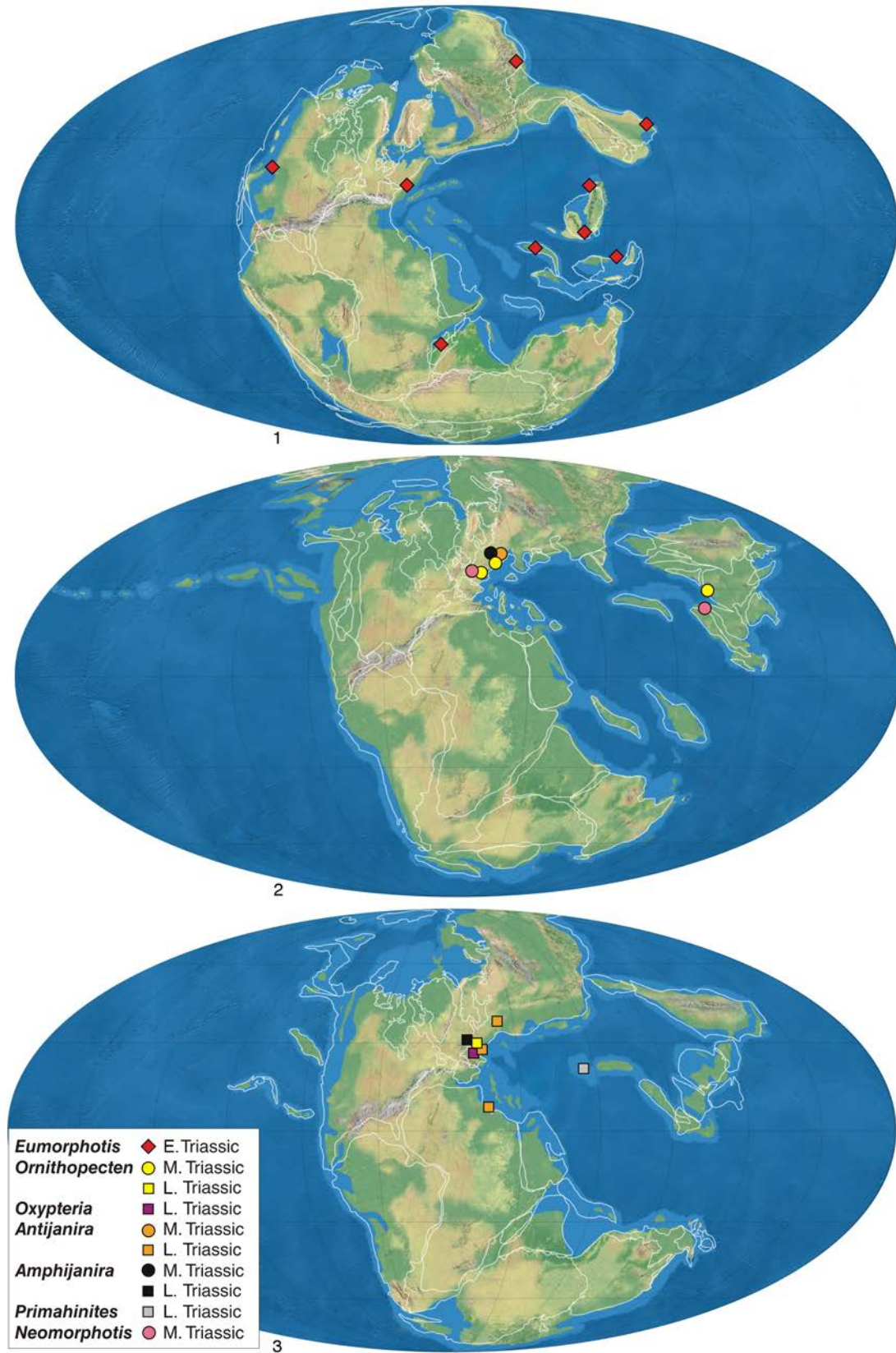


Figure 25. Paleogeographical distribution of Aviculopectinidae (*Eumorphotis*, *Ornithopecten*, *Oxypteria*, *Antijanira*, *Amphijanira*, *Primahinrites*, *Neomorphotis*). 1, Early Triassic; 2, Middle Triassic; 3, Late Triassic–Early Jurassic.

Tethys domain: Late Triassic: Carnian of Italy (Bittner, 1895; Leonardi, 1943; Carter, 1990a); Norian of Iran (Hautmann, 2001a, 2001b; Fürsich & Hautmann, 2005); Rhaetian of Burma (Healey, 1908).

Paleoautoecology.—B, E, S, C, Sed; C. *Eoplicatula* cemented to the substrate by its right valve. According to Hautmann (2001b), it was a reef-builder organism.

Mineralogy.—Bimineralic (Carter, 1990a, p. 223; Hautmann, 2001b). Outer shell layer: calcite (prismatic-foliated). Middle shell layer: aragonite (cross-lamellar). Inner shell layer: aragonite (prismatic-cross-lamellar).

Genus PSEUDOPLACUNOPSIS Bittner, 1895, p. 215

Type species.—*Pseudoplacunopsis affixa* Bittner, 1895, p. 215.

Remarks.—After Todd and Palmer (2002), who proposed that *Placunopsis* Morris & Lycett, 1853 in 1851–1855, p. 5, is a genus belonging to the Jurassic family Anomiidae, several species that were traditionally attributed to this genus were rejected, as they did not have a byssal foramen, and they were regarded as terquemids (=prospondylids) instead. While Hölder (1990) considered species from Triassic and Cretaceous ages to be within *Placunopsis*, Todd and Palmer (2002) proposed that their affinities are uncertain, and their knowledge is based on new well-preserved materials. We believe that many of the Triassic species referred to *Placunopsis* and included into the family Terquemiidae Cox, 1964, among them the so-called false oyster, are, in fact, true plicatulids and should be referred to *Pseudoplacunopsis*. Checa and others (2003) resampled the Middle Triassic (Ladinian) localities studied by Schmidt (1935) and Márquez-Aliaga, Hirsch, and López-Garrido (1986) from the Betic ranges (Jaen), and they obtained several thousand specimens of *Placunopsis flabellum* Schmidt, 1935, in which only the calcite microstructure of the right valves (the cemented ones) was preserved. In tens of specimens, details of the hinge could be observed, showing an elongated ligament furrow bordered by two crura diverging from the beak and pits corresponding to the other valve crura and inserted below the hinge line. The external ornamentation presented antimarginal thick ribs, and thus the species was referred to *Enantiostreon*; but hinge characters indicate that *P. flabellum* was a true plicatulid. Subsequently, one of the authors (Márquez-Aliaga) found identical hinge characters in specimens from Ladinian beds of the Iberian range (Cuenca) attributed to *Placunopsis teruelensis* Wurm, 1911. This species is ornamented by fine ribs. There are many Middle Triassic nominal species assigned to this genus, which could, in fact, be regarded as synonyms due to the variability of the cemented valve. Among the finely ornamented species, *P. plana* (Giebel, 1856) from the Germanic Muschelkalk could include as synonyms the following names: *alpina* Winkler, 1859, *schaftlautli* Winkler, 1859, *teruelensis* Wurm, 1911, and *filicostata* Hölder, 1990. Within the heavily ornamented species, *matricula* Quenstedt, 1852 in 1851–1852, could include as a synonym *flabellum* Schmidt (Checa & others, 2003). Recently, Posenato (2008b) developed similar ideas.

Stratigraphic range.—Middle Triassic (Anisian)—Upper Triassic (Rhaetian) (Posenato, 2008b; Márquez-Aliaga, Damborenea, & Goy, 2008a). Cox and others (1969) assigned it an Upper Triassic range, and Hautmann (2001a) also considered that it ranged from the Carnian, but new records, as discussed above, confirmed its

presence in Middle Triassic deposits. Regarding the upper extension of its stratigraphic range, Hautmann (2001a) considered that *Pseudoplacunopsis* lived until Kimmeridgian times, represented by the species *Plicatula ogerieni* Loriol, 1904. Hautmann (2001a) did not make any comments about this species, nor did we find any record of the genus for the Jurassic; and its last appearance seems to be Rhaetian. It is interesting to note that most references to this genus are based on the diagnosis given by Bittner (1895) and Cox (1924), and not on the emended one by Hautmann (2001a), as the hinge and the ligament area are rarely preserved in specimens attributed to this genus.

Paleogeographic distribution.—Tethys and Circumpacific (Fig. 23).

Tethys domain: Middle Triassic: Anisian of Italy (Posenato, 2008b); Ladinian of Spain (Schmidt, 1935; Márquez-Aliaga, 1985; Martínez & Márquez-Aliaga, 1992; López-Gómez & others, 1994; Márquez-Aliaga & Ros, 2002; Márquez-Aliaga, Budurov, & Martínez, 1996; Márquez-Aliaga & others, 2004), Germany (Hagdorn & Simon, 1983; Hölder, 1990), France (Brocard & Philip, 1989), Israel (Lerman, 1960), Poland (Assmann, 1916), Italy (Posenato, 2002), Jordan (Cox, 1924); Late Triassic: Carnian of Spain (Martín-Algarra, Solé de Porta, & Márquez-Aliaga, 1995), Italy (Bittner, 1895; Leonardi, 1943); Norian–Rhaetian of Iran (Hautmann, 2001b); Rhaetian of Austria (Posenato, 2008b), Spain (Márquez-Aliaga, Damborenea, & Goy, 2008b; Márquez-Aliaga & others, 2010).

Circumpacific domain: Middle Triassic: Ladinian of Nevada (United States) (Waller in Waller & Stanley, 2005).

Paleoautoecology.—B, E, S, C, Sed; C. *Pseudoplacunopsis* was a cementing bivalve. It attached to the substrate by its right valve, and according to Hautmann (2001a), it was a reef builder. Márquez-Aliaga and Martínez (1994) studied its behavior as an epizoan organism.

Mineralogy.—Bimineralic (De Renzi & Márquez-Aliaga, 1980; Márquez-Aliaga & Márquez, 2000). Outer shell layer: calcite (foliated). Inner shell layer: aragonite (cross-lamellar).

Superfamily PTERINOPECTINOIDEA Newell, 1938

Family PTERINOPECTINIDAE Newell, 1938

Genus CLARAIA Bittner, 1901a, p. 568

Type species.—*Posidonomya clarae* Hauer, 1850, p. 112.

Remarks.—Several taxa related to *Claraia* will not be considered in this analysis for various reasons: either they are regarded as synonyms of *Claraia* or their separation at generic level is not justified. These taxa are: *Pseudoclaraiia* Zhang, 1980, p. 438, 443, *Pteroclaraiia* Guo, 1985, p. 150, 265, *Guichiella* J. Li & Ding, 1981, p. 328–329, *Claraioides* Z. Fang, 1993, p. 653, 660, *Epiclaraiia* Gavrilova, 1995, p. 156, and *Rugiclaraiia* Waterhouse, 2000, p. 179 (see discussion for each of them in Genera not Included, p. 156).

Stratigraphic range.—upper Permian (Wuchiapingian)—Lower Triassic (middle Olenekian) (F. Yang, Peng, & Gao, 2001; McRoberts, 2010). For a long time, *Claraia* was regarded as a Lower Triassic index fossil. Cox and others (1969) assigned it a Lower Triassic range with a cosmopolitan distribution. Later, Nakazawa and others (1975) reported *Claraia bioni* Nakazawa in Nakazawa & others, 1975, from upper Permian sediments. Since then, there were many new upper Permian records (H. Yin, 1983; F. Yang, Peng, & Gao, 2001; Z. Fang, 1993, 2003; Gao, Yang, & Peng, 2004; Kotlyar, Zakharov, & Polubotko, 2004; He, Feng, & others, 2007; He, Shi, & others,

2007). Boyd and Newell (1979) reported *Claraia? posidoniformis* Termier & Termier, 1977, from Tunisian Guadalupian beds, but they doubted the generic relations of this species, because it shows some features that are not typical of *Claraia*.

Paleogeographic distribution.—Cosmopolitan (Fig. 24). During the late Permian, *Claraia* was widely distributed, mainly in the eastern part of Tethys. During the Early Triassic, it was abundant almost everywhere that beds of this age occur. For this reason, even though it was not reported from certain areas, a cosmopolitan distribution is given.

Tethys domain: late Permian: Kashmir (India) (Nakazawa & others, 1975); Wuchiapingian of China (F. Yang, Peng, & Gao, 2001); Changhsingian of China (Z. Zhang, 1980; H. Yin, 1983, 1990; Z. Fang, 1993, 2003; F. Yang, Peng, & Gao, 2001; Gao, Yang, & Peng, 2004; Z. Chen, Kaiho, & others, 2006; He, Feng, & others, 2007; He, Shi, & others, 2007), northwestern Caucasus (Russia) (Kotlyar, Zakharov, & Polubotko, 2004; Ruban, 2006a); Early Triassic: Pamir (Afghanistan) (Polubotko, Payevskaya, & Repin, 2001), Himalayas (Nepal) (Waterhouse, 2000), Italy (Leonardi, 1935; Broglio-Loriga, Masetti, & Neri, 1982; Neri, Pasini, & Posenato, 1986; Broglio-Loriga & others, 1988, 1990; Posenato, 1988; Posenato, Sciunnach, & Garzanti, 1996; Fraiser & Bottjer, 2007a, 2007b), China (Hsu, 1936–1937; F. Wu, 1985; Z. Li & others, 1986; Lu & Chen, 1986; S. Yang, Wang, & Hao, 1986; Z. Yang & others, 1987; Ling, 1988; M. Wang, 1993; Tong & Yin, 2002), Ussuriland (Russia) (Kiparissova, 1938); Induan of China (C. Chen, 1982; F. Yang, Peng, & Gao, 2001; He, Feng, & others, 2007), Italy (Leonardi, 1960), Malaysia (Ichikawa & Yin, 1966; Tamura & others, 1975), Vietnam (Vu Khuc & Huyen, 1998), Alberta (Canada) (Newell & Boyd, 1995; McRoberts, 2010); Olenekian of Mangyshlak (Kazakhstan) (Gavrilova, 1995), China (H. Yin, 1990; J. Chen & Komatsu, 2002), Pakistan (Nakazawa, 1996), Vietnam (Komatsu & Huyen, 2006).

Circumpacific domain: Early Triassic: Wyoming and Idaho (United States) (Newell & Kummel, 1942), Alberta (Canada) (Newell & Boyd, 1970), Japan (Nakazawa, 1971; Hayami, 1975); Induan of Nevada (United States) (Ciriacks, 1963; Schubert, 1993; Newell & Boyd, 1995; Schubert & Bottjer, 1995; Boyer, Bottjer, & Droser, 2004; Fraiser & Bottjer, 2007a, 2007b).

Boreal domain: late Permian: eastern Greenland (Newell & Boyd, 1995), Nova Zemla (Arctic Ocean) (Muromtseva, 1984); Early Triassic: Queen Elizabeth Islands (Arctic Archipelago, Canada) (Tozer, 1961, 1962, 1970).

Paleoautoecology.—B-Ps, E, S, Epi, Se-FaM. Several modes of life have been attributed to *Claraia*, ranging from benthic epibyssate (Z. Fang, 1993; F. Yang, Peng, & Gao, 2001) to pseudoplanktonic and even occasional swimmer (F. Yang, Peng, & Gao, 2001). *Claraia* shell morphology subtly changed through time. These differences are primarily related to the morphology of the byssal notch, the ornamentation, and the shape of the auricles (F. Yang, Peng, & Gao, 2001; He, Feng, & others, 2007). Permian forms had a more developed and deep byssal notch, shells were small in size, thin, and slightly inequivalve; they were interpreted as living epibyssate with the capacity to swim occasionally (F. Yang, Peng, & Gao, 2001). However, due to the associated fauna, e.g., ammonoids, they were also interpreted as pseudoplanktonic (H. Yin, 1983). Nevertheless, according to F. Yang, Peng, and Gao (2001), features present in

Permian forms were unsuited to this mode of life. On the other hand, in the Triassic forms, the byssal notch was shallower, which is associated with increased mobility (Z. Fang, 1993; see also He, Feng, & others, 2007, table 1), and the shells were less ornamented (F. Yang, Peng, & Gao, 2001). These forms were also interpreted by F. Yang, Peng, and Gao (2001) as being pseudoplanktonic bivalves that attached themselves to pieces of wood or algae.

The genus occurred primarily in deep-water Permian deposits, but, by the Triassic, it was in all types of environments, from shallow to deep (F. Yang, Peng, & Gao, 2001). This fact was related to an opportunistic behavior during recovery from the Permian–Triassic (P/T) extinction event (Schubert & Bottjer, 1995; Rodland & Bottjer, 2001). This success during the Triassic appears to be related to the morphological change, since Permian forms with a deep byssal notch did not survive the P/T event; however, the forms with a shallower byssal notch diversified enormously [from 3 species in late Permian to over 30 in the Triassic (He, Feng, & others, 2007)]. According to F. Yang, Peng, and Gao (2001), this was also related to the mode of life of *Claraia* larvae, which probably had a veliger planktonic stage. The deep-water habitats in which mostly Permian forms were found were interpreted by Gao, Yang, and Peng (2004) as potential refuges for those forms that survived and reached the Early Triassic. It is hard to assign a unique mode of life to all species of *Claraia*, since they have a wide range of morphological features that suggests that some species could have been epibenthic, pseudoplanktonic, and even occasional swimmers (He, Feng, & others, 2007).

Mineralogy.—Bimineralic (Boyd & Newell, 1976; Newell & Boyd, 1985, 1995; Carter, 1990a, 1990b). Outer shell layer: calcite (prismatic). Inner shell layer: aragonite (?).

Superfamily AVICULOPECTINOIDEA Meek & Hayden, 1864
Family AVICULOPECTINIDAE Meek & Hayden, 1864
Genus EUMORPHOTIS Bittner, 1901a, p. 566

Type species.—*Pseudomonotis telleri* Bittner, 1898, p. 710.

Stratigraphic range.—Lower Triassic (Induan–Olenekian) (Broglio-Loriga & Mirabella, 1986). Cox and others (1969) assigned it a Lower Triassic–Upper Triassic range. However, Broglio-Loriga and Mirabella (1986) did a comprehensive study on *Eumorphotis*, and they noted that Middle and Upper Triassic forms were highly dubious, and therefore they restricted the range of *Eumorphotis* to the Lower Triassic. Newell and Boyd (1995) assigned it the same range. Furthermore, these authors argued that *Heteropecten* Kegel & Costa, 1951, and *Eumorphotis* were virtually indistinguishable and that the reason for proposing *Eumorphotis* was more to separate the Paleozoic from the Triassic forms than to recognize significant morphological differences between the two groups. In fact, Newell and Boyd (1995) considered that some specimens attributed by Bittner (1901b) to the Triassic *Eumorphotis* from eastern Siberia are similar to *Heteropecten*. Moreover, *Eumorphotis* was also reported from the upper Permian, but Broglio-Loriga and Mirabella (1986) doubted all these records, because they were based on poorly preserved material. Posenato, Pelikán, and Hips (2005) proposed a new species, *Eumorphotis lorigae* Posenato, Pelikán, & Hips, 2005, and they referred it to the upper Permian (upper Changhsingian), but, as indicated by the authors, this age is only provisionally based on bivalves and brachiopods, and thus we will not take this record into account until new data allow a more precise age determination.

Paleogeographic distribution.—Tethys and Circumpacific (Fig. 25).

Tethys domain: Early Triassic: Italy (Bittner, 1912; Leonardi, 1935; Broglio-Loriga, Masetti, & Neri, 1982; Neri & Posenato, 1985; Broglio-Loriga & Mirabella, 1986, and references therein; Neri, Pasini, & Posenato, 1986; Broglio-Loriga & others, 1990), Ussuriland (Russia) (Kiparisova, 1938), Vietnam (Vu Khuc & Huyen, 1998), Pakistan (Nakazawa, 1996), Malaysia (Ichikawa & Yin, 1966), China (Hsu, 1936–1937; Z. Yang & Yin, 1979; C. Chen, 1982; F. Wu, 1985; S. Yang, Wang, & Hao, 1986; Ling, 1988; H. Yin, 1990; Tong & others, 2006); Induan of southern China (Hautmann & others, 2011).

Circumpacific domain: Early Triassic: western United States and Japan (Newell & Kummel, 1942; Ciriacks, 1963; Schubert, 1993; Newell & Boyd, 1995; Boyd, Nice, & Newell, 1999; Fraiser & Bottjer, 2007a), Japan (Nakazawa, 1961, 1971; Hayami, 1975; Kashiya & Oji, 2004).

Paleoautoecology.—B, E, S, Epi, Sed; By. According to key features present in different species of this genus (elongated anterior auricles, byssal notch in adults), and, following S. M. Stanley's (1970, 1972) criteria, *Eumorphotis* could be an epibyssate bivalve. Together with *Claraia*, *Promyalina*, and *Unionites*, *Eumorphotis* was one of the dominant bivalves in the Early Triassic seas (Fraiser & Bottjer, 2007a).

Mineralogy.—Bimineralic (Carter, 1990a, p. 241). There are no available data about *Eumorphotis* shell mineralogy or microstructure. Data provided for family Aviculopectinidae. Outer shell layer: calcite (prismatic-homogeneous-foliated). Inner shell layer: aragonite (nacreous-cross-lamellar).

Genus ORNITHOPECTEN Cox, 1962, p. 596

Type species.—*Aviculopecten bosniae* Bittner, 1903, p. 592.

Remarks.—Cox (1962) proposed *Ornithopecten* to accommodate several Triassic species that were previously attributed to *Aviculopecten* M'Coy, 1851, p. 171 (which is actually regarded a strictly Paleozoic genus).

Stratigraphic range.—Middle Triassic (Anisian)—Upper Triassic (Carnian) (Diener, 1923; Allasinaz, 1972). Cox and others (1969) assigned it a Middle–Upper Triassic range. According to Diener (1923), the species assigned to *Ornithopecten* by Cox (1962) were reported from Anisian and Carnian beds. Subsequently, the genus was reported from the Lower Triassic of China, but there are several problems with these records. The only reference we could locate in which the material was described and figured is Z. Yang and others (1987). A new species was described there: *Ornithopecten? magnautilus* Yin, but this was only doubtfully assigned to *Ornithopecten*, and, as noted by the authors, it might be better located within *Eumorphotis* Bittner, 1901a, with which we agree. The other papers where the genus was mentioned from the Triassic age (e.g., Z. Chen, Shi, & Kaiho, 2004; Z. Chen & McNamara, 2006; Z. Chen, Shi, & others, 2006) do not have figures or descriptions; furthermore, they do not mention the original source of data, so they are not taken into account.

Paleogeographic distribution.—Tethys (Fig. 25).

Tethys domain: Middle Triassic: Anisian of Yugoslavia (Allasinaz, 1972), China (H. Yin, 1985; J. Chen & Stiller, 2007), Alps (Diener, 1923); Ladinian of China (H. Yin, 1985), southern Alps (Bittner, 1985; Diener, 1923); Late Triassic: Carnian of the Alps (Diener, 1923).

Paleoautoecology.—B, E, S, Epi, Sed; By. Following the guidelines provided by S. M. Stanley (1970, 1972), *Ornithopecten* was most likely an epibyssate bivalve, and the byssus was placed under the anterior auricle.

Mineralogy.—Bimineralic (Carter, 1990a, p. 241). There are no data about *Ornithopecten* shell. Data provided for family Aviculopectinidae. Outer shell layer: calcite (prismatic-homogeneous-foliated). Inner shell layer: aragonite (nacreous-cross-lamellar).

Genus OXYPTERIA Waagen, 1907, p. 93

Type species.—*Aviculopecten (Oxypteria) bittneri* Waagen, 1907, p. 93.

Stratigraphic range.—Upper Triassic (Carnian) (Cox & others, 1969). Waagen (1907) proposed the genus on the basis of material from Carnian beds of southern Tyrol. The only other references that could be located are Diener (1923) and Cox and others (1969), who repeated the information in Waagen.

Paleogeographic distribution.—western Tethys (Fig. 25).

Tethys domain: Late Triassic: Carnian of southern Tyrol (Italian Alps) (Waagen, 1907; Diener, 1923; Cox & others, 1969).

Paleoautoecology.—B, E, S, Epi, Sed; By. Since all that is known of this monospecific genus is a left valve, it is difficult to speculate how it lived. We assign it the dominant mode of life in the family Aviculopectinidae.

Mineralogy.—Bimineralic (Carter, 1990a, p. 241). There are no data about *Oxypteria* shell. Data provided for family Aviculopectinidae. Outer shell layer: calcite (prismatic-homogeneous-foliated). Inner shell layer: aragonite (nacreous-cross-lamellar).

Genus ANTIJANIRA Bittner, 1901c, p. 49

Type species.—*Pecten hungaricus* Bittner, 1901c, p. 48.

Remarks.—According to Allasinaz (1972), Bittner proposed the name *Antijanira* to accommodate a group of Triassic species with a particular ornamentation type. However, Bittner did not provide a true diagnosis, nor did he indicate the similarities and differences with other taxa (Allasinaz, 1972). Probably for this reason, Newell and Boyd (1995) placed *Antijanira* in synonymy with *Leptocondria* Bittner, 1891, p. 101. Allasinaz (1972) provided an adequate diagnosis and discussed its similarities with other taxa, so the genus will be considered valid here and included in the Aviculopectinidae, according to this author. Cox and others (1969) and Carter (1990a) regarded it a member of Pectinidae, as did other authors (Kobayashi & Tamura, 1983a; Gou, 1993), who also considered it a subgenus of *Chlamys* Röding in Bolten, 1798. However, Johnson and Simms (1989) suggest allocation in Aviculopectinidae is supported by the shell structure and the aviculopectinid-type ligament.

Stratigraphic range.—Middle Triassic (Anisian)—Upper Triassic (Carnian) (Allasinaz, 1972). Cox and others (1969) assigned it an Upper Triassic range in Hungary and Sepkoski (2002) a Triassic (Anisian–Carnian) range, taking data from Hallam (1981), who considered it to be present only in the European Carnian, and Hayami (1975), who reported it from Anisian and Ladinian beds. Although the Anisian records appeared in Bittner (1903), Cox and others (1969) did not take them into account. On the other hand, Allasinaz (1972) did consider them, and we follow him.

Paleogeographic distribution.—western Tethys (Fig. 25). The distribution of this genus was limited to the Tethys domain. Waller and Stanley (1998) found a fragment of scallop that could be attributed to *Antijanira amphidoxa* (Bittner, 1903) from Middle Triassic beds of Nevada, but Waller and Stanley (2005) later included this specimen in *Oxytoma* (*Oxytoma*) *grantsvillensis* Waller in Waller & Stanley, 2005. Although *Antijanira* was reported from the Upper Triassic of China (Kobayashi & Tamura, 1983a; Gou, 1993), we cannot be sure of its presence in this area, since the only available described and figured specimens appeared in Gou (1993), and neither the auricles nor the ligament area are seen in them; moreover, neither the description nor the ornamentation match with the diagnosis given by Allasinaz (1972). Z. Fang and others (2009) tentatively suggested *Halobia* (*Enormihalobia*) Yin & Gan in Gan & Yin, 1978, p. 352, is a junior synonym of *Antijanira*. If this synonymy is accepted, the distribution of *Antijanira* extended to the Eastern Tethys (Carnian of Guizhou province).

Tethys domain: Middle Triassic: Anisian of Yugoslavia (Bittner, 1903; Allasinaz, 1972); Late Triassic: Carnian of Alps (Italy) (Bittner, 1895, 1901a; Allasinaz, 1972; Johnson & Simms, 1989), Tripoli-Garian region (Libya) (Desio, Rossi Ronchetti, & Vigano, 1960), Hungary (Bittner, 1912).

Paleoautoecology.—B, E, S, Epi, Sed; By. According to S. M. Stanley (1970), bivalves that are able to swim possess a symmetrical shell, equal auricles, and an umbonal angle greater than 105°. In the specimens described by Allasinaz, the umbonal angle is usually about 90°, but the angles given by Allasinaz (1972, p. 275) for some specimens from Zardini's collection often exceed 100° and even reach 115°. However, the auricles are not equal (see description in Allasinaz, 1972, p. 271), and in the anterior one, there is a deep byssal groove; also, not all species have a perfectly symmetrical shell, so it is likely that *Antijanira* species lived epibyssate with the sagittal plane in a horizontal position, interpreted by S. M. Stanley (1970) as being very stable since it increases the surface area in contact with the substrate. In addition, the auricles of these species have different convexity, suggesting they were not well adapted for swimming (S. M. Stanley, 1970).

Mineralogy.—Biminerale (Allasinaz, 1972; Carter, 1990a, p. 255, 262). Allasinaz (1972) described the shell microstructure of *Antijanira* with an external shell layer of prismatic calcite in the right valves and fibrous in the left. Carter (1990a) described the microstructure of the group *Antijanira* as grade 2. Although there are differences between the valves, the outer layer is always calcitic and the middle and inner layers are aragonitic. Outer shell layer: calcite (prismatic-homogeneous). Middle and inner shell layers: aragonite (cross-lamellar).

Genus AMPHIJANIRA Bittner, 1901c, p. 49

Type species.—*Pecten janirula* Bittner, 1895, p. 160.

Stratigraphic range.—Middle Triassic (Anisian)—Upper Triassic (Carnian) (Allasinaz, 1972). The range provided by both Cox and others (1969) and Sepkoski (2002) is similar to *Antijanira* (see stratigraphic range for *Antijanira*). Following Allasinaz (1972), we assign a Anisian–Carnian range.

Paleogeographic distribution.—western Tethys (Fig. 25).

Tethys domain: Middle Triassic: Anisian of Yugoslavia (Bittner, 1903; Allasinaz, 1972); Late Triassic: Carnian of the Alps (Italy) (Bittner, 1895; Allasinaz, 1972).

Paleoautoecology.—B, E, S, Epi, Sed; By. *Amphijanira* had an equivalve shell, the auricles were very different, with the posterior one being smaller and separated from the shell and the anterior one with a pronounced byssal notch (Allasinaz, 1972), and thus it is very unlikely that it could swim. It probably lived attached by the byssus.

Mineralogy.—Biminerale (Carter, 1990a, p. 255, 262). Although there are no specific data for *Amphijanira* shells, we assign the same data as *Antijanira*, following Carter, who provided the same information for the entire *Antijanira* Group. Outer shell layer: calcite (prismatic-homogeneous). Middle shell layer: aragonite (cross-lamellar). Inner shell layer: aragonite (cross-lamellar).

Genus PRIMAHINNITES Repin, 1996, p. 367

Type species.—*Primahinnites iranica* Repin, 1996, p. 367.

Remarks.—Repin (1996) included *Primahinnites* within the family Prospondylidae, but he only had a complete right valve and five fragments of right and left valves. Hautmann (2001b) obtained new and better preserved material, in which he observed certain key features, such as the ctenolium, and he included the genus in the family Aviculopectinidae; indeed, he emended the diagnosis. Repin's (1996) allocation was erroneous because none of his specimens had the cementation area preserved, but they had a byssal notch instead, described as being small (Hautmann, 2001b).

Stratigraphic range.—Upper Triassic (Norian–Rhaetian) (Hautmann, 2001b). Although originally Repin (1996) reported *Primahinnites* only from the upper Norian, later Hautmann (2001b) reported it from the Rhaetian as well.

Paleogeographic distribution.—Tethys (Fig. 25).

Tethys domain: Late Triassic: Norian of Iran (Repin, 1996; Hautmann, 2001b); Rhaetian of Iran (Hautmann, 2001b).

Paleoautoecology.—B, E, S, Epi, Sed; By. Hautmann (2001b) described a well-developed byssal notch below the anterior auricle of the right valve, so he considered it to be an epibyssate bivalve.

Mineralogy.—Biminerale (Carter, 1990a, p. 241). There are no data about *Primahinnites* shell mineralogy. Data provided for family Aviculopectinidae. Outer shell layer: calcite (prismatic-homogeneous-foliated). Inner shell layer: aragonite (nacreous-cross-lamellar).

Genus NEOMORPHOTIS H. Yin & Yin, 1983, p. 155

Type species.—*Neomorphotis gigantea* H. Yin & Yin, 1983, p. 155.

This species was regarded as a synonym of *Eumorphotis bubabeensis* Lu by Fang & others, 2009, p. 36.

Remarks.—*Neomorphotis* was originally included in the family Pectinidae, but H. Yin (1985) and Posenato (2008b) transferred it to Aviculopectinidae. Due to its relationship with *Eumorphotis*, this seems appropriate.

Stratigraphic range.—Middle Triassic (Anisian) (Posenato, 2008b). According to Z. Fang and others (2009), the genus was proposed by H. Yin and Yin in 1983 from Middle Triassic beds of China. All records are from the Anisian (e.g., Lu & Chen, 1986; Ling, 1988; Sha, Chen, & Qi, 1990; Posenato, 2008b), but we are not certain which species were included in the genus by the authors, and thus the range will remain temporarily as Anisian until we have access to more information.

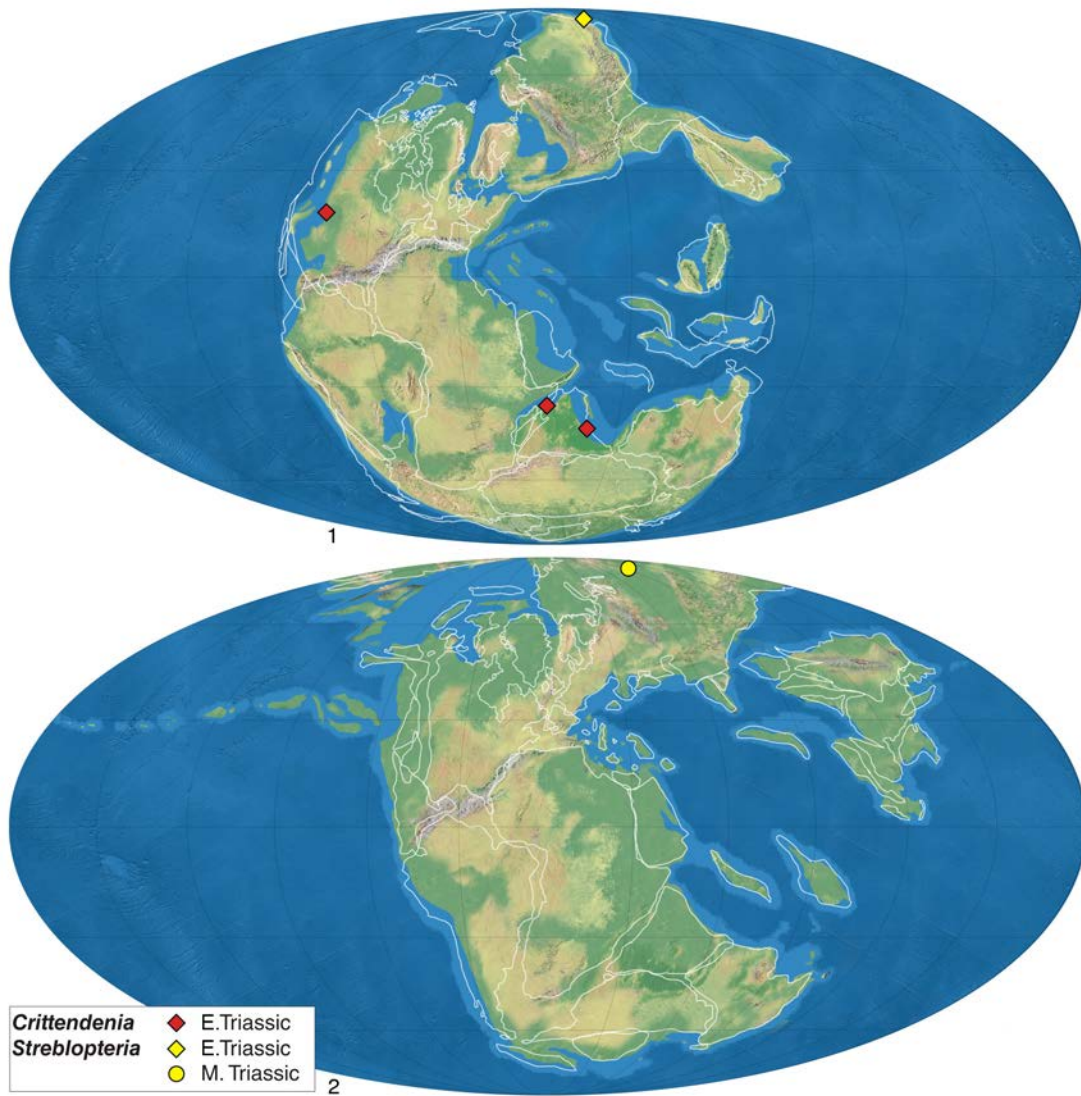


Figure 26. Paleogeographical distribution of Deltopectinidae (*Crittendenia*, *Streblopteria*). 1, Early Triassic; 2, Middle Triassic.

Posenato (2008b) raised the possibility that *Pseudomonotis beneckei* Bittner, 1900 (according to this author, included by H. Yin & Yin in *Neomorphotis*) is a junior synonym *Neomorphotis compta* (Goldfuss, 1833 in 1833–1841). If we accept this synonymy, the genus would be also present in the Lower Triassic, as *P. beneckei* was mentioned for this age by several authors. However, we included this species in *Eumorphotis* following Broglio-Loriga and Mirabella (1986). H. Yin (1985) considered that the genus was also present in the Olenekian, data incorporated by Sepkoski (2002).

Paleogeographic distribution.—Tethys (Fig. 25).

Tethys domain: Middle Triassic: Anisian of the Dolomites (Italy) (Posenato, 2008a, 2008b), southern China (Lu & Chen, 1986; Ling, 1988; Sha, Chen, & Qi, 1990).

Paleoautoecology.—B, E, S, Epi, Sed; By. At least *N. compta*, according to the description offered by Posenato (2008b), prob-

ably was an epibyssate bivalve, since it has an inequivalve shell and a deep byssal notch in the right valve. Moreover, taphonomic evidence also supports this mode of life (see Posenato, 2008b, p. 101).

Mineralogy.—Bimineralic (Posenato, 2008b). Posenato (2008b, p. 101) indicated about *N. compta* (Goldfuss, 1833 in 1833–1841): “shell wall is thin, bimineralic, and consisting of an outer calcitic layer and an inner, thin, calcitized layer.”

Family DELTOPECTINIDAE Dickins, 1957

Genus CRITTENDENIA Newell & Boyd, 1995, p. 52

Type species.—*Crittendenia kummeli* Newell & Boyd, 1995, p. 53.

Remarks.—Newell and Boyd (1995) provisionally included their new genus in Deltopectinidae due to external similarities with *Streblopteria* M’Coy, 1851, in the absence of characters from

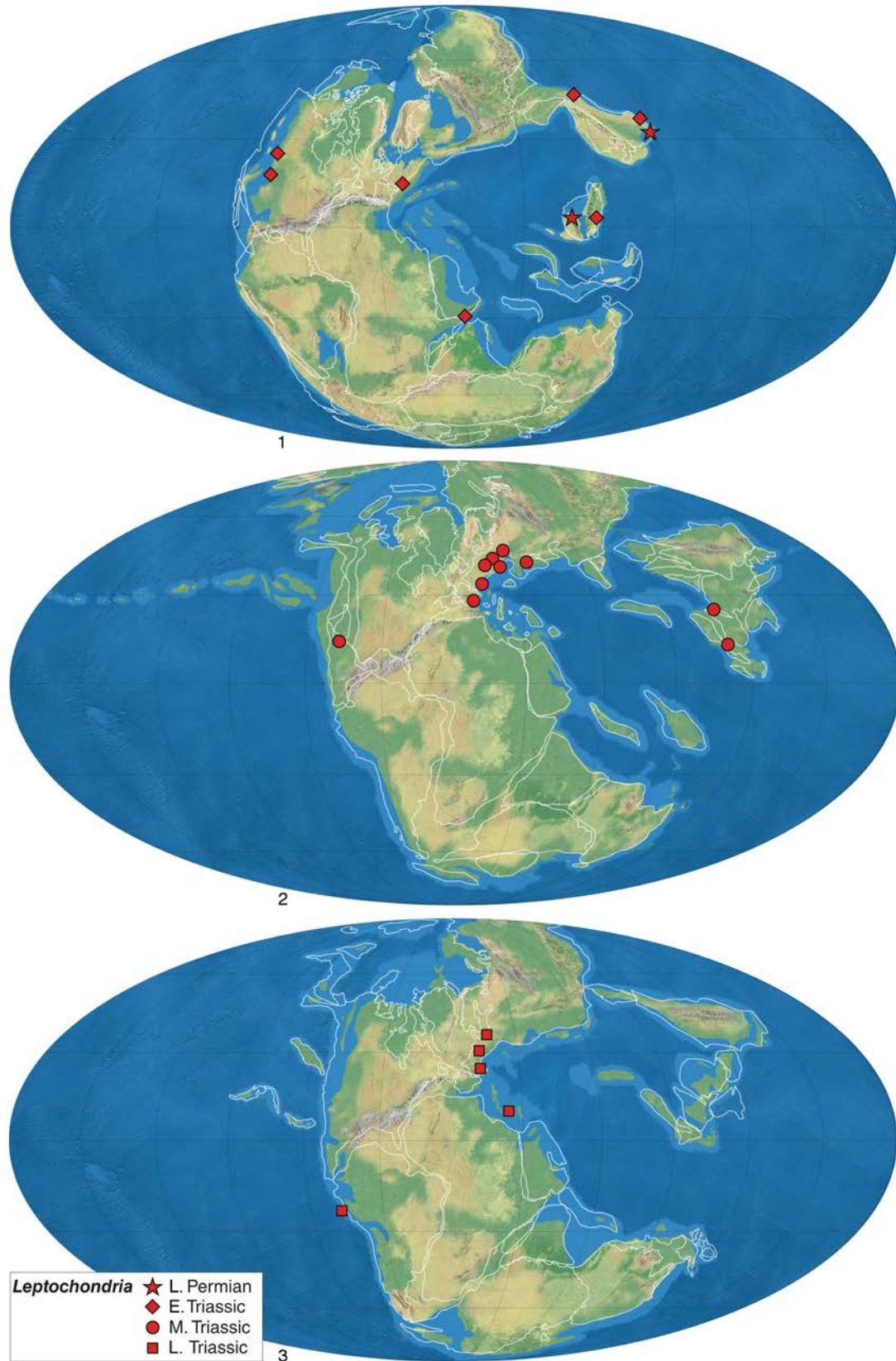


Figure 27. Paleogeographical distribution of Leptochondriidae (*Leptochondria*). 1, late Permian–Early Triassic; 2, Middle Triassic; 3, Late Triassic–Early Jurassic.

the ligament area and microstructure of the shell. Besides the type species, recorded from the Thaynes Formation in Nevada, they also included *Pseudomonotis decidens* Bittner, 1899, which was referred to *Claraia* and *Streblopteria* by other authors (see Newell & Boyd, 1995, p. 52–53). Gavrilova (1996), ignoring Newell and Boyd's paper, proposed a new subgenus of *Claraia*, *Bittnericlaraia* Gavrilova, with *Pseudomonotis decidens* Bittner, 1899, as type.

Newell and Boyd (1995) have a few contradictions, however: in the text, they mentioned *P. decidens* as being collected in Salt Range, Pakistan, and referred it to their figure 39. In this figure explanation, the given name is *Crittendenia kummeli* from the Lower Triassic of Salt Range, Pakistan. Furthermore, they considered *C. kummeli* as being present in Nevada and in Pakistan. This was used by Nakazawa (1996) to regard *C. kummeli* as a synonym of *B. decidens*. But taking into account that the ligament area is not known in any of these species, this synonymy is not clearly justified (Waterhouse, 2000). Waterhouse (2000) saw a clear relationship between *Claraia* and *Crittendenia*, and he referred the latter to the Pterinopectinidae. Furthermore, this author included in *Crittendenia* several new species, plus those included by Gavrilova (1996) in *Claraia* (*Bittnericlaraia*), but Waterhouse had a concept of the genus that is totally different from the original authors. In the absence of more information about key characters of the genus, as discussed above, we provisionally accept the allocation of Newell and Boyd (1995).

Stratigraphic range.—Lower Triassic (Newell & Boyd, 1995). *Crittendenia* was only reported from Lower Triassic (Newell & Boyd, 1995).

Paleogeographic distribution.—Tethys and Circumpacific (Fig. 26).

Tethys domain: Early Triassic: Pakistan (Newell & Boyd, 1995), Himalayas (Bittner, 1899), Nepal (Waterhouse, 2000).

Circumpacific domain: Early Triassic: Nevada (United States) (Newell & Boyd, 1995; Fraiser & Bottjer, 2007a).

Paleoautoecology.—B-Ps, E, S, Epi, Sed-FaM; By. Newell and Boyd (1995) mentioned a deep byssal notch in *Crittendenia* diagnosis, so this is an epibyssate bivalve. In addition, it was often found in association with ammonoids, and the umbilical area of ammonoids is sometimes xenomorphic on the bivalve shell. Therefore, Newell and Boyd (1995) postulated that *Crittendenia* could have had a pseudoplanktonic (attached to objects by the byssus) or even pseudopelagic mode of life (attached by byssus to the shells of live ammonoids).

Mineralogy.—Bimineralic (Waller, 1978). There are no data on the mineralogy and microstructure of *Crittendenia* shell. Due to the uncertainties about its familial assignation, we cannot use here the predominant data from the family. In the diagnosis provided by Waller (1978) for the order Pectinoida, he indicated that the shell is bimineralic.

Genus STREBLOPTERIA M'Coy, 1851, p. 170

Type species.—*Meleagrina laevigata* M'Coy, 1844, p. 80.

Stratigraphic range.—Carboniferous (Mississippian)—Middle Triassic (Anisian) (Dagys & Kurushin, 1985; Newell & Boyd, 1995). *Streblopteria* is a distinctive Paleozoic genus (Newell, 1938; Nakazawa & Newell, 1968; Hayami & Kase, 1977; Waterhouse, 1978; Boyd & Newell, 1979; Newell & Boyd, 1987, among others). However, Newell and Boyd (1995, p. 50) argued that it was also reported

from the Middle Triassic of Siberia: "Distribution: Cosmopolitan, Miss.-Perm., M. Trias. of Arctic Siberia (*vide* Kurushin, 1982, p. 60)." In fact, ten years earlier, Dagys and Kurushin (1985) had described and listed the species referred by Newell and Boyd (1995): *Streblopteria newelli* Kurushin, 1982, and a new species, *S. jakutica* Kurushin in Dagys & Kurushin, 1985, the first being reported from the Olenekian and Anisian and the second from the Olenekian.

Paleogeographic distribution.—Boreal (Fig. 26). During the Carboniferous and the Permian, it had a cosmopolitan distribution (Newell & Boyd, 1995). Specifically, it was reported from the upper Permian of Nepal (Waterhouse, 1978), China (H. Yin, 1983; Z. Yang & others, 1987; M. Wang, 1993; He, Feng, & others, 2007), and the boreal region of Russia (Astafieva, 1998).

Boreal domain: Early Triassic: Olenekian of northern Siberia (Dagys & Kurushin, 1985); Middle Triassic: Anisian of northern Siberia (Dagys & Kurushin, 1985).

Paleoautoecology.—B, E, S, Epi, Sed; By. Within pectinoids, two groups can be recognized regarding their mode of life (S. M. Stanley, 1972): epibyssate bivalves, which are characterized by different convexity in both valves, the anterior auricle being more developed than the posterior one, and having a byssal sinus throughout its ontogeny; and others, also epibyssate but which developed swimming abilities, which are more symmetrical with both valves being equally convex, with auricles of the same shape and size, and an umbonal angle greater than 90°. *Streblopteria* features indicate it belongs in the first group.

Mineralogy.—Bimineralic (Waller, 1978). According to Newell and Boyd (1985), the outer shell layer of *Streblopteria* was fibrous prismatic in both valves. The inner shell layers are not known, but Waller (1978), in the diagnosis of the order Pectinoida, indicated that the shell was bimineralic.

Superfamily PSEUDOMONOTOIDEA Newell, 1938

Family LEPTOCHONDRIIDAE Newell & Boyd, 1995

Genus LEPTOCHONDRIA Bittner, 1891, p. 101

Type species.—*Pecten aeolicus* Bittner, 1891, p. 101.

Stratigraphic range.—middle Permian (Guadalupian)—Upper Triassic (Norian) (Cox, 1949; Newell & Boyd, 1995). Although Cox and others (1969) assigned it a Lower–Upper Triassic range, new records expanded the range of this genus. *Leptochondria* was reported from the middle Permian of Texas and Wyoming (United States) (Boyd & Newell, 1995) and from the upper Permian (Nakazawa & Newell, 1968; He, Feng, & others, 2007). Waller and Stanley (2005) reported *Leptochondria* from upper Permian of Pakistan, allegedly taking their data from Newell and Boyd (1995), but there the genus was mentioned only from the Lower Triassic of Pakistan. The youngest record is Norian (Cox, 1949; Newell & Boyd, 1995).

Paleogeographic distribution.—Tethys and Circumpacific (Fig. 27).

Tethys domain: late Permian: Changhsingian of southern China (Y. Zhang, 1981; H. Yin, 1983; He, Feng, & others, 2007); Early Triassic: Induan of Pakistan (Nakazawa, 1996); Olenekian of southern China (Sha, 1995, 1998; Sha & Grant-Mackie, 1996; Sha, Johnson, & Fürsich, 2004), Italy (Neri & Posenato, 1985; Posenato, 2008a); Middle Triassic: Poland (Senkowiczowa, 1985); Anisian of Italy, Yugoslavia, and Bulgaria

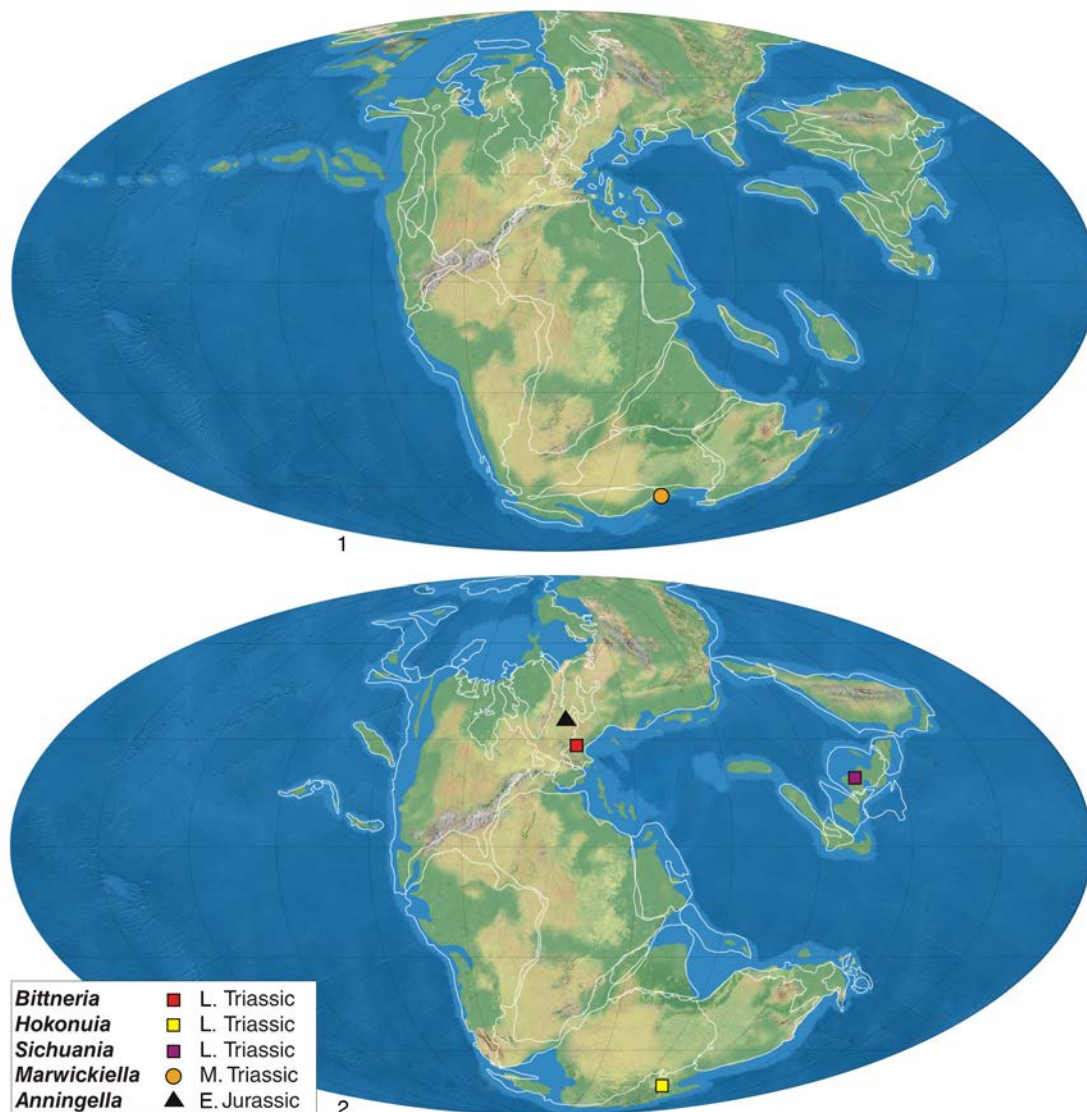


Figure 28. Paleogeographical distribution of Buchiidae (*Bittneria*, *Hokouia*, *Sichuania*, *Marwickiella*, *Anningella*). 1, Middle Triassic; 2, Late Triassic–Early Jurassic.

(Allasinaz, 1972), southern China (Komatsu, Chen, & others, 2004); Anisian–Ladinian of Hungary (Szente, 1997), northern Vietnam (Komatsu, Huyen, & Huu, 2010); Ladinian of Italy (Allasinaz, 1972), Spain (Márquez-Aliaga, 1983, 1985; Márquez-Aliaga, Hirsch, & López-Garrido, 1986; Márquez-Aliaga & Montoya, 1991; Freneix, 1999; Niemeyer, 2002; Márquez-Aliaga & Ros, 2003), Carpathians (Slovakia) (Kochanová, Mello, & Siblík, 1975); Late Triassic: Carnian of Italy and Yugoslavia (Allasinaz, 1972); Norian of Hungary (Allasinaz, 1972), Anatolia (Turkey) (Diener, 1923).

Circumpacific domain: late Permian: Japan (Nakazawa & Newell, 1968; Hayami, 1975; Hayami & Kase, 1977); Early Triassic: Ussuriland (Russia) (Kiparisova, 1938); Olenekian of Nevada (United States) (Newell & Boyd, 1995; Boyer, Bottjer, & Droser, 2004;

Fraiser & Bottjer, 2007a), Utah (United States) (Boyer, Bottjer, & Droser, 2004; Fraiser & Bottjer, 2007a), Japan (Nakazawa, 1961, 1971; Fraiser & Bottjer, 2007a); Middle Triassic: Ladinian of Nevada (United States) (Waller & Stanley, 2005); Late Triassic: Norian of Peru (Cox, 1949).

Paleoautoecology.—B, E, S, Epi, Sed; By. According to the diagnosis provided by Newell and Boyd (1995), there is a wide byssal notch in the right valve. It was most likely an epibyssate bivalve. Sha and Grant-Mackie (1996) proposed a possible pseudoplanktonic mode of life for *Leptochondria*.

Mineralogy.—Bimineralic (Waller & Stanley, 2005). Waller and Stanley (2005) assumed bimineralic mineralogy, due to the differential dissolution of the shell layers in their specimens of *Leptochondria shoshonensis* Waller in Waller & Stanley, 2005.

Superfamily MONOTOIDEA Fischer, 1887 in 1880–1887

Family BUCHIIDAE Cox, 1953

Genus BITTNERIA Broili, 1904, p. 168

Type species.—*Avicula? efflata* Broili, 1904, p. 167.

Remarks.—Broili (1904) proposed the genus *Bittneria* based on *Avicula? efflata*, and he included it in the family Aviculidae, although he noted that it could be considered as being intermediate between *Avicula* and *Pecten*. This allocation is doubtful, because only one left valve was then available. Subsequently, Cox and others (1969) included it in the family Buchiidae, also dubiously. The systematic position of this genus is especially problematic, because the hinge structure is not known (Sha & Fürsich, 1994). These authors related *Bittneria* to *Aucellina* Pompeckj, 1901.

Stratigraphic range.—Upper Triassic (Carnian) (Broili, 1904). The genus was proposed by Broili (1904) as being from Carnian sediments, and little else is known about it. Cox and others (1969) assigned the same range. Subsequently, new material was found at the same stage by Fürsich and Wendt (1977).

Paleogeographic distribution.—western Tethys (Fig. 28). Although J. Chen (1982a) described a new species from the Carnian of southern China (*Bittneria? hunanensis* J. Chen, 1982a), it was only doubtfully assigned to the genus, so we are not considering it.

Tethys domain: Late Triassic: Carnian of southern Alps (Broili, 1904; Waagen, 1907; Fürsich & Wendt, 1977).

Paleoautoecology.—B, E, S, Epi, Sed; By. According to the diagnosis offered by Cox and others (1969), the anterior left auricle is separated from the disk by a deep sinus from where the byssus would probably emerge. *Bittneria* was probably an epibyssate bivalve.

Mineralogy.—?Bimineralic (Carter, 1990a, p. 234). There are no data for the shell of *Bittneria*. We cannot use the characteristic features of the family due to its doubtful systematic allocation. Nevertheless, it is likely that *Bittneria* had a bimineralic shell, as did most members of the Order Pectinioida.

Genus HOKONUIA Trechmann, 1918, p. 202

Type species.—*Hokonua limaeformis* Trechmann, 1918, p. 204.

Remarks.—Although *Hokonua* was related to the families Pergamidiidae (Trechmann, 1918; Waterhouse, 1960), Myalinidae (Trechmann, 1918; Wilckens, 1927) and Pteriidae (Marwick, 1953), it is now referred to Buchiidae (Cox & others, 1969; H. J. Campbell, 1983; Begg & Campbell, 1985; Sha & Fürsich, 1994).

Stratigraphic range.—Upper Triassic (upper Carnian–Norian) (H. J. Campbell, 1983). The genus was first described from the upper Carnian (Trechmann, 1918). It was later reported from Norian beds (H. J. Campbell, 1983). According to the latest stratigraphic revision (H. J. Campbell & Raine in Cooper, 2004), the type species ranges from Oretian to Warepan (=uppermost Carnian and Norian).

Paleogeographic distribution.—Austral (Fig. 28). J. Chen (1982a) reported *Hokonua* sp. from the Carnian of southern China, but the figured specimen (pl. II, 14) is not consistent with the diagnosis of the genus.

Austral domain: Late Triassic: latest Carnian–Norian of New Zealand (Trechmann, 1918; Wilckens, 1927; Marwick, 1953; Waterhouse, 1960; H. J. Campbell, 1983; Grant-Mackie, 1984).

Paleoautoecology.—B, E, S, Epi, Sed; By. Like the other members of the family Buchiidae, *Hokonua* was an epibyssate bivalve. The byssus

emerged through the deep byssal notch in the right valve (Waterhouse, 1960). Although it was suggested that some buchiids might have a pseudoplanktonic mode of life (Wignall & Simms, 1990), we do not believe *Hokonua* is among them, since its distribution is very limited.

Mineralogy.—Bimineralic (Waterhouse, 1960; Begg & Campbell, 1985; Carter, 1990a; Carter, Barrera, & Tevesz, 1998, p. 1002). Carter, Barrera, and Tevesz (1998) indicated that the inner shell layer of *Hokonua* was probably aragonitic, in contrast to other buchiids, which had three calcitic shell layers. Outer shell layer: calcite (prismatic). Middle shell layer: calcite (foliated). Inner shell layer: aragonite (homogeneous).

Genus SICHUANIA Chen in Gu & others, 1976, p. 151

Type species.—*Sichuania difformis* Chen in Gu & others, 1976, p. 151.

Remarks.—*Sichuania* Chen, 1976, was also described as a new genus in Wen and others (December 1976). Chen (in Gu & others, 1976) included *Sichuania* in the Buchiidae. This was followed by Sha, Chen, and Qi (1990), but, although *Sichuania* had the typical form of shells of the family Buchiidae, it lacked a right anterior auricle, and, for this reason, Sha and Fürsich (1994) suggested that it belongs neither to Buchiidae nor to Monotoidea. But as these authors did not propose a new assignment, *Sichuania* is here treated in this family, while awaiting more information.

Stratigraphic range.—Upper Triassic (Norian) (Chen in Gu & others, 1976). *Sichuania* was first described by Chen in Wen and others (1976) from the Norian of China (Sichuan and Yunnan provinces). Later, it was also reported from Rhaetian beds (Hautmann, 2001b), although without a description or the original source data. Waterhouse (1980b) provisionally attributed his supposedly Lower Triassic specimens from New Zealand to *Sichuania* (?*Sichuania marwicki* Waterhouse, 1980b). But the sediments in which he found the specimens were not of that age, and the specimens were not well accommodated in this genus (see discussion for *Marwickiella*, p. 79).

Paleogeographic distribution.—Eastern Tethys (Fig. 28). Hautmann (2001b) mentioned *Sichuania* from the Norian and Rhaetian beds of Tibet and the Himalayas, but he did not indicate the source of the data. Kobayashi and Tamura (1983a) also quoted it from the Upper Triassic in several Chinese provinces and southern Tibet, but this record does not have a source of original data.

Tethys domain: Late Triassic: Norian of China (Chen in Gu & others, 1976; Sha, Chen, & Qi, 1990).

Paleoautoecology.—B, E, S, Epi, Sed; By. According to the translation of the original generic diagnosis provided by Waterhouse (1980b), the shell is inequivalve, with the left valve being more prominent and convex than the right, and it had a byssal sinus. Due to these characteristics, *Sichuania* should be regarded as an epibyssate bivalve, although Sha, Chen, and Qi (1990) only doubtfully assigned it this mode of life.

Mineralogy.—?Bimineralic (Carter, 1990a, p. 234). There are no data on *Sichuania* shell mineralogy and structure. Since its systematic position is not known, we cannot assign it the dominant mineralogy in the family. Nevertheless, it likely had a bimineralic shell, like most members of the order Pectinioida.

Genus MARWICKIELLA Sha & Fürsich, 1994, p. 21

Type species.—? *Sichuania marwicki* Waterhouse, 1980b, p. 1.

Remarks.—Waterhouse (1980b) tentatively assigned his specimens to *Sichuania*, thinking that they belonged to the family Buchiidae. We have already seen that *Sichuania* is probably not a buchiid, as it lacked the typical anterior auricle. But Waterhouse's specimens have this auricle and other diagnostic features of the family Buchiidae (Begg & Campbell, 1985; Sha & Fürsich, 1994). Since seemingly this species did not fit into any Buchiidae, Begg and Campbell (1985, p. 739) argued that it represented a new genus, and later Sha and Fürsich (1994) proposed the name *Marwickiella* for it.

Stratigraphic range.—Middle Triassic (Anisian). Although Waterhouse (1980b) originally referred the beds with ?*Sichuania marwicki* to the Lower Triassic, Begg (1981) showed that the areas where Waterhouse collected this species were in fact of lower Anisian age.

Paleogeographic distribution.—Austral (Fig. 28).

Austral domain: Middle Triassic: Anisian of New Zealand (Waterhouse, 1980b; Begg, 1981; Begg & Campbell, 1985).

Paleoautoecology.—B, E, S, Epi, Sed; By. According to the description provided by Waterhouse (1980b) for the only species included in the genus, it was probably an epibyssate bivalve.

Mineralogy.—Bimineralic. According to Waterhouse (1980b), his specimens had a thin calcitic shell, although he did not perform microstructural studies of any kind. We assign the dominant mineralogy of family Buchiidae.

Genus ANNINGELLA Cox, 1958, p. 44

nom. nov. pro Anningia Cox, 1936, p. 468, *non* Broom, 1927, p. 227 (Amniota)

Type species.—*Anningia carixensis* Cox, 1936, p. 468.

Remarks.—Little is known about *Anningella*, because it is only known from its right valve. According to Sha and Fürsich (1994), it is practically indistinguishable from *Chaenocardia* Meek & Worthen, 1869 (a Carboniferous genus not discussed). In their opinion, this genus would be better located in the Asoellidae, but in the absence of any further study, we follow Cox and others (1969) and include it in the Buchiidae.

Stratigraphic range.—Lower Jurassic (Hettangian–Sinemurian) (Hallam, 1987; Warrington & Ivimey-Cook, 1990). Cox (1936) described the genus *Anningia* (renamed *Anningella* by Cox [1958]) from the Liassic of Dorset. Subsequently, Cox and others (1969) assigned it a lower Lower Jurassic range. There are some inconsistencies in the literature regarding the stratigraphic range of this genus; most authors reported it from Sinemurian beds of England (Hallam, 1976, 1977, 1987; Liu, 1995; Aberhan, 2001); however, Sepkoski (2002) assigned it a Rhaetian–Sinemurian range, allegedly taking data from Hallam (1977, 1981), but, in this last paper, the genus is not mentioned. Hallam and El Shaarawy (1982) quoted *Anningella* from the “Penarth group” of Rhaetian age, but later Warrington and Ivimey-Cook (1990) indicated that *Anningella* had its origin in the *Planorbis* zone (=Hettangian) of the Bristol Channel area, so we believe its presence in the Rhaetian is unlikely.

Paleogeographic distribution.—western Tethys (Fig. 28).

Tethys domain: Early Jurassic: Hettangian of England (Warrington & Ivimey-Cook, 1990); Sinemurian of England (Hallam, 1976, 1977, 1987; Liu, 1995; Aberhan, 2001).

Paleoautoecology.—B, E, S, Epi, Sed; By. Like the other members of the family Buchiidae, *Anningella* was an epibyssate bivalve.

Mineralogy.—Bimineralic (Carter, 1990a, p. 234). There are no data on the shell of *Anningella*. Nevertheless, it likely had a bimineralic shell, like most members of the Order Pectinioida.

Family MONOTIDAE Fischer, 1887 in 1880–1887**Genus MONOTIS Bronn, 1830a, p. 284**

Type species.—*Pectinites salinarius* von Schlotheim, 1820, p. 230.

Remarks.—Although Cox and others (1969) only considered two subgenera of *Monotis*, *M. (Monotis)* and *M. (Entomonotis)* Marwick, 1935, p. 298, in the past three decades many more were named: *Pacimonotis* Grant-Mackie & Silberling, 1990; *Eomonotis* Grant-Mackie, 1978a, p. 102; *Inflatomonotis* Grant-Mackie, 1978a, p. 105; *Maorimonotis* Grant-Mackie, 1978a, p. 108; 1978d. Although these subgenera group species with different morphotypes and are biostratigraphically useful, they are not based on phylogenetic relationships (McRoberts, Krystyn, & Shea, 2008). However, McRoberts (2010) considered *Eomonotis* at genus level, following Tozer (1980). *Monotis* had a wide paleogeographic distribution during the Late Triassic and is a good biochronologic indicator, due to its relatively rapid morphologic change; thus, despite its limited stratigraphic range, many authors studied them from this point of view.

Stratigraphic range.—Upper Triassic (Norian–lower Rhaetian) (McRoberts, Krystyn, & Shea, 2008). Until very recently, *Monotis* was believed to be completely extinguished at the Norian–Rhaetian boundary (Wignall & others, 2007), but McRoberts, Krystyn, and Shea (2008) reported it from the lower Rhaetian.

Paleogeographic distribution.—Cosmopolitan (Fig. 29). McRoberts (1997a) mentioned *Monotis* from the Norian of Mexico, but he neither described nor figured the material.

Tethys domain: Late Triassic: Norian of Slovenia (Jurkovsek, 1982a, 1982b), China (C. Chen & Yu, 1976; J. Chen & Yang, 1983), Afghanistan (Polubotko, Payevskaya, & Repin, 2001), Iran (Westermann & Seyed-Emami, 1981; Hautmann, 2001b), western Caucasus (Russia) (Ruban, 2006a), northern Alps (Austria) (Grant-Mackie & Silberling, 1990; McRoberts, Krystyn, & Shea, 2008); Rhaetian of northern Alps (Austria) (McRoberts, Krystyn, & Shea, 2008; McRoberts, 2010).

Circumpacific domain: Late Triassic: Norian of British Columbia (Ward & others, 2004; Wignall & others, 2007), Alaska (accreted terranes) (Grant-Mackie & Silberling, 1990; Silberling, Grant-Mackie, & Nichols, 1997), Peru (Jaworski, 1922; Steinmann, 1929; Prinz, 1985), Bolivia (Beltan & others, 1987; Suarez-Riglos & Dalenz-Farjat, 1993), Chile (Thiele, 1967; Westermann, 1970; Z. Fang & others, 1998), Nevada (United States) (Grant-Mackie & Silberling, 1990), California (McRoberts, 2010), Japan (Nakazawa, 1964; Hayami, 1975; Ando, 1983, 1984, 1986, 1987; Ando, Noda, & Sato, 1987).

Austral domain: Late Triassic: Norian of New Zealand (Grant-Mackie, 1976, 1978a, 1978b, 1978c, 1978d, 1980a, 1980b; H. J. Campbell, 1983; MacFarlan, 1998).

Boreal domain: Late Triassic: ?Carnian, Norian of Primorie (Kiparisova, 1972); Norian of northeastern Russia (Kiparisova, Bychkov, & Polubotko, 1966; Kurushin, 1990; Klets, 2006), several localities

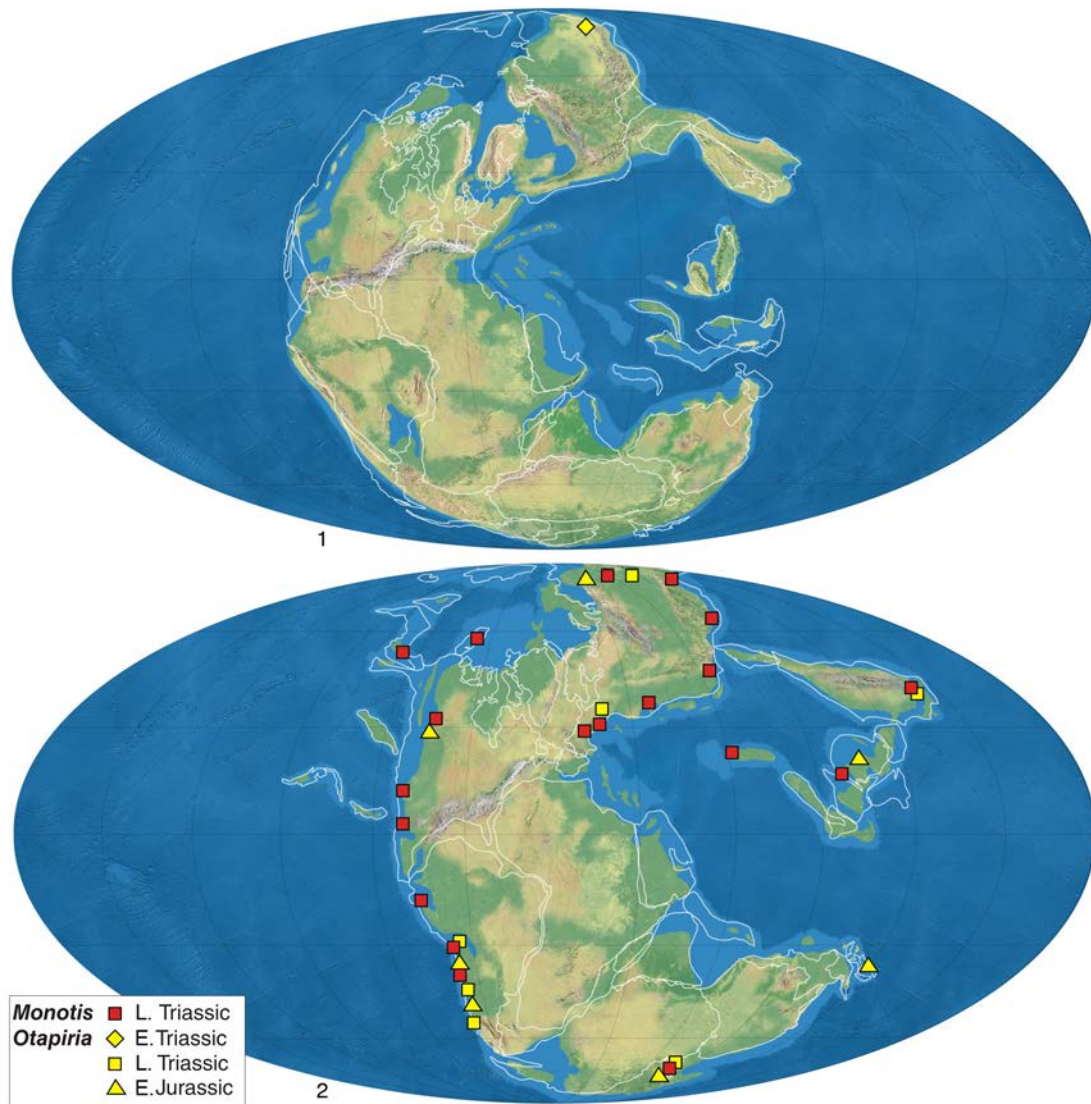


Figure 29. Paleogeographical distribution of Monotiidae (*Monotis*, *Otapiria*). 1, Early Triassic; 2, Late Triassic–Early Jurassic.

of Russia (Payevskaya, 1985), Alaska (Arctic terranes) (Silberling, Grant-Mackie, & Nichols, 1997), Arctic Archipelago (Canada) (Tozer, 1970).

Paleoautoecology.—B-Ps, E, S, Epi, Sed-FaM; By. Much has been speculated about the mode of life of *Monotis*. The interpretations range from benthic epibyssate on hard substrate (S. M. Stanley, 1972; Hallam, 1981; McRoberts, Krystyn, & Shea, 2008), byssate on aquatic plants (Ando, 1987; Hautmann, 2001b), pseudoplanktonic (Hayami, 1969a; S. M. Stanley, 1972; Silberling, Grant-Mackie, & Nichols, 1997) and even nektonic (Jefferies & Minton, 1965). These interpretations were based on the *Monotis* shell morphology and on the facies where different species are typically found.

A nektonic mode of life was proposed by Jefferies and Minton (1965) but was rejected by several authors (S. M. Stanley, 1972; Ando, 1987), since it is unlikely that *Monotis* could swim with its inequilateral and inequivalve shell, and some species had a byssal notch (Ando, 1987). According to S. M. Stanley (1972), a benthic

mode of life for some species and a pseudoplanktonic one for others would be more in agreement with the stratigraphic and taphonomic evidence. One of the strongest arguments in favor of a pseudoplanktonic mode of life is the great paleogeographic distribution *Monotis* had, but this could also be explained by a long-lasting planktotrophic larval stage, which is difficult to corroborate when the protoconch is not preserved. The genus is also usually found in deep-water environments, often deficient in oxygen, but this is not always the case, since Ando (1987) reported that some Japanese species were found in shallow, well-oxygenated environments. A pseudoplanktonic mode of life is also plausible with *Monotis* morphology, as it had a thin shell and its anterior auricle formed a pseudoctenolium, which indicates that the shell attached to objects by its byssus (Silberling, Grant-Mackie, & Nichols, 1997). Furthermore, the preferential orientation of the shells found in the fossil record, with the concave side upward, suggests they fell floating through the water column toward the bottom, in low-turbulence environments and with little

post mortem transport (Silberling, Grant-Mackie, & Nichols, 1997). However, McRoberts, Krystyn, and Shea (2008) explain this orientation by suggesting that *Monotis* was epibenthic and lived in this position on the bottom and in cave fissures.

According to criteria by Wignall and Simms (1990) to distinguish between obligate and facultative pseudoplanktonic bivalves, and taking into account everything mentioned above, *Monotis* could be facultative, as it is not usually associated with objects suitable for fixation. As mentioned above, it is often, but not always (see Ando, 1987), found associated with deep facies. Moreover, it is often found in low-oxygen facies, and this could have several explanations, from shells falling into these facies because they had a pseudoplanktonic mode of life, or the presence of some kind of symbiotic organisms that made living in those environments possible, although there is no evidence to support this last possibility (A. G. Fischer & Bottjer, 1995).

According to this evidence, we agree with S. M. Stanley (1972) and consider that some species were epibyssate on the bottom and others might have had a facultative pseudoplanktonic mode of life.

Mineralogy.—?Calcitic (Carter, 1990a, p. 248; Carter, Barrera, & Tevesz, 1998). According to Carter, Barrera, and Tevesz (1998), members of family Monotidae have three calcitic shell layers, although Carter (1990a) noted that the presence of a thin sublayer of aragonite in the inner or middle shell layer of one or both valves was possible. According to the emended diagnosis offered by Carter (1990a) for the family Monotidae, the shell is built of foliated calcite with a thin homogeneous layer within one or both valves.

Genus OTAPIRIA Marwick, 1935, p. 302

Type species.—*Pseudomonotis marshalli* Trechmann, 1923, p. 270.

Remarks.—According to Begg and Campbell (1985), Damborenea (1987b, 2002a), Ando (1987), and Carter (1990a), we include *Otapiria* in Monotidae (see Damborenea, 1987b, p. 154, for discussion on this topic); although Cox and others (1969), like other later authors (e.g., J. Yin, H. Yao, & Sha, 2004) included it in Aviculopectinidae. We consider *Lupherella* Imlay, 1967, p. 8, as a subgenus of *Otapiria* and *Pleuromysidia* Ichikawa, 1954, p. 52, as a synonym of *Otapiria* (see discussion in Genera not Included, p. 167).

Stratigraphic range.—Lower Triassic (Olenekian)—Upper Jurassic (Kimmeridgian) (Dagys & Kurushin, 1985; Damborenea, 1987b). Cox and others (1969) assigned it an Upper Triassic (Rhaetian)—Upper Jurassic (Tithonian) range. Damborenea (1987b), in her exhaustive review of the species that were attributed to the genus, recorded Kimmeridgian as the youngest record, as did Sha (1996). It is thought that *Otapiria* originated during the Early Triassic in the Boreal domain (Dagys & Kurushin, 1985), although it was not until Carnian times that this genus began to be abundant (Ando, 1988). Dagys and Kurushin (1985) proposed a new subgenus and new species, *Otapiria (Praeotapiria) bakevilliaeformis* from Lower Triassic beds. According to Ando (1988), this new subgenus is unnecessary, since morphological differences with other species of *Otapiria* are very subtle.

Paleogeographic distribution.—Cosmopolitan (Fig. 29). According to Sha (1996), *Otapiria* originated in the Boreal domain and probably also in the Austral, and its distribution was most likely conditioned by water temperature and substrate. It was especially recorded at high and middle latitudes and adapted to low temperatures (Damborenea,

1993). It is regarded as a bipolar (Damborenea, 1996a) or antitropical taxon (Sha, 1996). According to Sha (1996), during the Early Triassic–Late Jurassic interval, it was widely distributed in Austria, Carpathians, Alaska, northern and northeastern Siberia, Japan, New Caledonia, New Zealand, Peru, Chile, Argentina, Colombia, and Ecuador. It was only known from northeastern Siberia, New Zealand, and Chile from the Late Jurassic. Damborenea (1986) regarded this as a circumpacific genus with sporadic appearances in the Tethys, and this is corroborated by our data.

Tethys domain: Late Triassic: Norian of Austria (Grant-Mackie & Zapfe, 1973; Zapfe, 1973); Rhaetian of Austria (Zapfe, 1973; McRoberts, 2010); Early Jurassic: southeastern China (J. Yin, H. Yao, & Sha, 2004).

Circumpacific domain: Late Triassic: Carnian of Japan (Hayami, 1975; Ando, 1988); Norian of Chile (Chong & Hillebrandt, 1985; Covacevich, Pérez, & Escobar, 1991), Japan (Ando, 1988); Early Jurassic: Hettangian–Sinemurian of Chile (Escobar, 1980); Sinemurian of Canada (Poulton, 1991; Aberhan, 1998a, 1998b), Chile (Covacevich & Escobar, 1979; Aberhan, 1993, 1994a, 1998b).

Austral domain: Late Triassic: ?Andes (Argentina) (Covacevich, Pérez, & Escobar, 1991; Riccardi & others, 1997, 2004); Rhaetian of New Zealand (Marwick, 1953; Grant-Mackie, 1960) and Argentina (Damborenea & Manceñido, 2012); Early Jurassic: Hettangian–Sinemurian Neuquén basin (Argentina) (Damborenea, 1987b, 1993, 1996a, 2002a; Damborenea & Manceñido, 2005b), New Zealand (Marwick, 1953; Grant-Mackie, 1960), New Caledonia (Marwick, 1953).

Boreal domain: Early Triassic: Siberia (Dagys & Kurushin, 1985); Late Triassic: Carnian of Primorie (Kiparisova, 1972); Norian of Siberia (Okuneva, 1985, 1986); Norian–Rhaetian of Siberia (Klets, 2006); Early Jurassic: Hettangian–Sinemurian of Siberia (Polubotko, 1968b).

Paleoautoecology.—B, E, S, Epi, Sed; By. Ando (1988), after studying the environments and taphonomy related to *Otapiria*, concluded that it was probably an epibyssate bivalve. Although wood fragments were found associated with *Otapiria dubia* (Ichikawa, 1954), there was no evidence that the bivalve was attached to them. However, due to the shell orientation, they probably attached to each other by their byssus. Both the sediments in which *Otapiria* is usually found and its orientation indicate that its mode of life was different from *Monotis* (Ando, 1988). An epibyssate mode of life was also proposed for other species of *Otapiria* (Gruber, 1984).

Mineralogy.—?Calcitic (Carter, 1990a). No data are known on *Otapiria* shell microstructure. According to the emended diagnosis offered by Carter (1990a) for the family Monotidae, the shell is composed of foliated calcite with a thin homogeneous outer layer on one or both valves. Carter, Barrera, and Tevesz (1998) assigned a calcitic mineralogy to the three shell layers of family Monotidae members.

Family OXYTOMIDAE Ichikawa, 1958

Genus OXYTOMA Meek, 1864, p. 39

Type species.—*Avicula muensteri* Bronn, 1830b, p. 164.

Stratigraphic range.—?Lower Triassic, Middle Triassic (Ladinian)—Upper Cretaceous (Maastrichtian) (Abdel-Gawad, 1986; Waller & Stanley, 2005). Cox and others (1969) assigned a Upper Triassic–Upper Cretaceous range. However, over the years, *Oxytoma*

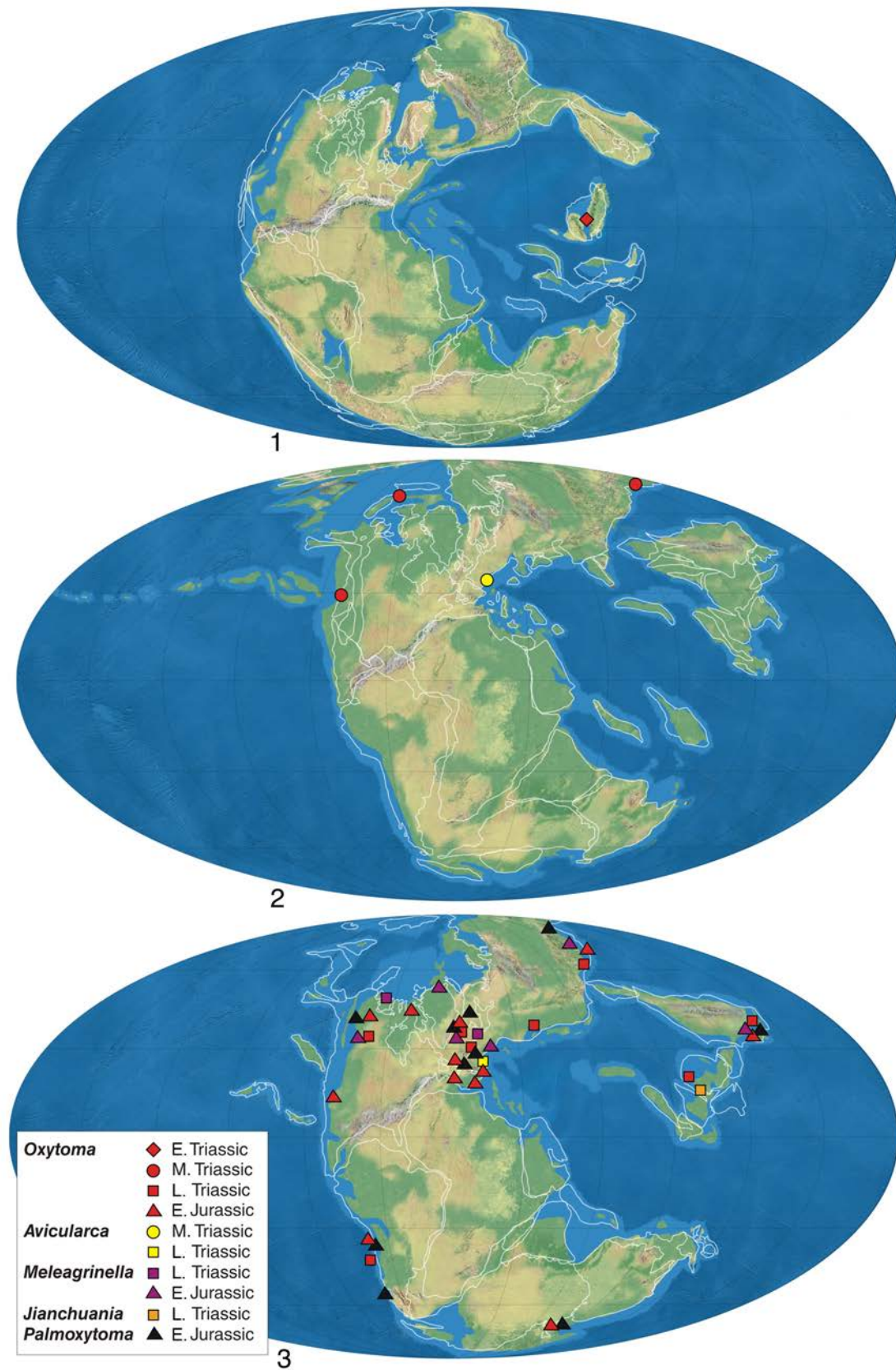


Figure 30. Paleogeographical distribution of Oxytomidae (*Oxytoma*, *Avicularca*, *Meleagrinnella*, *Jianchuania*, *Palmoxytoma*). 1, Early Triassic; 2, Middle Triassic; 3, Late Triassic–Early Jurassic.

was repeatedly reported from Middle Triassic sediments. Waller (in Waller & Stanley, 2005, p. 38) considered that the oldest records of the genus to be *Oxytoma* sp. aff. *O. inaequivalve* Sowerby var. *intermedia* Emmerich, and *Oxytoma* sp. aff. *Oxytoma mojsisovicsi* Teller, from Triassic beds of Fujian province in southeastern China. They assumed a Lower Triassic age, because these species appeared to be associated with *Eumorphotis*. They also noted that *Oxytoma scythicum* (Wirth, 1936), reported from the Lower Triassic, was later assigned to *Towapteria* (family Bakevelliidae).

Paleogeographic distribution.—Cosmopolitan (Fig. 30).

Tethys domain: Early Triassic: ?southern China (Waller & Stanley, 2005); Late Triassic: China (J. Chen, 1982a); Norian of western Carpathians (Kollarova & Kochanová, 1973); Rhaetian of the Alps (Austria) (Tanner, Lucas, & Chapman, 2004; Tomašových, 2006a), England (Ivimey-Cook & others, 1999); Early Jurassic: Sinemurian of England, France, Spain, and Portugal (Liu, 1995), Italy (Monari, 1994), Hungary (Szente, 1996).

Circumpacific domain: Middle Triassic: Ladinian of Nevada (Waller & Stanley, 2005); Late Triassic: ?Chile (Moscoso & Covacevich, 1982; Damborenea, 1987b); Carnian of Japan (Hayami, 1975; Ando, 1988); Norian of Japan (Nakazawa, 1956, 1963, 1964; Hayami, 1975); Norian or Rhaetian of Chile (Chong & Hillebrandt, 1985); Rhaetian of Canada (Wignall & others, 2007); Early Jurassic: Hettangian of Nevada (United States) (Guex & others, 2003; Lucas & Tanner, 2004); Hettangian–Sinemurian of Chile (Escobar, 1980; Aberhan, 1994a), Canada (Poulton, 1991; Aberhan, 1998a, 1998b; Aberhan, Hrudka, & Poulton, 1998); Sinemurian of Japan (Hayami, 1975).

Austral domain: Early Jurassic: Hettangian–Sinemurian of New Zealand (Marwick, 1953).

Boreal domain: Middle Triassic: Ladinian of Siberia (Klets, 2006), Arctic Archipelago (Canada) (Tozer, 1961); Late Triassic: Primorie (Kiparisova, 1972); Early Jurassic: Hettangian–Sinemurian of Greenland (Liu, 1995), northeastern Russia (Milova, 1988).

Paleoautoecology.—B-Ps, E, S, Epi, Sed-FaM; By. Species belonging to *Oxytoma* had a well-developed byssal notch, suggesting that they were epibyssate bivalves. They had an elongated posterior auricle, and thus *Oxytoma* was compared with *Pteria* regarding its mode of life (Cox & others, 1969), living attached by the byssus to hydrozoa, shells, or other objects (Fürsich, 1980). According to Sha (1991), *Oxytoma* larvae were probably planktotrophic. However, some species, such as *Oxytoma inaequivalve* (J. Sowerby, 1819), most likely could also have had a pseudoplanktonic mode of life, because they were found attached to *Echioceras* shells (Sinemurian of Dorset) (Wignall & Simms, 1990, fig. 3). The evidence suggests that *O. inaequivalve* specimens were fixed to the ammonoids when they were alive.

Mineralogy.—Calcitic (Carter, 1990a, p. 249). Waller (in Waller & Stanley, 2005) suggested a probably entirely calcitic shell for their specimens of *Oxytoma* (*Oxytoma*) *grantsvillensis* Waller in Waller & Stanley, 2005, since there was no evidence of differential recrystallization of the inner shell layer. For the family Oxytomidae, Carter (1990a) indicated that the shells were mostly calcitic, but they could have had a very thin aragonitic middle layer of cross-lamellar microstructure; however, there is no record of this middle shell layer in *Oxytoma*. Outer shell layer: calcite (simple prismatic). Middle and inner shell layers: calcite (foliated).

Genus AVICULARCA Bubnoff, 1821, p. 281

Type species.—*Avicula cardiiformis* Münster, 1841, p. 78.

Stratigraphic range.—Middle Triassic (Ladinian)–Upper Triassic (Carnian). Cox and others (1969) assigned it an Upper Triassic range in the southern Alps. The type species was reported from sediments of this age (Wissman & Münster, 1841), and later, the genus was mentioned by Laube (1865) as being from the same stage. However, Bubnoff (1821) proposed *Avicularca* as a subgenus of *Avicula*, and he included three new species from the Italian Ladinian. Sepkoski (2002) assigned it a Carnian, ?Rhaetian range, following Crame (1996), but the last author did not adequately substantiate this range.

Paleogeographic distribution.—western Tethys (Fig. 30).

Tethys domain: Middle Triassic: Ladinian of Pedrazzo (Italy) (Kutassy, 1931); Late Triassic: southern Alps (Italy) (Wissman & Münster, 1841; Laube, 1865).

Paleoautoecology.—B, E, S, Epi, Sed; By. According to the generic diagnosis offered by Cox and others (1969, p. 344), *Avicularca* was probably an epibyssate bivalve.

Mineralogy.—Unknown. There are no data about *Avicularca* shell mineralogy. Since the allocation of this genus by Cox and others (1969) was doubtful, we cannot assign the predominant mineralogy of family Oxytomidae.

Genus MELEAGRINELLA Whitfield, 1885, p. 71

Type species.—*Avicula curta* Hall, 1852, p. 412.

Stratigraphic range.—Upper Triassic (Norian)–Lower Cretaceous (Albian) (Tozer, 1970; Wen, 1999). Although Cox and others (1969) assigned it an Upper Triassic (Rhaetian)–Upper Jurassic range, *Meleagrinnella* was later reported from the Lower Cretaceous: Berriasian (X. Li, 1990), Valanginian (Kaim, 2001), and Albian (Wen, 1999). There are some disagreements regarding the origin of *Meleagrinnella*. Sepkoski (2002) recorded that it ranges from Rhaetian times, based on data provided by Crame (1996), who surely followed Cox and others (1969). *Meleagrinnella* was quoted from the Norian of British Columbia associated with *Monotis* (Westermann & Verman, 1967; Wignall & others, 2007), but specimens were neither figured nor described. The same occurred in the paper by Klets (2006), who considered *Meleagrinnella* to have originated during the Anisian in the Boreal domain. He probably based this on data in Dagys and Kurushin (1985), who included *Avicula polaris* Kittl, 1907, and *Pseudomonotis tasaryensis* Voronetz, 1936, in *Meleagrinnella*, and quoted the Anisian of Siberia from them. *Avicula polaris* was also reported from Carnian beds of Norway (Diener, 1923). Nevertheless, we leave this record as questionable, since we were unable to confirm this information, as none of these authors mentioned the original records. Tozer (1970) recorded *Meleagrinnella antiqua* Tozer from the Norian of the Arctic Archipelago, and this age will be taken provisionally as the first record of the genus.

Paleogeographic distribution.—Tethys, Circumpacific, and Boreal (Fig. 30). Although *Meleagrinnella* was present from the Late Triassic, it started to be more abundant and widely distributed during the Pliensbachian (Marwick, 1953; Duff, 1975; Wen, 1982; Pugaczewska, 1986; Jaitly, 1988; X. Li & Grant-Mackie, 1994; J. Chen, 1999; Harries & Little, 1999; Damborenea, 2002a; Delvene, 2003;

Fraser, Bottjer, & Fischer, 2004; Kenig & others, 2004; Fürsich & others, 2005; Fürsich & Thomsen, 2005; Zakharov & others, 2006).

Tethys domain: Late Triassic: Rhaetian of Austria (Hallam & El Shaarawy, 1982; Early Jurassic: Hettangian–Sinemurian of northwestern Europe (Aberhan, 2001); Sinemurian of Europe (Quenstedt, 1856–1858), England (Liu, 1995).

Circumpacific domain: Early Jurassic: ?Hettangian of Canada (Poulton, 1991); Sinemurian of Japan (Hayami, 1961, 1975), Canada (Poulton, 1991; Aberhan, 1998a, 1998b).

Boreal domain: Late Triassic: Norian of Arctic Archipelago (Canada) (Tozer, 1970); Early Jurassic: Hettangian of northeastern Russia (Sey & others, 1981; Damborenea & others, 1992); Hettangian–Sinemurian of Greenland (Liu, 1995).

Paleoautoecology.—B-Ps, E, S, Epi, Sed-FaM; By. The external morphology of *Meleagrinnella* suggests an epibyssate mode of life. Duff (1975) considered that while *Meleagrinnella* may not have been strictly benthic, it may have attached to algae or even floating objects such as wood fragments, implying a pseudoplanktonic mode of life. Duff (1975) classified it as pendent. It is often reported from bituminous shales. However, Kaim (2001) found *Meleagrinnella* specimens associated with cemented oysters; therefore, in this case, the mode of life was not necessarily pseudoplanktonic.

Mineralogy.—Bimineralic (Carter, 1990a, p. 249). Outer shell layer: calcite (prismatic). Middle shell layer: aragonite (cross-lamellar, in right valve). Inner shell layer: calcite (foliated).

Genus JIANCHUANIA J. Chen & Chen, 1980, p. 57, 59

Type species.—*Pteria? problematica* J. Chen in Ma & others, 1976, p. 287.

Stratigraphic range.—Upper Triassic (?Rhaetian) (J. Chen & Chen, 1980). J. Chen and Chen (1980) proposed *Jianchuania* and reported it from Upper Triassic beds of Yunnan (China), but they did not specify the stage. However, in the systematic discussion of the genus, they suggested that the specimens described by Healey (1908) as *Conocardium?* sp. and *Conocardium superstes* Healey, 1908, from the Rhaetian of Burma, are very similar and appeared in coeval deposits.

Paleogeographic distribution.—Eastern Tethys (Fig. 30). *Jianchuania* was endemic to Yunnan province, China.

Tethys domain: Late Triassic: ?Rhaetian of Yunnan (China) (J. Chen & Chen, 1980).

Paleoautoecology.—B, E, S, Epi, Sed; By. *Jianchuania* had a strongly inequilateral and inequivalve shell, with a deep byssal notch and an elongated posterior auricle, similar to *Pteria*. It was probably an epibyssate bivalve.

Mineralogy.—Bimineralic. There are no data about *Jianchuania* shell mineralogy. We therefore used data provided for the family Oxytomidae.

Genus PALMOXYTOMA Cox, 1962, p. 593

Type species.—*Pecten cygnipes* Young & Bird, 1822, p. 235.

Remarks.—Although Cox (1962) proposed *Palmoxytoma* as subgenus of *Oxytoma* and this was maintained in Cox and others (1969), we consider *Palmoxytoma* to be at the generic level following Damborenea (2002a).

Stratigraphic range.—Lower Jurassic (Hettangian–Pliensbachian) (Cox, 1962). Cox and others (1969) assigned the genus as lower to middle Lower Jurassic range, and this is maintained here. Although there are many papers that regard its origin as Hettangian (see paleogeographic distribution below), Guex and others (2003) and Lucas and Tanner (2004) recorded *Palmoxytoma* from Rhaetian beds of Nevada, but they neither described nor figured the specimens. Some species such as *Oxytoma mojsisovicsi* Teller, 1886, *Oxytoma koniensis* Tuchkov, 1956, and *Oxytoma gizhigensis* Milova, 1976, which are transitional between *Oxytoma* Meek, 1864, and *Palmoxytoma*, were considered to be in *O. (Palmoxytoma)* by some authors (e.g., Milova, 1976; but see Hayami, 1975), and if they were accepted as belonging to *Palmoxytoma*, its range would be extended to Upper Triassic.

Paleogeographic distribution.—Cosmopolitan (Fig. 30). *Palmoxytoma* had a bipolar distribution during the Hettangian (Damborenea, 1993; Sha, 1996; Aberhan, 1998b, 1999), and it appears to have been restricted to the Boreal domain during the Pliensbachian (Damborenea, 1993). Although it was also present in the Tethys and Circumpacific domains, it was not recorded at low paleolatitudes.

Tethys domain: Early Jurassic: Hettangian of England, Sweden, France, Switzerland (Cox, 1962).

Circumpacific domain: Early Jurassic: Hettangian of Chile (Aberhan, 1994a); Sinemurian of Canada (Poulton, 1991; Aberhan, 1998a), Japan (Hayami, 1975).

Austral domain: Early Jurassic: Hettangian of Argentina (Riccardi & others, 1991; Damborenea, 2002a; Damborenea & Manceñido, 2005b; Damborenea & Lanés, 2007), New Zealand (Trechmann, 1923).

Boreal domain: Early Jurassic: Hettangian of northeastern Siberia (Polubotko, 1968b).

Paleoautoecology.—B, E, S, Epi, Sed; By. We assign a mode of life similar to *Oxytoma*, but there is no evidence for a pseudoplanktonic mode of life.

Mineralogy.—Calcitic (Carter, 1990a, p. 249; Carter, 1990b, p. 371). Carter (1990b, p. 371) indicated that the outer shell layer of the type species of *Palmoxytoma* was built of prismatic calcite. We assume a calcitic mineralogy, as in *Oxytoma*, since there is no evidence of an aragonitic middle shell layer.

Family ASOELLIDAE Begg & Campbell, 1985

Begg and Campbell (1985) proposed the family Asoellidae, naming *Asoella* Tokuyama, 1959c, as type genus and including their new genus *Etalia*.

Genus ASOELLA Tokuyama, 1959c, p. 2

Type species.—*Eumorphotis (Asoella) confertoradiata* Tokuyama, 1959c, p. 4.

Remarks.—Although Cox and others (1969) included *Asoella* in the Aviculopectinidae following the original reference, Begg and Campbell (1985) proposed the family Asoellidae to accommodate *Asoella*, *Etalia* Begg & Campbell, 1985, p. 727, and probably also *Aucellina* Pompeckj, 1901, p. 365. They related and characterized these three genera in having edentulous hinges and a subumbonal resilifer with anterior and posterior areas.

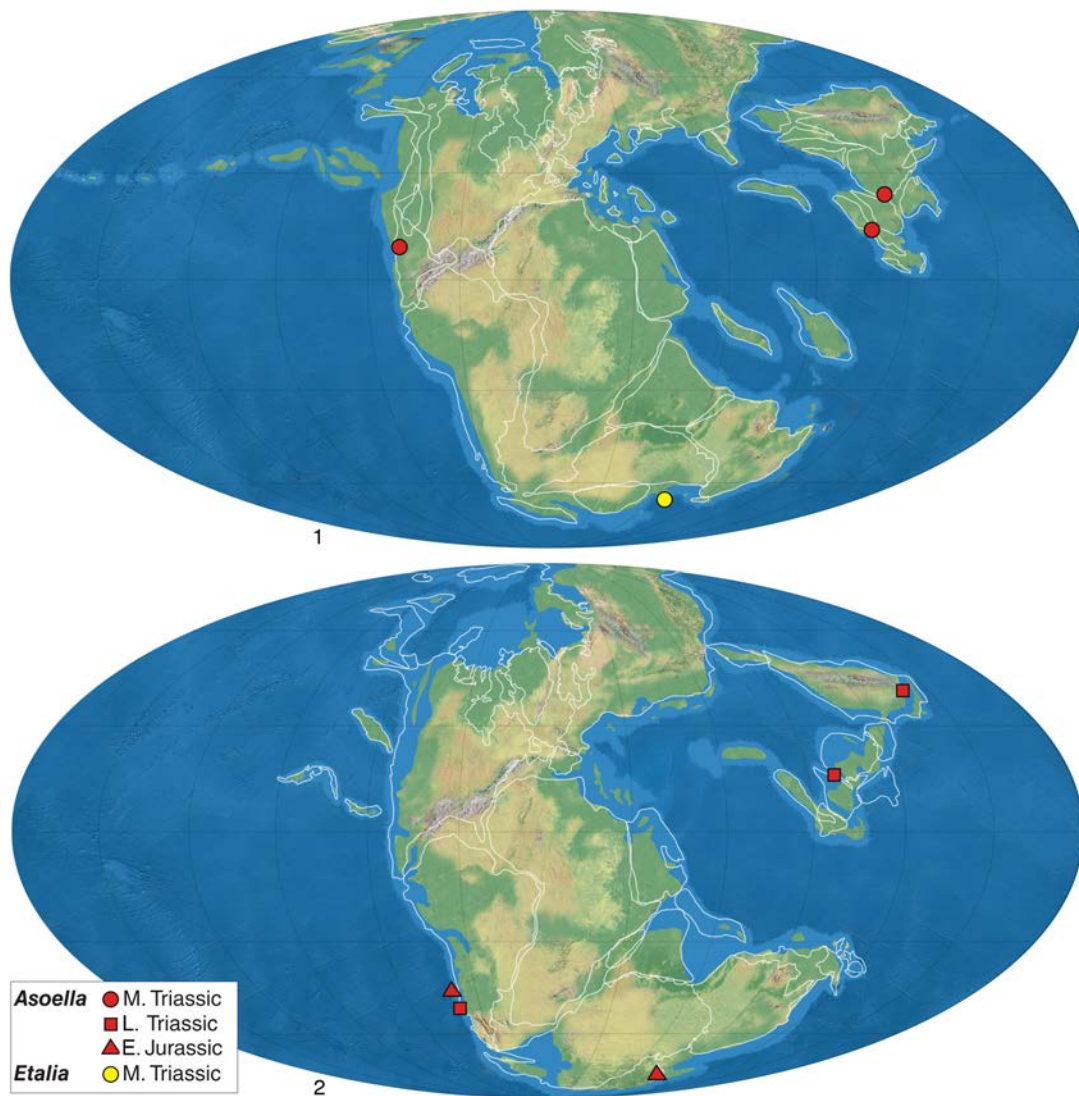


Figure 31. Paleogeographical distribution of Asoellidae (*Asoella*, *Etalia*). 1, Middle Triassic; 2, Late Triassic–Early Jurassic.

Stratigraphic range.—Middle Triassic (Anisian)–Lower Jurassic (Pliensbachian) (Sha, Chen, & Qi, 1990; Damborenea, 2002a). Cox and others (1969) assigned this genus a Norian range in Japan, since at that time only that information was available. Sepkoski (2002), based on Hayami (1975) and H. Yin (1985), assigned it an Anisian–Norian range. Regarding the origin of *Asoella*, it seems reasonably acknowledged that it was present in the Anisian of China (Kobayashi & Tamura, 1983b; H. Yin, 1985; Sha, Chen, & Qi, 1990; Tong & Liu, 2000) and Vietnam (Komatsu, Huyen, & Huu, 2010). Tong and Liu (2000) reported *Asoella illyrica* and *Asoella subillyrica* from the Anisian of China, but K. Huang and Opdyke (2000) suggested that the former is currently *Leptochondria illyrica* (Bittner) (see K. Huang & Opdyke, 2000, p. 80; Waller & Stanley, 2005, p. 35). Lu and Chen (1986) doubtfully assigned *Leptochondria subparadoxica* H. Yin & Yin to *Asoella*. As we have observed in these Chinese publica-

tions, there seems to be some confusion between *Leptochondria* and *Asoella*; *Asoella* records from the Middle Triassic of China should be reviewed. In addition, Waller and Stanley (2005) indicated that their Ladinian specimens from the United States, if they really belong to *Asoella*, would be the oldest records of this genus. In principle, since we cannot access all the information related to *Asoella* from China, we provisionally use Anisian as the oldest record. Although *Asoella* was considered to have vanished at the end of the Late Triassic in the past (Hallam, 1981, 1990), in recent years, it was reported from Sinemurian and Pliensbachian beds of South America (Damborenea, 2002a) and Hettangian–Pliensbachian beds of New Zealand (MacFarlan, 1998; N. Hudson, 2003). Its presence in New Zealand is accepted with caution, since the specimens were not described.

Paleogeographic distribution.—Tethys, Circumpacific, and Austral (Fig. 31).

Tethys domain: Middle Triassic: Anisian of southern China (Sha, Chen, & Qi, 1990); Anisian–Ladinian of northern Vietnam (Komatsu, Huyen, & Huu, 2010); Late Triassic: Carnian of China (J. Chen, 1982a; X. Li, Meng, & Wang, 2005).

Circumpacific domain: Middle Triassic: Ladinian of ?Nevada (United States) (Waller & Stanley, 2005); Late Triassic: Carnian–Norian of Japan (Hayami, 1975).

Austral domain: Late Triassic: Argentina (Damborenea & Manceñido, 2012); Early Jurassic: Sinemurian of Argentina (Damborenea, 1996a, 2002a; Damborenea & Manceñido, 2005b; Damborenea & Lanés, 2007); Hettangian–Sinemurian of ?New Zealand (MacFarlan, 1998; N. Hudson, 2003).

Paleoautoecology.—B, E, S, Epi-Un, Sed; By-R. Begg and Campbell (1985, p. 727), in their diagnosis of superfamily Monotoidea, which includes Asoellidae, stated, “Byssate Pectinina with right valve against substrate and with a distinct byssal notch throughout life.” Damborenea (2002a) indicated that *Asoella asapha* (A. F. Leanza, 1942) was an epibyssate bivalve, at least in the juvenile stages, but it could have lived reclined on its right valve in the adult stage. Besides, since some species were consistently found in association with plant remains, it is possible that they could attach themselves to plants (Damborenea & Manceñido, 2012).

Mineralogy.—?Calcitic (Begg & Campbell, 1985; Carter, 1990a, p. 248). Begg and Campbell (1985) indicated that the outer shell layer was made of prismatic calcite. Carter (1990a) added that the shell was probably all foliated and calcitic, except the outer shell layer, which probably had a prismatic microstructure.

Genus ETALIA Begg & Campbell, 1985, p. 727

Type species.—*Etalia johnstoni* Begg & Campbell, 1985, p. 727.

Stratigraphic range.—Middle Triassic (Anisian) (Begg & Campbell, 1985). *Etalia* was originally reported from the Anisian beds of New Zealand, and no other record of the genus is known. Since it had a restricted stratigraphic range (Etalian, New Zealand regional stage correlated with Anisian), it is a good index fossil for this stage (Begg & Campbell, 1985; H. J. Campbell & Raine in Cooper, 2004).

Paleogeographic distribution.—Austral (Fig. 31).

Austral domain: Middle Triassic: Anisian of Nelson and Southland (New Zealand) (Begg & Campbell, 1985).

Paleoautoecology.—B, E, S, Epi, Sed; By. Begg and Campbell (1985) recorded some specimens in life position and demonstrated that they had a gregarious habit, attaching to each other by the byssus, and reclining the right valves on the substrate, leaving the left valve free to open or close the shell. Authors considered it to be an opportunistic bivalve, a rapid colonizer of shallow-water environments.

Mineralogy.—?Calcitic (Begg & Campbell, 1985; Carter, 1990a, p. 248). Begg and Campbell (1985) indicated that the outer shell layer of the right valves was made of prismatic calcite. Although they did not mention anything about the inner shell layers, they pointed out that the shell was thin and probably calcitic. Carter (1990a), discussing the family Asoellidae, noted that the shell is almost entirely composed of calcite and probably of foliated microstructure, but the outer shell layer of the right valve contained prismatic calcite.

Family PROSPONDYLIDAE Pchelincev, 1960

=Terquemiidae Cox, 1964

Due to the wide range of different opinions in the literature about relations of the various genera included in this family, and as it is not an objective of this paper to review all of them, we follow mainly Hautmann (2001a) in his analysis of Prospondylidae, since it seems the most appropriate.

Genus TERQUEMIA Tate in Woodward, 1868, p. 65

nom. nov. pro Carpenteria Eudes-Deslongchamps, 1860, p. 127, *non* Gray, 1858, p. 269

Type species.—*Carpenteria pectiniformis* Eudes-Deslongchamps, 1860, p. 130.

Remarks.—Most references to this genus are often based on badly preserved specimens, resulting in a poorly known genus (Damborenea, 2002a; Hautmann & Golej, 2004). The main difficulty is that several genera in this family are externally very similar, and if details of the hinge and other internal characters of the specimens cannot be observed, it is very difficult to know to which genus they belong.

Stratigraphic range.—Lower Jurassic (Sinemurian), ?Upper Jurassic (Hautmann & Golej, 2004). Although Cox and others (1969) assigned it an Upper Triassic–Upper Jurassic range, according to Hautmann (2001a, p. 344): “Most Triassic species assigned to *Terquemia* in lower publications actually belong to *Newaagia* or *Enantiostreon*. Although there are some incompletely preserved specimens which might belong to *Terquemia*, there is no unequivocal record from rocks older than Lower Jurassic.”

Ivimey-Cook and others (1999), and J. Yin and McRoberts (2006), reported *Terquemia difformis* (Schlotheim, 1820) from the Rhaetian of the Penarth Group (England) and from the Rhaetian–Hettangian transition layers in Tibet (China), respectively, but this species was referred to *Umbrostrea* by Márquez-Aliaga and others (2005), because it had an aragonitic inner shell layer (De Renzi & Márquez-Aliaga, 1980; Carter, 1990a; Carter, Barrera, & Tevesz, 1998) and ligament structure, hinge, and antimarginal ribs, typical of ostreids. J. Yin, Enay, and Wan (1999) reported it from Norian beds of the Himalayas (China), but they did not describe the material, and since we cannot be sure that it is really *Terquemia*, it will not be taken into account. The same occurs with most of the Triassic records of the genus. We follow Hautmann (2001a) in considering the oldest solid record to be Lower Jurassic. Regarding the youngest record accepted for *Terquemia*, it is hard to establish due to identification problems. Fürsich and Werner (1988) reported *Terquemia* from the Kimmeridgian of Portugal, but their specimens were only doubtfully assigned, as the specimens are articulated, and the hinge features, which are key to a proper allocation, cannot be seen. The same occurs with the specimens assigned by Damborenea (2002a) from the Toarcian of South America. No more records of *Terquemia* from the Upper Jurassic were found, apart from Fürsich and Werner (1988). Tentatively we indicate its range to be until the Upper Jurassic, following Hautmann and Golej (2004).

Paleogeographic distribution.—Tethys (Fig. 32). *Terquemia* was mentioned from the Tethys domain, but the only solid reference is in Hautmann and Golej (2004). Due to pending questions about the relationship of this genus, we cannot provide a complete distribution.

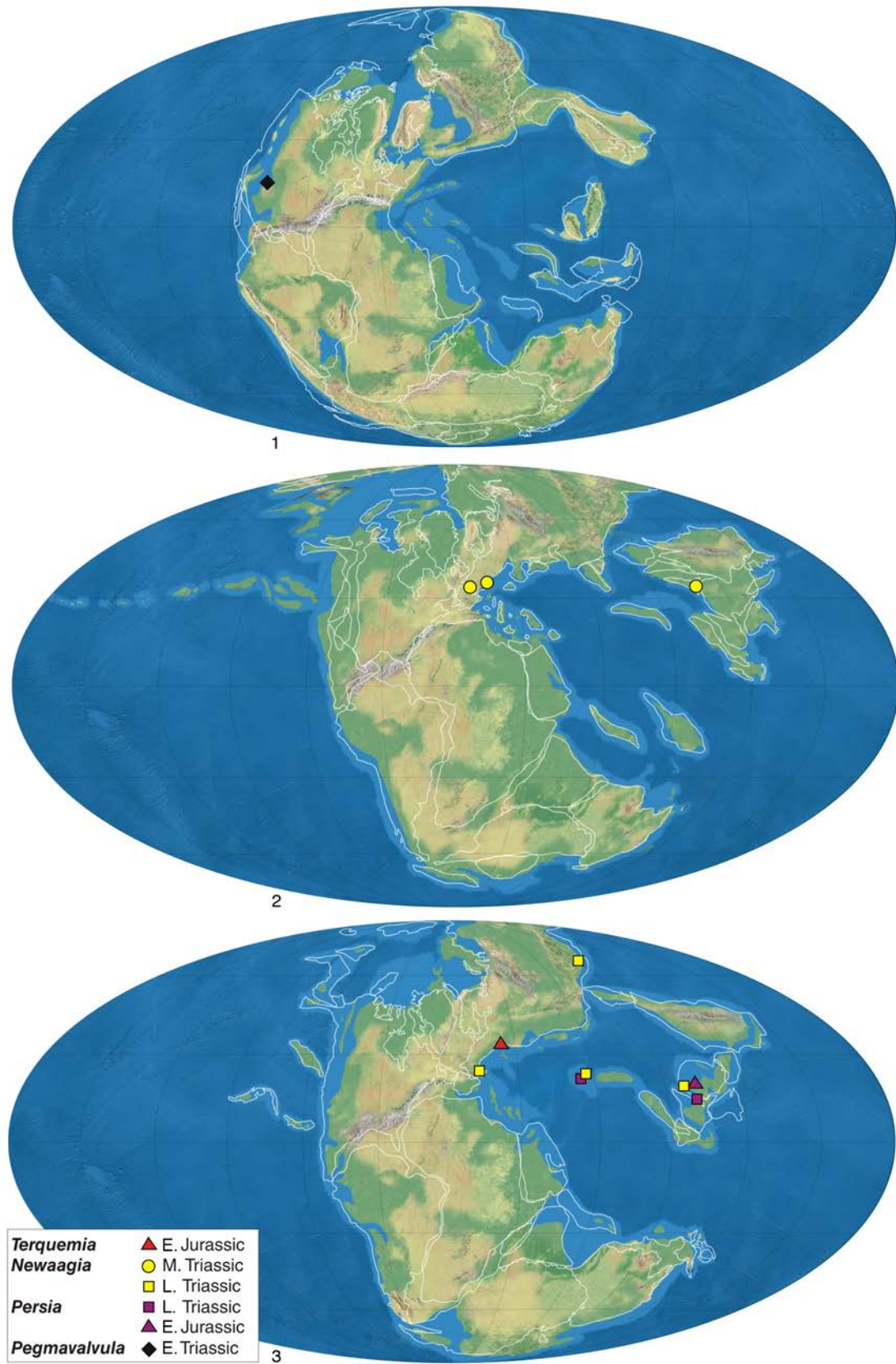


Figure 32. Paleogeographical distribution of Prospondyliidae (*Terquemia*, *Newaagia*, *Persia*, *Pegmaivalvula*). 1, Early Triassic; 2, Middle Triassic; 3, Late Triassic–Early Jurassic.

Tethys domain: Early Jurassic: Sinemurian of Western Carpathians (Slovakia) (Hautmann & Golej, 2004).

Paleoautoecology.—B, E, S, C, Sed; C. *Terquemia* was a cemented bivalve that attached to the substrate by its right valve, leaving the left one free. Unlike other cementing bivalves, such as *Persia*, *Terquemia* lacks byssal notch, so it should not have byssate juvenile stages. In many cases, shells of other bivalves were the substrate (Damborenea, 2002a).

Mineralogy.—Bimineralic (Hautmann & Golej, 2004). Hautmann and Golej (2004) described an outer shell layer subdivided into two sublayers, the outer prismatic and the inner foliated (both calcitic), in their specimens of *Terquemia* (*Dentiterquemia eudesdeslongchampsii*) Hautmann & Golej, 2004. The inner shell layer was recrystallized, but assuming that this layer microstructure was the same as in the rest of the family Prospodylidae, they believed it had a cross-lamellar microstructure (aragonitic).

Genus NEWAAGIA Hertlein, 1952, p. 275

nom. nov. pro Philippiella Waagen, 1907, p. 173, *non* Pfeffer in von Martens & Pfeffer, 1886, p. 119

Type species.—*Spondylus obliquus* Münster, 1841, p. 74.

Remarks.—Hertlein (1952) proposed the name *Newaagia* to replace *Philippiella* Waagen, 1907, as the latter name had already been used for another bivalve genus, *Philippiella* Martens & Pfeffer, 1886.

Some Triassic specimens attributed to *Spondylus* could better fit in *Newaagia* (Waller, 2006, p. 334): “So-called *Spondylus* from the Triassic, such as the many species described by Klipstein (1843 in 1843–1845), are spiny, multicostate bivalves cemented by their right valve and having ventrally migrating ligaments that leave a higher ligament area on the right valve than on the left. Although they superficially resemble *Spondylus*, those that I have examined have a pterioid-type resilium and lack hinge teeth. At least some of these are assignable to *Newaagia* Hertlein, 1952 . . .”

Stratigraphic range.—Middle Triassic (Anisian)—Upper Triassic (Rhaetian) (Hautmann, 2001a). Cox and others (1969) assigned it an Upper Triassic (Carnian) range, and, with some doubt, they noted its presence in the Permian. *Newaagia* was later regarded as an exclusively Mesozoic genus (Newell & Boyd, 1970). Sepkoski (2002), following H. Yin (1985), assigned it an Anisian–Carnian range. It was reported from the Anisian (H. Yin & Yin, 1983), and subsequently, from Norian and Rhaetian beds (Hautmann, 2001a, 2001b).

Paleogeographic distribution.—Eastern Tethys and Boreal (Fig. 32). *Newaagia* was reported from the Norian of China (Sha, Chen, & Qi, 1990), but this was based on only one badly preserved specimen. In addition, it was also reported from the Norian of northeastern Asia (Polubotko & Repin, 1990), but the specimens are not figured or described, and there is no other information about the genus from that area.

Tethys domain: Middle Triassic: Anisian of the Dolomites (Italy) (Posenato, 2008b), Dolomites (Switzerland) (Zorn, 1971), northwestern China (Qinghai province) (H. Yin & Yin, 1983); Late Triassic: Carnian of Italy (Leonardi, 1943; Allasinaz, 1966); Norian–Rhaetian of Iran (Hautmann, 2001a, 2001b; Fürsich & Hautmann, 2005); Rhaetian (transitional layers of Rhaetian–Hettangian) of Tibet (China) (J. Yin & McRoberts, 2006).

Boreal domain: Late Triassic: Carnian of Primorie (Kiparisova, 1972).

Paleoautoecology.—B, E, S, C, Sed; C. *Newaagia* was a cemented bivalve, attaching to hard substrates or to other shells by the umbonal area of the right valve (Newell & Boyd, 1970). It was a bioherm builder, according to Hautmann (2001b).

Mineralogy.—Bimineralic (Carter, 1990a, p. 251; Hautmann, 2001a). Outer shell layer: calcite (fibrous prismatic–foliated). Middle shell layer: aragonite (cross-lamellar–complex cross-lamellar). Inner shell layer: aragonite (simple prismatic).

Genus PERSIA Repin, 1996, p. 4 [365 in translation]

Type species.—*Persia monstrosa* Repin, 1996, p. 4 [365 in translation].

Remarks.—Although *Persia* had some external resemblance to *Newaagia* and *Terquemia*, it is distinguishable from both by differences in the auricles, ligament area, and ornamentation (see Repin, 1996, p. 365). *Persia* was emended by Hautmann (2001a). Although it was originally monospecific, subsequently J. Yin and McRoberts (2006) described a new species: *P. hallami* J. Yin & McRoberts, 2006.

Stratigraphic range.—Upper Triassic (Norian)—Lower Jurassic (lower Hettangian) (Repin, 1996; J. Yin & McRoberts, 2006). The genus was originally reported from the Norian of Iran (Repin, 1996), containing only the type species. Subsequently, it was found in Rhaetian beds of the same area (Hautmann, 2001a, 2001b) and in the Rhaetian–Hettangian transitional layers of Tibet (China) (J. Yin & McRoberts, 2006).

Paleogeographic distribution.—Tethys (Fig. 32).

Tethys domain: Late Triassic: Norian of Central Iran (Repin, 1996; Hautmann, 2001a, 2001b); Rhaetian of central Iran (Hautmann, 2001a, 2001b), Tibet (China) (J. Yin & McRoberts, 2006); Early Jurassic: early Hettangian of Tibet (China) (Tibeticum zone in J. Yin & others, 2007) (J. Yin & McRoberts, 2006).

Paleoautoecology.—B, E, S, C, Sed; C. The presence of a byssal notch between the anterior auricle and the disk may indicate that *Persia* had a byssate state before becoming cemented (Hautmann, 2001a). *Persia* was one of the reef-builder bivalves from the Late Triassic (Fürsich & Hautmann, 2005).

Mineralogy.—Bimineralic. Details of *Persia* shell microstructure are unknown. Probably it had a bimineralic shell, as do other members of family Prospodylidae.

Genus PEGMAVALVULA Newell & Boyd, 1970, p. 263

Type species.—*Pegmaulvula gloveri* Newell & Boyd, 1970, p. 263.

Stratigraphic range.—lower Permian (Artinskian)—Lower Triassic (Olenekian) (Newell & Boyd, 1970, 1995). Although, according to Hautmann (2001a), *Pegmaulvula* was a Paleozoic genus, there is evidence that at least one species, *P. triassica* Newell & Boyd, 1995, was present in the Lower Triassic (Newell & Boyd, 1995).

Paleogeographic distribution.—Circumpacific (Fig. 32). *Pegmaulvula* was reported from Guadalupian to Artinskian levels of North America (Newell & Boyd, 1970); it was also reported from Greece in Changhsingian beds (Clapham & Bottjer, 2007), although these authors did not figure or describe the specimens.

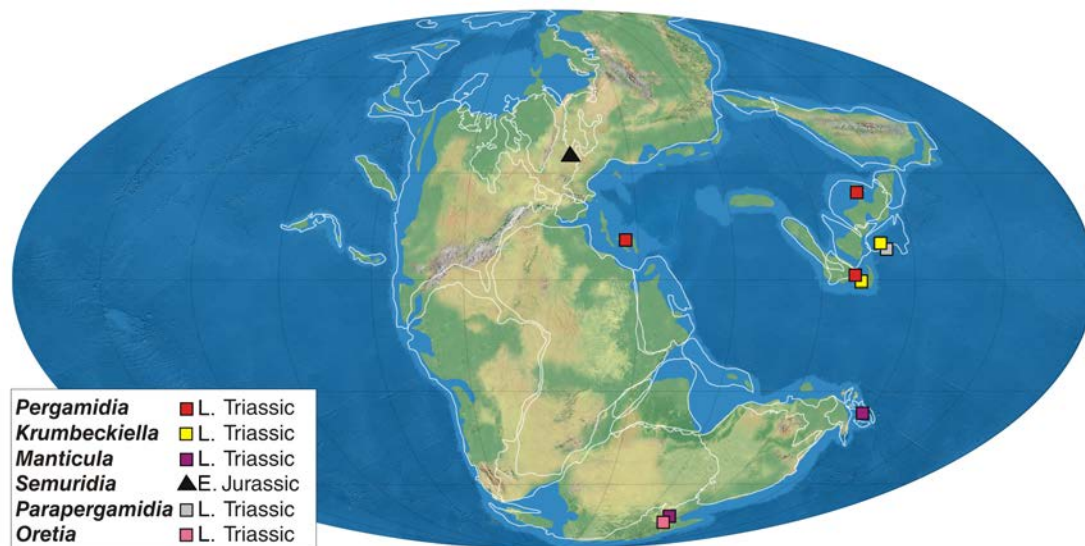


Figure 33. Paleogeographical distribution of Pergamidiidae (*Pergamidia*, *Krumbeckiella*, *Manticula*, *Semuridia*, *Parapergamidia*, *Oretia*). Late Triassic–Early Jurassic.

Circumpacific domain: Early Triassic: Olenekian of Nevada (United States) (Newell & Boyd, 1995).

Paleoautoecology.—B, E, S, C, Sed; C. Species belonging to *Pegmavalvula* were cemented to the substrate with almost the entire surface of the right valve (Newell & Boyd, 1995). Shells had a byssal notch in juvenile stages, but this was closed in the adult stage. This fact was interpreted as evidence that they had an early byssate phase (pectiniform stage) before cementing to the substrate (Newell & Boyd, 1970).

Mineralogy.—Bimineralic. *Pegmavalvula* shell mineralogy is not known. It was probably bimineralic, as were other members of family Prospendylidae.

Family PERGAMIDIIDAE Cox in Cox & others, 1969

Genus PERGAMIDIA Bittner, 1891, p. 103

Type species.—*Pergamidia eumenea* Bittner, 1891, p. 103.

Stratigraphic range.—Upper Triassic (Norian) (L. Lin & others, 2007). Cox and others (1969) assigned it a Norian range, which is confirmed by the reviewed literature. However, Sha and others (2005) indicated that *Pergamidia* lived from Carnian to Norian, but later, in another paper (L. Lin & others, 2007), *Pergamidia* was assigned an exclusively Norian genus.

Paleogeographic distribution.—Tethys (Fig. 33). *Pergamidia* was widely distributed throughout the Paleotethys suture, extending from the Carpathians to the Java Sea (Sha & others, 2005).

Tethys domain: Late Triassic: Norian of Turkey (Bittner, 1891, 1892), Timor (Indonesia) (Krumbeck, 1924), Yunnan province (China) (Cowper-Reed, 1927; Sha & others, 2005), Lungma region (China) (Wen & others, 1976), Qinghai province (China) (Sha, Chen, & Qi, 1990).

Paleoautoecology.—B, E, S, Epi, Sed; By. *Pergamidia* had a mytiliform shell and was monomyarian; it also had a very deep byssal notch, suggesting that it possessed a large byssus to attach itself to the substrate

(Sha & others, 2005). Due to the associated substrate type, its low diversity, and high abundance, it was probably able to put up with extreme conditions, even toxic environments (sulphuric) and those low in oxygen. They were found in large numbers in rift zones and island arcs, which were more or less affected by tectonic movements and volcanic activity. These types of environments imply shallow to deep waters and toxic sulfide seas (Sha & others, 2005). *Pergamidia* was considered an opportunist taxon capable of colonizing highly stressed environments where other organisms could not live, with very unstable populations that went extinct rapidly (Sha & Fürsich, 1994).

Mineralogy.—Bimineralic (Carter, 1990a, p. 196). There are no data about *Pergamidia* shell mineralogy. We assume a bimineralic shell, as in the other members of the order Pterioida.

Genus KRUMBECKIELLA Ichikawa, 1958, p. 196

nom. nov. pro Timoria Krumbeck, 1924, p. 218, *non* Kaye, 1919, p. 93

Type species.—*Timoria timorensis* Krumbeck, 1924, p. 221.

Remarks.—Krumbeck (1924) proposed the genus *Timoria*, being unaware that this name was already in use for an insect genus, *Timoria* Kaye, 1919. Ichikawa (1958) realized this and renamed the genus as *Krumbeckiella*.

Stratigraphic range.—Upper Triassic (Carnian–upper Rhaetian) (Sha, Chen, & Qi, 1990; J. Yin & McRoberts, 2006). The type species of *Krumbeckiella* was described by Krumbeck (1924) from the Norian of Timor, and this was the stratigraphic range assigned by Cox and others (1969). Subsequently, *Krumbeckiella* was also reported from upper Rhaetian beds (J. Yin & McRoberts, 2006). Sha, Chen, and Qi (1990) reported the genus from the Carnian, and it seems to be fairly common in sediments of that age (X. Wang & others, 2008).

Paleogeographic distribution.—Tethys (Fig. 33). Although the species *Krumbeckiella* cf. *timorensis* (Krumbeck, 1924) was men-

tioned from the Circumpacific domain by Newton (in Newton & others, 1987), Waller (in Waller & Stanley, 2005) showed that specimens described by Newton (in Newton & others, 1987) actually belong to *Mysidiella* Cox, 1964, and he renamed the species *Mysidiella newtonae* Waller in Waller & Stanley, 2005. In addition, Waller and Stanley (2005) reported the presence of *Krumbeckiella* at high paleolatitudes in the southern hemisphere, but we did not locate in the literature any reference of the genus from that area.

Tethys domain: Late Triassic: Carnian of Qinghai province (China) (Sha, Chen, & Qi, 1990); Norian of Timor (Indonesia) (Krumbeck, 1924), China (Wen & others, 1976), Tibet (China) (Kobayashi & Tamura, 1983a), Qinghai province (China) (Sha, Chen, & Qi, 1990); Rhaetian of Tibet (China) (J. Yin & McRoberts, 2006; J. Yin & others, 2007).

Paleoautoecology.—B, E, S, Epi, Sed; By. The mode of life of *Krumbeckiella* was probably similar to that of *Pergamidia*.

Mineralogy.—Bimineralic (Carter, 1990a, p. 196). *Krumbeckiella* shell mineralogy is unknown. As for other members of Pterioidea, it could have had a bimineralic shell.

Genus MANTICULA Waterhouse, 1960, p. 428

Type species.—*Mytilus problematicus* Zittel, 1864, p. 28.

Remarks.—Although the type species was related to *Mytilus* Linnaeus, 1758, and *Myalina* de Koninck, 1842 in 1841–1844, Waterhouse (1960) proposed the new genus *Manticula*, characterized by hinge details and shell microstructure. He did not provide a systematic allocation, but Cox and others (1969) referred it to the Pergamidiidae.

Stratigraphic range.—Upper Triassic (?Carnian–Norian), Lower Cretaceous (Berriasian) (Waterhouse, 1960; Crame, 1995). It was originally reported from the Otamitan (then regarded as Carnian) of New Zealand, and this was the stratigraphic range assigned by Cox and others (1969); subsequently, it was also reported from the Norian stage (Freneix & Avias, 1977), and now the Otamitan is correlated with the Norian (H. J. Campbell & Raine in Cooper, 2004). Crame (1995) reported it from the Early Cretaceous (Berriasian) of Antarctica and regarded *Manticula* as a Lazarus taxon, without Jurassic representatives, which survived in Antarctica that acted as a refuge.

Paleogeographic distribution.—Austral (Fig. 38).

Austral domain: Late Triassic: ?Carnian, Norian of New Zealand and New Caledonia (Wilckens, 1927; Waterhouse, 1960; Freneix & Avias, 1977; W. Zhang & Grant-Mackie, 2001).

Paleoautoecology.—B, E, S, Epi, Sed; By. Most probably, *Manticula* was an epibyssate bivalve, as were the other members of the Pergamidiidae; this is indicated by its mytiliform shell and the presence of byssal notch.

Mineralogy.—Bimineralic (Waterhouse, 1960; Carter, 1990a, p. 204). Outer shell layer: calcite (prismatic-homogeneous). Inner shell layer: aragonite (cross-lamellar).

Genus SEMURIDIA Melville, 1956, p. 116

Type species.—*Semuridia jacksoni* Melville, 1956, p. 116.

Remarks.—*Semuridia* was referred to the Pergamidiidae by Cox and others (1969); Waller and Stanley (2005) believed that

it may be included in another clade due to differences in shell microstructure and ligament area, together with other genera of the family such as *Pergamidia*, *Krumbeckiella*, and *Manticula*. Carter (1990a) already indicated that if the inner shell layer of *Semuridia* is really nacreous, as stated by Cox and others (1969), it should be separated from the group at a subfamily or even family level.

Stratigraphic range.—Lower Jurassic (Sinemurian) (Cox & others, 1969). *Semuridia* was only recorded from Sinemurian beds (Cox & others, 1969; Hallam, 1976, 1977, 1987; Liu, 1995).

Paleogeographic distribution.—western Tethys (Fig. 33).

Tethys domain: Early Jurassic: Sinemurian of England (Cox & others, 1969; Liu, 1995).

Paleoautoecology.—B, E, S, Epi, Sed; By. Like the rest of the Pergamidiidae, *Semuridia* is externally mytiliform, it had a byssal notch, and was monomyarian, so it is interpreted to be an epibyssate bivalve.

Mineralogy.—Bimineralic (Cox & others, 1969, p. 314; Waller & Stanley, 2005). According to Cox and others (1969), *Semuridia* inner shell layer was nacreous (aragonite). Waller and Stanley (2005, p. 9) stated, “its outer shell layer, although not described, appears to be columnar prismatic based on figures of the left valve of *Semuridia dorsetensis* (Cox, 1926) in Cox [and others] (1969, fig. C44.4a).”

Genus PARAPERGAMIDIA L. Lin & others, 2007, p. 110

Type species.—*Parapergamidia changtaiensis* L. Lin & others, 2007, p. 111.

Stratigraphic range.—Upper Triassic (?upper Carnian–lower Norian) (L. Lin & others, 2007). *Parapergamidia* occurs in the Norian and probably also in the upper Carnian (L. Lin & others, 2007).

Paleogeographic distribution.—Eastern Tethys (Fig. 33).

Tethys domain: Late Triassic: late Carnian–early Norian of western Sichuan (southwestern China) (L. Lin & others, 2007).

Paleoautoecology.—B, E, S, Epi, Sed; By. Externally similar to *Pergamidia*, the main differences are based on the shape of the retractor muscles and the thickness of the shell (L. Lin & others, 2007). The byssal retractor muscle scars of *Parapergamidia* are very prominent and indicate it was fixed by the byssus. It had the same external mytiliform appearance as other members of the family to which it belongs. Its mode of life was probably similar to *Pergamidia*. Interpretation of the facies in which it occurs shows that it lived in deep-water environments (L. Lin & others, 2007).

Mineralogy.—Bimineralic (Carter, 1990a, p. 196). *Parapergamidia* shell microstructure is unknown. Bimineralic mineralogy is assumed as in the other members of the order Pterioidea.

Genus ORETIA Marwick, 1953, p. 62

Type species.—*Oretia coxi* Marwick, 1953, p. 62.

Remarks.—Marwick (1953) included *Oretia* in the family Pterioidea, but later Cox and others (1969) attributed it to an uncertain family within the superfamily Pectinoidea. Waterhouse (1979a) emended the generic diagnosis, and he tentatively included it in Pergamidiidae, but he also found some similarities with Monotiidae and Mysidiellidae.

Stratigraphic range.—Upper Triassic (lower Norian) (Marwick, 1953; H. J. Campbell & Raine in Cooper, 2004). The genus is restricted to the Oretian (New Zealand local stage), and halobiid and

ammonoid correlations suggest a lowest Norian age (H. J. Campbell & Grant-Mackie, 2000); the stage was correlated with lower Norian (H. J. Campbell & Raine in Cooper, 2004).

Paleogeographic distribution.—Austral (Fig. 33).

Tethys domain: Late Triassic: early Norian of New Zealand (Marwick, 1953; Waterhouse, 1979a).

Paleoautoecology.—B, E, S, Epi, Sed; By. Probably epibyssate.

Mineralogy.—Unknown. *Oretia* shell microstructure is unknown. Since its allocation to the family Pergamidiidae is uncertain, we cannot assign the dominant mineralogy in the family.

Superfamily HALOBIOIDEA Kittl, 1912

Family HALOBIIDAE Kittl, 1912

Over the past three decades, a large number of genera and subgenera related to *Daonella* and *Halobia* were proposed (e.g., Polubotko, Payevskaya, & Repin, 2001; Kurushin & Truschelev, 2001). Some authors specializing in this group do not agree (see McRoberts, 1993, 2000, and H. J. Campbell, 1994) which criteria used to characterize these taxa are diagnostic features. The new taxa not taken into account in this paper are: *Perihalobia* Gruber, 1976; *Zittelihalobia* Polubotko, 1984; *Indigirohalobia* Polubotko, 1984; *Parahalobia* Yin & Hsu, 1938, in C. Chen, 1976; *Pacifihalobia* Polubotko, 1990; *Primahalobia* Polubotko, 1988; *Comatahalobia* Polubotko in Polubotko, Payevskaya, & Repin, 2001; *Magnolobia* Kurushin & Truschelev, 2001 (see discussion for each of them in Genera not Included, p. 156). McRoberts (1993, p. 201–202) considered *Perihalobia*, *Indigirohalobia*, *Zittelihalobia*, *Parahalobia*, and *Pacifihalobia* to be synonyms of *Halobia*. In his own words: “the characters employed to construct these new taxa are inconsistent with the included taxa, are too narrowly defined to accommodate reasonable amounts of variation, or were erected to fit an *a priori* assumption of inferred phylogenetic relations. Many of the characters used to define the above genera are probably best used in specific rank.” When Polubotko (1984) proposed the new genera, he emphasized the features related to the shape and size of the auricles and the type of ornamentation, characters used previously as diagnostic at the species level. In addition, there are a number of *Daonella* subgenera that were taken into account by Sepkoski (2002), which will not be considered here either: *Dipleurites* Kittl, 1912; *Moussonella* Turculet, 1972; *Grabella* Turculet, 1972; *Arzelella* Turculet, 1972; *Loemmelella* Turculet, 1972; *Pichlerella* Turculet, 1972; and *Longidaonella* Farsan, 1972; Sepkoski (2002) based these data on H. Yin (1985). *Pichlerella* and *Arzelella* are here regarded as subgenera of *Daonella* (Schatz, 2001b, 2004).

Halobia and *Daonella* were traditionally distinguished by the presence or absence of an anterior auricle, but in the publication of papers by Gruber (1976) and Polubotko (1984, 1988, 1990), there is no consensus about which characters are best suited to distinguish at subgeneric and generic levels (H. J. Campbell, 1994). A thorough review of the group is badly needed to establish the criteria for generic, subgeneric, and specific level discrimination, in order to restore stability, which this group had until the 1970s. In our opinion, the diverse senses in which members of the group were used, depended in part on the taxon concept of different authors. Sometimes, depending on the use to be given to the different taxa proposed, the list tends to swell

as a matter of convenience, for example, in biostratigraphy. We believe that new taxa should be defined as biological concepts, as far as possible.

We include *Daonella* Mojsisovics, 1874; *Aparimella* H. J. Campbell, 1994; *Halobia* Bronn, 1830a; and *Enteropleura* Kittl, 1912, in this family, following H. J. Campbell (1994), McRoberts (2000), and Waller and Stanley (2005). According to McRoberts (2000, p. 600), the first three are distinguished: “*Daonella* lacks an anterior auricle, *Aparimella* possesses an upper anterior auricle, and *Halobia* has a two-fold anterior auricle” (byssal tube of H. J. Campbell, 1994). *Daonella* is similar to *Enteropleura*, but its ornamentation is less marked, and the ligament is alivincular, very similar to *Bositra* De Gregorio, 1886 (Waller & Stanley, 2005).

One of the difficulties with this group is that the shell is very thin and the specimens are often found with the dorsal part broken, so that unless they are very well preserved, the ligament area cannot be observed. Many of the references in the literature were based on shell fragments or on internal and external molds only, and hence the confusion between genera is common.

The great abundance and distribution of halobiids during the Triassic and their high speciation rate made their species very useful as biochronological indicators, which is not common among bivalves.

Genus HALOBIA Bronn, 1830a, p. 282

Type species.—*Halobia salinarum* Bronn, 1830a, p. 282.

Stratigraphic range.—Upper Triassic (lower Carnian–middle Norian) (McRoberts, 1993, 2000). Although Cox and others (1969) assigned to *Halobia* a Middle–Upper Triassic range, according to McRoberts (2000, p. 602), *Halobia* did not appear until the early Carnian, because, “Earlier reports of Ladinian *Halobia* have now been determined to be either species belonging to other taxa such as *Daonella* and *Aparimella* (e.g., Campbell, 1994), or assigned to younger strata . . .”

Paleogeographic distribution.—Cosmopolitan (Fig. 34). Although *Halobia* was considered to be a taxon with cosmopolitan distribution, according to McRoberts (1997b), it is not known in South America. However, Pérez-Barría (2004, 2006) reported *Halobia* from the Upper Triassic of Chile, but no systematic treatment of the specimens was made.

Tethys domain: Late Triassic: China (Cowper-Reed, 1927; Gou, 1993), Timor and Sumatra (Indonesia) (Krumbeck, 1914, 1924; Gruber in Kristan-Tollman, Barkham, & Gruber, 1987); Carnian of Tibet (China) (Sha, Johnson, & Fürsich, 2004), Qinghai province (China) (Sha, Chen, & Qi, 1990; Sha, 1995, 1998; Sha & Grant-Mackie, 1996), Xizang province (China) (C. Chen, 1982), Yugoslavia (Jurkovsek & Kolar-Jurkovsek, 1986), Italy (Leonardi, 1943; Nicora & others, 2007; McRoberts, 2010); Carnian–Norian of Slovakia (Kochanová, 1987), Sicilia (Italy) (Cafiero & Capoa de Bonardi, 1982; see records for European distribution), Apennines (Italy) (Capoa de Bonardi, 1970), Yugoslavia (Cafiero & Capoa de Bonardi, 1980), China (Wen & others, 1976), ?Singapore (Kobayashi & Tamura, 1968a), Turkey (Allasinaz, Gutnic, & Poisson, 1974); Norian of Tibet (China) (Sha, Johnson, & Fürsich, 2004), Qinghai province (China) (Sha, Chen, & Qi, 1990; Sha, 1995, 1998; Sha & Grant-Mackie, 1996), southern Russia (Okuneva, 1985, 1987), Austria (McRoberts, 2010).

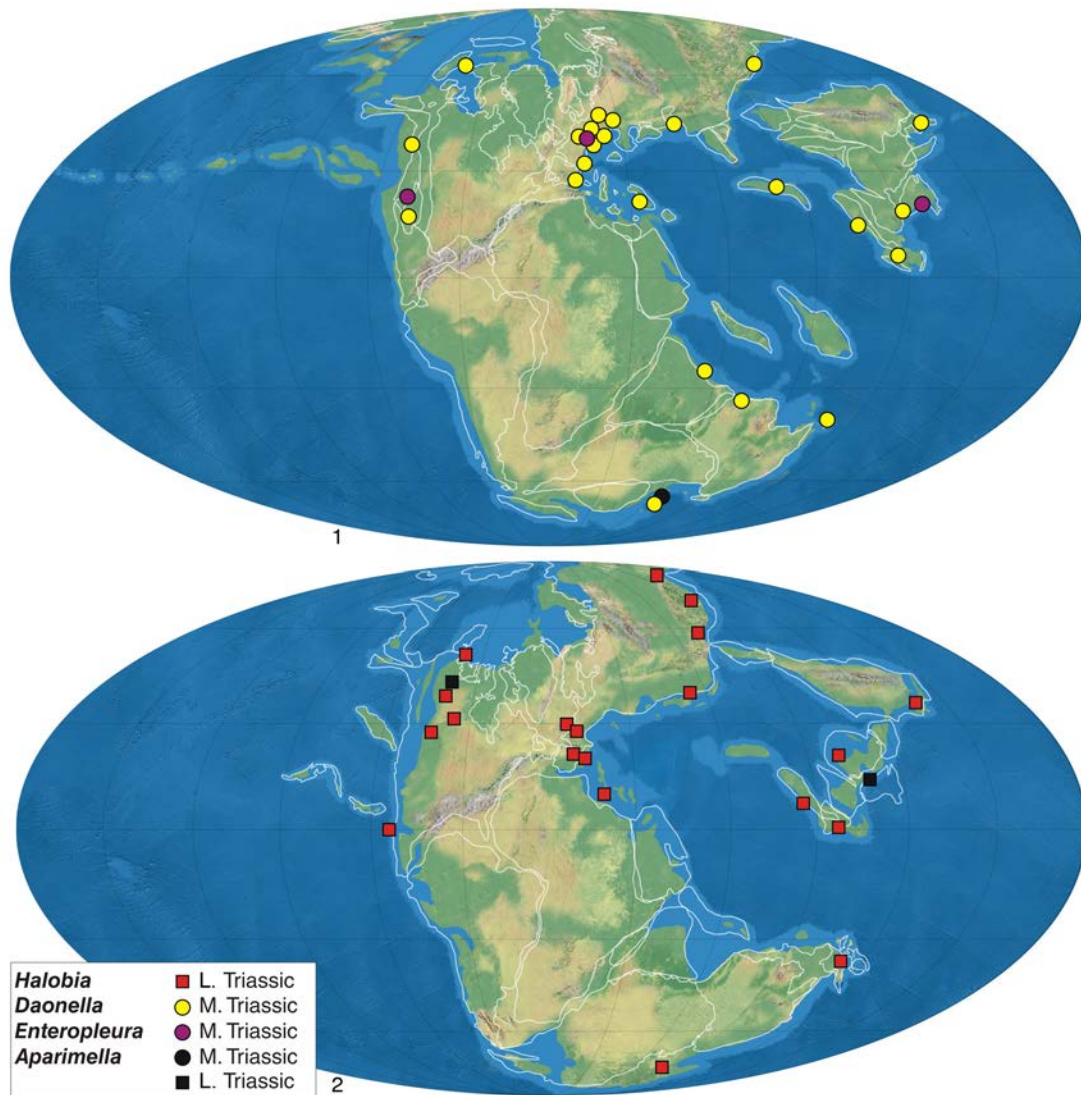


Figure 34. Paleogeographical distribution of Halobiidae (*Halobia*, *Daonella*, *Enteropleura*, *Aparimella*). 1, Middle Triassic; 2, Late Triassic.

Circumpacific domain: Late Triassic: early Carnian of British Columbia (Canada) (McRoberts, 2000), Japan (Ando, 1988); Carnian–Norian from various localities in North America (J. P. Smith, 1927; McRoberts, 1993, 1997b), Mexico (Lucas & González-León, 1994), Japan (Kobayashi & Ichikawa, 1949a; Nakazawa, 1964; Hayami, 1975; Tamura & others, 1975; Tanaka, 1989); Norian of British Columbia (McRoberts, 2010).

Austral domain: Late Triassic: ?Carnian, Norian of New Zealand and New Caledonia (Trechmann, 1918; Wilckens, 1927; Marwick, 1953; Grant-Mackie, 1960; H. J. Campbell, 1982, 1994).

Boreal domain: Late Triassic: Carnian of Svalbard (H. J. Campbell, 1994), Arctic Canada (McRoberts, 2010), Primorie (Kiparisova, 1972); Carnian–Norian of Arctic zone of Canada (Tozer, 1961, 1962; McRoberts, 1997b), Siberia (McRoberts, 1997b and references therein); Norian of Svalbard (H. J. Campbell, 1994).

Paleoautoecology.—B-Ps, E, S-Ch, Epi-Un, Sed-FaM; By-R. Many authors have speculated about mode of life of halobiids; Jefferies and Minton (1965), Hayami (1969a), S. M. Stanley (1972), Seilacher (1990), H. J. Campbell (1994), Etter (1996), McRoberts (1997b), Waller (in Waller & Stanley, 2005), and Schatz (2005), among many others.

To explain their wide distribution, association with low oxygen facies, morphology, and population structure, different modes of life were postulated: benthic semi-infaunal, benthic epifaunal on the substrate associated with chemosynthetic bacteria, epibyssate on plants or seaweed, pseudoplanktonic fixed to floating objects or other living organisms (such as ammonoids), nektonic (see Schatz, 2005). There are arguments for and against almost all suggested modes of life (good reviews of this topic are in H. J. Campbell, 1994, and Schatz, 2005).

Possibly several modes of life can be assigned to the species of this group (H. J. Campbell, 1994), although Schatz (2005) sup-

ported an epibenthic pleurothetic mode of life on soft substrate and adapted to low oxygen environments for daonellids, as the thin shell could have facilitated the oxygen exchange in these extreme environments. However, other authors, such as McRoberts (1997b) and H. J. Campbell (1994), suggested that a pseudoplanktonic mode of life cannot be ruled out, although Schatz (2005) argued that the morphology exhibited by daonellids and other evidence does not support this hypothesis. The wide distribution of these bivalves may be due to long-term planktotrophic larvae (H. J. Campbell, 1994; McRoberts, 1997b, 2000; Sha, 2003). The external morphology of some species could fit into a swimming mode of life (subcircular form, equivalve, and short hinge line), but the adductor muscle scar is small and falls just below the umbo, and the shells are too thin (Schatz, 2005). The discussion is far from settled, and it is possible that the different morphologies of members of the group indicate slightly different modes of life.

Mineralogy.—Bimineralic (H. J. Campbell, 1994). Outer shell layer: calcite (prismatic). Middle shell layer: aragonite (homogeneous). Inner shell layer: calcite (foliated or lamellar).

Genus DAONELLA Mojsisovics, 1874, p. 7

Type species.—*Halobia lommeli* Wissmann in Wissmann & Münster, 1841, p. 22.

Stratigraphic range.—Middle Triassic (Anisian–Ladinian). Cox and others (1969) assigned *Daonella* a Triassic range. The range is currently limited to the Middle Triassic. *Daonella pichleri* Mojsisovics, 1874, was mentioned also from the Carnian by Capoa and Capoa de Bonardi (1980), but Schatz (2001b) reviewed this species and included it within the subgenus *Pichlerella*, and he limited its range to the *archelaus* zone (upper Ladinian). McRoberts (2010) mentioned that several occurrences of *Daonella* from lower Carnian beds are known, but they remain poorly documented.

Paleogeographic distribution.—Cosmopolitan (Fig. 34).

Tethys domain: Middle Triassic: China (Cowper-Reed, 1927; Lu & Chen, 1986); Anisian of southern China (Komatsu, Chen, & others, 2004), Malaysia (Vu Khuc & Huyen, 1998), Slovakia (Kochanová, 1985), Germany (Bartholomä, 1983), Switzerland (Zorn, 1971); Anisian–Ladinian of Italy (Pinna & Teruzzi, 1991; Brack & Rieber, 1993), southern China (J. Chen & others, 1992), Switzerland (Rieber, 1968, 1969); Ladinian of Spain (Schmidt, 1935; Llopis Lladó, 1952; Vía & Villalta, 1975; Vía, Villalta, & Esteban, 1977; Márquez-Aliaga, 1983, 1985; Budurov & others, 1991; Márquez-Aliaga & Martínez, 1996; Márquez-Aliaga & others, 2002, 2004; Márquez-Aliaga & Ros, 2002, 2003), southern Alps (Switzerland) (Schatz, 2001a), Italy (Kittl, 1912; Scandone & Capoa de Bonardi, 1966; Capoa de Bonardi, 1970; Schatz, 2001b), Bosnia, Romania, Turkey, India, Vietnam (Schatz, 2001b, and references therein), Timor (Indonesia) (Krumbeck, 1924), Malaysia (Vu Khuc & Huyen, 1998), Bulgaria (Budurov & others, 1991), southern Russia (Okuneva, 1985), Slovenia (Jurkovsek, 1983, 1984), Yugoslavia (Ramovs & Jurkovsek, 1983a, 1983b; Jurkovsek, 1983), China (Wen & others, 1976), Slovakia (Kochanová, Mello, & Siblík, 1975), Bulgaria (Stefanov, 1963), Timor (Indonesia) (Krumbeck, 1924), Afghanistan (Farsan, 1972, and references therein).

Circumpacific domain: Middle Triassic: Anisian of Japan (Nakazawa, 1961), Nevada (United States) (McRoberts, 2010); Ladinian of Japan (Hayami, 1975; Tamura & others, 1975).

Austral domain: Middle Triassic: Anisian of New Zealand and New Caledonia (H. J. Campbell, 1994).

Boreal domain: Middle Triassic: Anisian of Svalbard (H. J. Campbell, 1994); Anisian–Ladinian of Arctic Archipelago (Canada) (Tozer, 1961, 1962, 1970); Ladinian of northeastern Asia (Kurushin & Truschelev, 2001), Svalbard (H. J. Campbell, 1994; McRoberts, 2010), British Columbia (McRoberts, 2010).

Paleoautoecology.—B-Ps, E, S-Ch, Epi-Un, Sed-FaM; By-R. See *Halobia* (p. 91).

Mineralogy.—Bimineralic (H. J. Campbell, 1994). Outer shell layer: calcite (prismatic). Middle shell layer: aragonite (homogeneous). Inner shell layer: calcite (foliated or lamellar).

Genus ENTEROPLEURA Kittl, 1912, p. 162

Type species.—*Daonella guembeli* Mojsisovics, 1874, p. 8.

Remarks.—The systematic position of *Enteropleura* varied throughout its history, from a synonym of *Daonella* (Krumbeck, 1924) to a subgenus of *Daonella* (Capoa de Bonardi, 1970) or valid genus as interpreted by Cox and others (1969) and here. Although the genus was not widely understood, and somewhat neglected, several recent studies (Hopkin & McRoberts, 2005; Waller & Stanley, 2005; J. Chen & Stiller, 2007) clarified its position. Following these papers, the species of the genus are: *E. guembeli* Mojsisovics, 1874; *E. bittneri* Kittl, 1912; *E. lamellosa* (Kittl, 1912); *E. jenksi* Hopkin & McRoberts, 2005; *E. walleri* Chen & Stiller, 2007. The species *boeckhi* Mojsisovics, 1874 (quoted as *Daonella (Enteropleura) boeckhi* by Capoa de Bonardi, 1970) is regarded as a *Daonella* (J. Chen & Stiller, 2007). *Enteropleura* sp. A Waller in Waller & Stanley, 2005, is the same as *Enteropleura jenksi* Hopkin & McRoberts, 2005.

Stratigraphic range.—Middle Triassic (middle Anisian) (Waller & Stanley, 2005). According to the species included in the genus, its stratigraphic range is middle Anisian and not Anisian–Norian, as assigned by Cox and others (1969). Broglio-Loriga and others (1999) reported *Enteropleura* from the Carnian of the Dolomites (Italy), but this will not be taken into account, because the figured specimen lacks the dorsal part, critical to establish proper relations.

Paleogeographic distribution.—Tethys and Circumpacific (Fig. 34).

Tethys domain: Middle Triassic: middle Anisian of Guangxi province (southern China) (J. Chen & Stiller, 2007), Hungary (Kittl, 1912).

Circumpacific domain: Middle Triassic: middle Anisian of Nevada (United States) (Hopkin & McRoberts, 2005; Waller & Stanley, 2005).

Paleoautoecology.—B-Ps, E, S-Ch, Epi-Un, Sed-FaM; By-R. See *Halobia* (p. 91).

Mineralogy.—Bimineralic (Waller & Stanley, 2005, p. 23–24). According to Waller and Stanley (2005), their specimens of *E. jenksi* provided the following information: Outer shell layer: calcite (prismatic). Middle shell layer: aragonite (?). Inner shell layer: calcite (?).

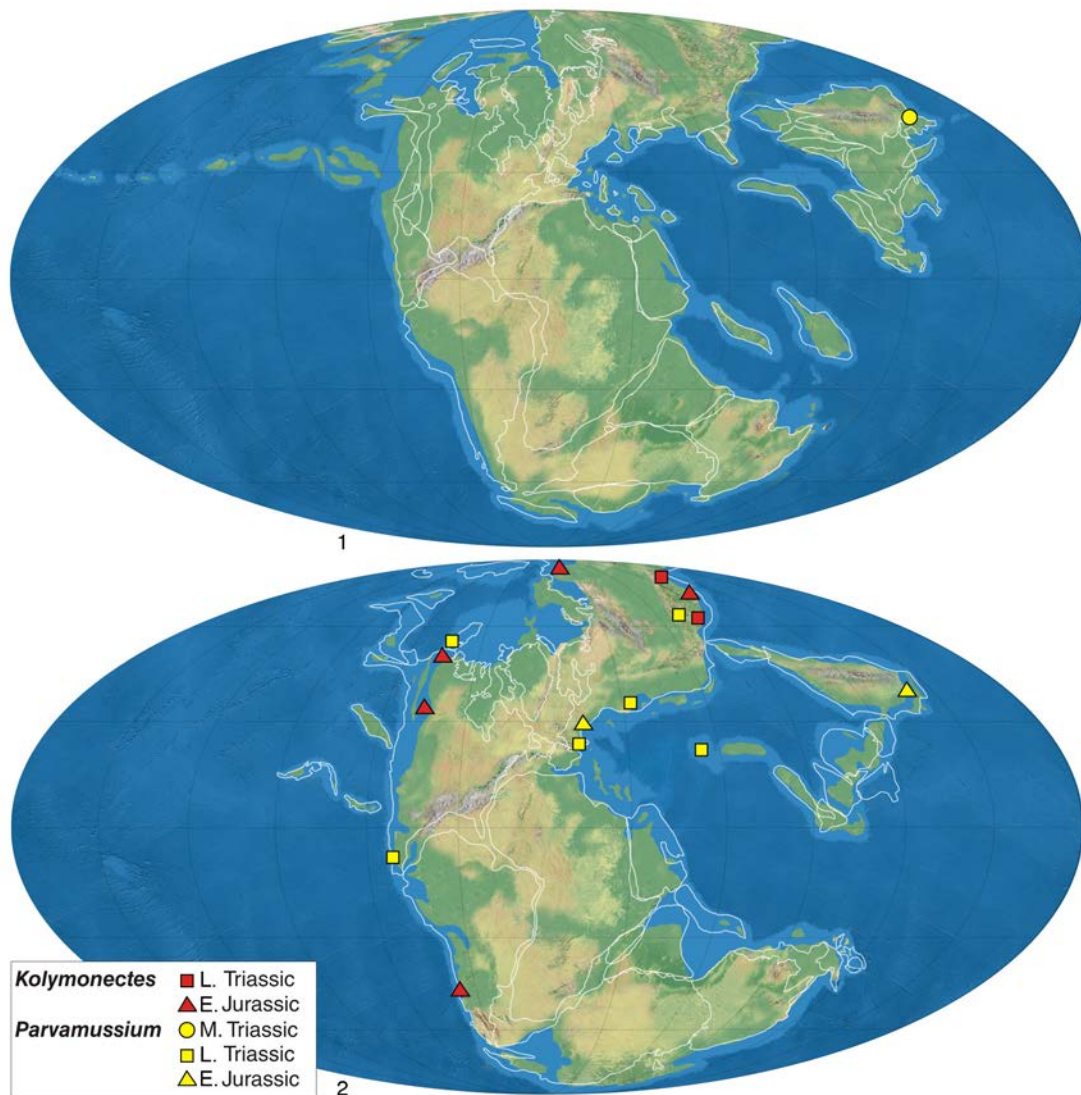


Figure 35. Paleogeographical distribution of Propeamussiidae (*Kolymonectes*, *Parvamussium*). 1, Middle Triassic; 2, Late Triassic–Early Jurassic.

Genus APARIMELLA H. J. Campbell, 1994, p. 65

Type species.—*Daonella apteryx* Marwick, 1953, p. 53.

Stratigraphic range.—Middle Triassic (upper Anisian)–Upper Triassic (lower Carnian) (H. J. Campbell, 1994). The stratigraphic range of *Aparimella* extends from Anisian to Carnian (H. J. Campbell, 1994).

Paleogeographic distribution.—Eastern Tethys, Austral, and Boreal (Fig. 34).

Tethys domain: Late Triassic: early Carnian of Yunnan (southern China) (J. Chen, 1982c).

Austral domain: Middle Triassic: late Anisian of New Zealand (H. J. Campbell, 1994); late Ladinian of New Zealand (Marwick, 1953; H. J. Campbell, 1994).

Boreal domain: Late Triassic: early Carnian of Svalbard (H. J. Campbell, 1994).

Paleoautoecology.—B-Ps, E, S-Ch, Epi-Un, Sed-FaM; By-R. See *Halobia* (p. 91).

Mineralogy.—Bimineralic (H. J. Campbell, 1994, p. 55). There are no specific data for *Aparimella* shell microstructure. We assign the data provided by H. J. Campbell (1994) for the family Halobiidae. Outer shell layer: calcite (prismatic). Middle shell layer: aragonite (homogeneous). Inner shell layer: calcite (foliated or lamellar).

Superfamily PECTINOIDEA Wilkes, 1810

Family PROPEAMUSSIIDAE Abbot, 1954

Genus KOLYMONECTES Milova & Polubotko in Bychkov & others, 1976, p. 67

Type species.—*Aequipecten* (?) *anjuensis* Milova, 1969, p. 182.

Remarks.—Milova and Polubotko proposed *Kolymonectes* as a new genus in two almost simultaneous papers (in Bychkov & others, 1976, July 26; and in Milova, 1976, August 28).

Although *Kolymonectes* was regarded a member of the family Entoliidae by some authors (e.g., Polubotko & Milova, 1986), we include it in the family Propeamussiidae, following Damborenea (1998, 2002a), on the basis of the lack of ctenolium and the presence of calcite in the prismatic outer layer of the shell, two diagnostic characters of this family (Damborenea, 1998). This same approach was followed by Aberhan (1998a). However, Waller (2006) included it in the family Entolioididae Waller, 2006. *Kolymonectes* is regarded as a member of a propeamusiid group without internal ribs (Damborenea, 1998).

Stratigraphic range.—Upper Triassic (?Norian)—Lower Jurassic (lower Toarcian) (Damborenea, 2002a). *Kolymonectes* appeared in the upper Norian of the Boreal domain (Milova & Polubotko in Milova, 1976); Kurushin (1990) and Polubotko and Repin (1990) recorded *Kolymonectes* from the upper Norian (=?Rhaetian) and Hettangian. Aberhan (1998a) believed that the genus was present until the Middle Jurassic, but he did not indicate the source of this information. The youngest checked records of the genus are upper Pliensbachian (Damborenea, 2002a, 2002b) and lower Toarcian (e.g., Damborenea & others, 1992). Zakharov and others (2006) considered the record to be the lower Toarcian of northern Siberia and the Arctic area, but they did not figure or describe any specimen from that age.

Paleogeographic distribution.—Circumpacific, Austral, and Boreal (Fig. 35). *Kolymonectes* was distributed in the Boreal domain during the Late Triassic and exhibited a bipolar distribution during the Early Jurassic (Damborenea, 1993, 1996a, 1998, 2001), and although it was also reported from the Circumpacific domain, these records are located at high paleolatitudes.

Boreal domain: Late Triassic: northeastern Russia (Damborenea, 1998); Norian of northeastern Asia (Kurushin, 1990; Polubotko & Repin, 1990); late Norian–Rhaetian of Siberia (Milova & Polubotko in Milova, 1976); Early Jurassic: Hettangian–Sinemurian of northeastern Russia (Milova, 1988); ?Hettangian, Sinemurian of Magadan (Russia) (Polubotko & Milova, 1986), Arctic zone of Canada (Aberhan, Hrudka, & Poulton, 1998); Sinemurian of northern Russia (Milova & Polubotko in Milova, 1976).

Circumpacific domain: Early Jurassic: Sinemurian of western Canada (Aberhan, 1998a, 1998b).

Austral domain: Early Jurassic: Hettangian–Sinemurian of Argentina (Damborenea & Manceñido, 2005b); Sinemurian of Argentina (Damborenea, 1998, 2002a).

Paleoautoecology.—B, E, S, Un, FaM; R-Sw. In adult specimens, the byssal gape is not usually observed. *Kolymonectes* probably had an earlier byssate stage, but adults lived reclining on the substrate (Damborenea, 1998, 2002a). According to S. M. Stanley (1972), it was probably a good swimmer, since it had a thin shell, the valves were of the same convexity, the auricles were equal, and the umbonal angle was large enough to allow swimming cycles. Propeamussiids are currently restricted to deep environments, but this was not the case during the Jurassic, as they were present both in deep environments associated with low-oxygen facies (without other benthic organisms), and in coastal environments (Damborenea, 1998, 2002a).

Mineralogy.—Bimineralic (Damborenea, 1998). Damborenea (1998) proposed the presence of a calcitic outer shell layer at least in the right valve, based on indirect evidence, provided by the

shell of specimens of *Kolymonectes weaveri* Damborenea, 1998. She also stated that the observed characters of the shell agree with the distribution of the shell layers in the family Propeamussiidae (see mineralogy for *Parvamussium* below).

Genus PARVAMUSSIUM Sacco, 1897, p. 48

Type species.—*Pecten (Pleuonectes) duodecimlamellatum* Bronn, 1831, p. 116.

Remarks.—Sacco (1897) distinguished 3 subgenera of *Amussium*: *Propeamussium*, species without ornamentation and large size, Eocene–Recent; *Parvamussium*, species very similar to *Propeamussium* but smaller, Cretaceous–Recent; and *Variamussium*, small shells internally ribbed, which include Jurassic forms, some Tertiary, and some modern forms. Subsequently, Cox and others (1969) regarded *Variamussium* as a junior synonym of *Parvamussium*, so that the arrangement was as follows: *Propeamussium (Propeamussium)* and *Propeamussium (Parvamussium)*. Unfortunately, the stratigraphic ranges assigned to the two groups in Cox and others (1969) were mixed, and, from then on, *Propeamussium sensu stricto* was frequently cited from the Lower Jurassic, but these species should have been included in *Parvamussium* instead. Both groups are now recognized at the generic level (see Damborenea, 1998, p. 148–149). *Parvamussium* and *Propeamussium* can be distinguished as follows (Damborenea, 1998, p. 149): “In *Propeamussium*, no external sculpture, no byssal notch, equal auricles and a lateral gape, and, in *Parvamussium*, smaller size, well developed ornamentation on right valve, byssal notch and no lateral gape.”

Propeamussium is not included here because its revised stratigraphic range is from the Cretaceous to the present (see discussion in Genera not Included, p. 168).

Filamussium Waller, 2006 (type species: *Pecten schafhäutli* Winkler, 1859) is not included here, as we believe the proposition of this genus was unnecessary in view of the above (see discussion in Genera not Included, p. 161).

Following these arguments, specimens from the Triassic and Lower Jurassic (until Sinemurian) assigned to *Propeamussium (Propeamussium)* by Johnson (1984) and J. Yin and Grant-Mackie (2005), to *Propeamussium (Variamussium)* by Hautmann (2001b), and to *Propeamussium* by McRoberts (1997a), are considered to belong in *Parvamussium*.

Stratigraphic range.—Middle Triassic (Anisian)—Holocene (Nakazawa, 1961; Damborenea, 1998). Cox and others (1969) assigned to *Parvamussium* an Upper Cretaceous–Holocene range, but we explained above why we consider *Parvamussium* to range from the Triassic to the Recent. Although it was more abundant during the Late Triassic, especially during the Norian (see paleogeographic distribution, above), its oldest record is from the Anisian of Japan with *Propeamussium (Variamussium)* n. sp. indet. (Nakazawa, 1961).

Paleogeographic distribution.—Tethys, Circumpacific, and Boreal (Fig. 35). Although during our study interval we only find records from the Tethys and Circumpacific domains, later in the Jurassic the genus was also distributed in South America (Aberhan, 1994a, 1998b; Damborenea, 2002a) and Tibet (J. Yin & Grant-Mackie, 2005).

Tethys domain: Late Triassic: Norian of Iran (Hautmann, 2001b), western Carpathians (Kochanová, 1967; Kollarova & Kochanová, 1973); Rhaetian of Lombardy (Italy) (Allasinaz, 1962), Iran (Haut-

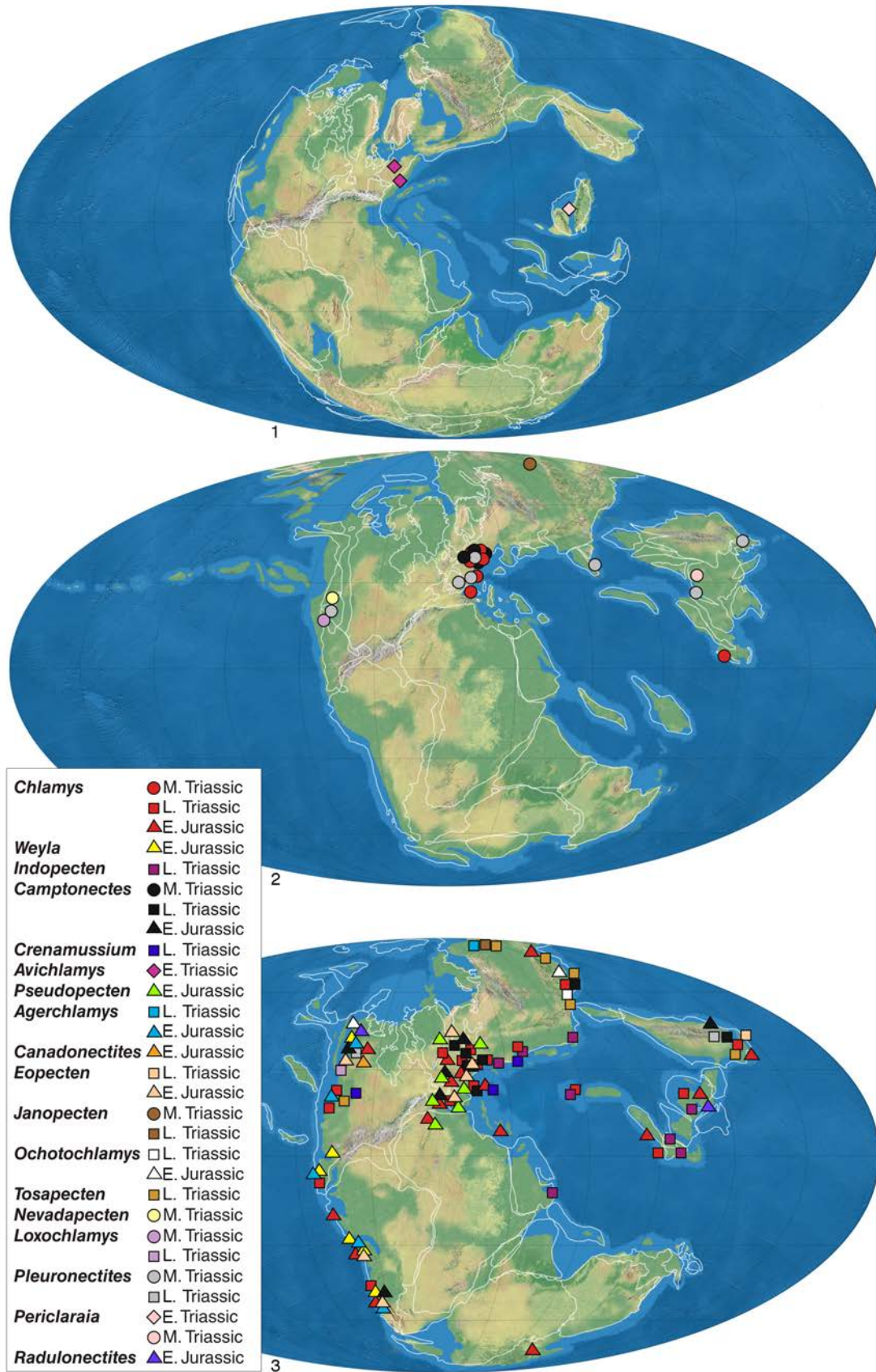


Figure 36. Paleogeographical distribution of Pectinidae (*Chlamys*, *Weyla*, *Indopecten*, *Camptonectes*, *Crenamussium*, *Avichlamys*, *Pseudopecten*, *Agerchlamys*, *Canadonectites*, *Eopecten*, *Janopecten*, *Ochotochlamys*, *Tosapecten*, *Nevadapecten*, *Loxochlamys*, *Pleuronectites*, *Periclararia*, *Radulonectites*). 1, late Permian–Early Triassic; 2, Middle Triassic; 3, Late Triassic–Early Jurassic.

mann, 2001b); Early Jurassic: Sinemurian of ?Europe (Johnson, 1984).

Circumpacific domain: Middle Triassic: Anisian of Japan (Nakazawa, 1961); Late Triassic: Norian of Sonora (Mexico) (McRoberts, 1997a); Early Jurassic: Japan (Hayami, 1957b).

Boreal domain: Late Triassic: Norian of Arctic zone of Canada (Tozer, 1962).

Paleoautoecology.—B, E, S, Un, FaM; R-Sw. Most Recent species live in deep-water environments, their shells are very fragile, and this is a good place to be safe from predators (Beesley, Ross, & Wells, 1998). Some species can live 600 m deep, although they are also found in shallow water. They live freely reclining (Waller, 2006), and at least juveniles have a byssate stage in (Johnson, 1984; Damborenea, 2002a). Although a pseudoplanktonic mode of life was suggested for some propeamussiids, there is no morphological evidence (Johnson, 1984). Living species, at least, of *Parvamussium* can probably swim for short distances, since it is known that they feed on pelagic organisms (and benthic ones), and they may even actively catch them. A swimming habit is entirely compatible with their morphology (Johnson, 1984).

Mineralogy.—Bimineralic (Waller, 2006; but see Carter, 1990a, p. 256–257). Outer shell layer: calcite (prismatic). Middle shell layer: calcite (foliated). Inner shell layer: aragonite (cross-lamellar).

Family PECTINIDAE Wilkes, 1810

Genus CHLAMYS Röding in Bolten, 1798, p. 161

Type species.—*Pecten islandicus* Müller, 1776, p. 248.

Remarks.—A synapomorphy of the subfamily Chlamyidae is the presence of aragonite cross-lamellar structure in the shell (Waller & Marinovich, 1992), but this feature only occurs in the specimens younger than the Tertiary. The inclusion of large numbers of Mesozoic species in the genus used in its broadest sense is an unsolved problem, and a review of *Chlamys* and other related genera diagnoses is needed (Damborenea, 2002a).

Although *Praechlamys* Allasinaz, 1972, was considered as a genus by some authors (e.g., Waller & Marinovich, 1992; Monari, 1994; Szente, 1996; Damborenea, 2002a), it was originally proposed as a subgenus of *Chlamys*. Other authors (e.g., Posenato, 2008b) still regard it as a subgenus of *Chlamys*, while Hautmann (2001b) questioned its validity altogether, since, in his opinion, the type of ornamentation is not an important taxonomic character at subgenus level. But Allasinaz (1972) used mainly differences in ornamentation to separate the subgenera *C.* (*Chlamys*), *C.* (*Praechlamys*), and *C.* (*Granulochlamys*). Until this controversy is solved, *Praechlamys* is here taken in its original sense. It is necessary to establish the diagnostic characters that define each taxon, because the diagnosis given by Allasinaz (1972) was too lax (Damborenea, 2002a). Some of the Triassic species traditionally attributed to *Chlamys* could fit into *Praechlamys* if considered at generic level, with an emended diagnosis, but other species are difficult to accommodate in other genera, and therefore a new taxon is required for them (Damborenea, 2002a).

As this discussion is beyond the scope of this paper, *Chlamys* is considered in a broad sense and present in the Triassic, but this is just a temporary solution for a group that has been particularly problematic since its conception.

Stratigraphic range.—Middle Triassic (Anisian)—Holocene (Cox & others, 1969; Waller, 2006). Cox and others (1969) assigned it a Triassic–Holocene range. According to Waller (2006), the oldest member of the subfamily Chlamyidae is *Praechlamys reticulata* (Schlotheim, 1823 in 1822–1823) from the Anisian of Germany, but Hautmann (2010) stated that this species was not a pectinid. There are older records (e.g., *Praechlamys wuxingensis* Li, in Nanjing Institute of Geology and Mineral Resources, 1982, from the Lower Triassic of China), but those specimens are very doubtful pectinids (see Waller, 2006, p. 331).

Paleogeographic distribution.—Cosmopolitan (Fig. 36).

Tethys domain: Middle Triassic: Anisian of Bosnia (Allasinaz, 1972), Italy (Posenato, 2008b), Switzerland (Zorn, 1971); Ladinian of Italy (Rossi Ronchetti, 1959; Allasinaz, 1972), Germany (Allasinaz, 1972), Spain (Márquez-Aliaga, 1983, 1985; López-Gómez & others, 1994), Slovakia (Kochanová, Mello, & Siblík, 1975), Malaysia (Tamura, 1973); Late Triassic: China (Wen & others, 1976; J. Chen, 1982a; Gou, 1993); Carnian of Italy (Allasinaz, 1966, 1972; Fürsich & Wendt, 1977), Switzerland, Hungary, and Bosnia (Allasinaz, 1972), Carpathians (Hungary) (Turculet, 1988), Spain (Martín-Algarra, Solé de Porta, & Márquez-Aliaga, 1995); Norian–Rhaetian of Iran (Hautmann, 2001b); Rhaetian of Czech Republic (Allasinaz, 1972), Austria (Allasinaz, 1972; Johnson, 1984), England (Johnson, 1984; Ivimey-Cook & others, 1999), Italy (Allasinaz, 1962; Johnson, 1984), Tibet (China) (J. Yin & McRoberts, 2006); Early Jurassic: Hettangian of England and France (Johnson, 1984; Liu, 1995), Italy (Allasinaz, 1962; Gaetani, 1970; Johnson, 1984), Wales (Johnson, 1984), Tibet (China) (J. Yin & McRoberts, 2006); Hettangian–Sinemurian of Spain (Calzada, 1982); Sinemurian of Switzerland (Johnson, 1984), Austria and Hungary (Szente, 1996), England, France, Spain, and Morocco (Liu, 1995), Vietnam (Sato & Westermann, 1991), Turkey (M. A. Conti & Monari, 1991).

Circumpacific domain: Late Triassic: Japan (Nakazawa, 1952; Tokuyama, 1959b); Carnian of Japan (Hayami, 1975); Norian of Oregon (United States) (Newton, 1986; Newton in Newton & others, 1987); Rhaetian of Nevada (United States) (Laws, 1982; Hallam & Wignall, 2000), Sonora (Mexico) (McRoberts, 1997a); Early Jurassic: Hettangian of Peru (Johnson, 1984); Hettangian–Sinemurian of Chile (Aberhan, 1994a); Sinemurian of western Canada (Aberhan, 1998a), Japan (Hayami, 1964, 1975).

Austral domain: Late Triassic: Rhaetian of Argentina (Riccardi & others, 2004); Early Jurassic: Hettangian–Sinemurian of Argentina (Damborenea, 2002a), of New Zealand (Damborenea & Manceñido, 1992); Sinemurian of Argentina (Damborenea & Manceñido, 2005b).

Boreal domain: Late Triassic: Carnian of Primorie (Kiparisova, 1972); Early Jurassic: Hettangian of northeastern Russia (Milova, 1976); Sinemurian of northeastern Russia (Polubotko & Milova, 1986).

Paleoautoecology.—B, E, S, Epi-Un, FaM; By-R-Sw. As inferred by functional morphology (Johnson, 1984), most fossil species probably lived attached by the byssus, at least during juvenile stages, in the same way that living species do. Many of them would be able to swim as well. Depending on the substrate in which they lived, they could spend most of their life as epibyssate on hard substrates. Other species are found in soft substrates, and these have spiny shells and probably lived reclined, using the spines to anchor them. See

Johnson (1984) for a broad discussion on the ecology and modes of life of several species.

Mineralogy.—Bimineralic (Carter, 1990a, p. 260). The group is very heterogeneous, and it is difficult to generalize about the microstructure of the shell layers (for details on the various species, see Carter (1990b, p. 381–383).

Genus WEYLA J. Böhm, 1922, p. 138

Type species.—*Pecten alatus* Buch, 1838, p. 55.

Remarks.—Although Damborenea (1987b) and Damborenea and Manceñido (1988) regarded *Weyla* as a neitheid, this family was not included in the systematic arrangement proposed by Amler (1999), which is followed here. Waller (2006) included this genus in the family Pectinidae by the presence of ctenolium.

Stratigraphic range.—Lower Jurassic (Hettangian–Toarcian) (Damborenea & Manceñido, 1988; Aberhan, 1994a). Cox and others (1969) assigned it a Upper Triassic–Middle Jurassic range, but they included three subgenera: *W.* (*Weyla*) from the Lower Jurassic, *W.* (*Pseudovola*) Lissajous, 1923, p. 169, from the Middle Jurassic, and *W.* (*Tosapecten*) Kobayashi & Ichikawa, 1949b, p. 166, from the Upper Triassic. Currently, *Pseudovola* and *Tosapecten* are considered to be separate genera (Hayami, 1975; Damborenea, 1987b), so the remaining range is Lower Jurassic. We include two subgenera of *Weyla* from the Lower Jurassic, *W.* (*Weyla*) and *W.* (*Lywea*) Damborenea, 1987b. Damborenea and Manceñido (1988) indicated that the genus was present from Sinemurian to Toarcian, and subsequently it was found in Hettangian deposits (Aberhan, 1994a; Liu, 1995; Damborenea, 1996a). Lucas and Estep (1997, p. 45, fig. 1c and 1d) mentioned and figured *Weyla* from Carnian beds of Sonora (Mexico), but these specimens were reassigned to *Mysidioptera* by Damborenea in Damborenea and Gonzalez-León (1997); Lucas and Estep (1997) also reported other specimens from the Sinemurian of the same area.

Paleogeographic distribution.—Circumpacific and Austral (Fig. 36). Although the genus is also present in the Tethys domain, it is recorded there only after the beginning of the Pliensbachian (Calzada, 1982; Liu, 1995; Fraser, Bottjer, & Fischer, 2004; Valls, Comas-Rengifo, & Goy, 2004). The genus originated in the Pacific margin and then extended to the western Tethys through the Hispanic Corridor or Proto-Atlantic (Damborenea & Manceñido, 1979, 1988; Aberhan, 2001). See Damborenea and Manceñido (1979) for a complete distribution of the genus.

Circumpacific domain: Early Jurassic: Hettangian–Sinemurian of western Canada (Aberhan, 1998a), Mexico and Texas (Liu, 1995), Chile (Aberhan, 1994a); Sinemurian of Sonora (Mexico) (Damborenea in Damborenea & González-León, 1997; Lucas & Estep, 1997; Scholz, Aberhan, & González-León, 2008), Chile (Escobar, 1980), Peru (Rangel, 1978).

Austral domain: Early Jurassic: Sinemurian of Argentina (Damborenea & Manceñido, 2005b; Damborenea & Lanés, 2007).

Paleoautoecology.—B, Se, S, Un, Sed; R. From the observation of specimens in life position and analysis of the shell morphology (Damborenea & Manceñido, 1979, 1988; Damborenea, 1987b), it was inferred that *Weyla* was sedentary and lived semi-infaunally as a recliner, without byssus attachment in the adult stage.

Mineralogy.—Bimineralic (Carter, 1990a, p. 260, 263). Little is known about the microstructure of the shell of *Weyla*; the inner shell layer is aragonitic and with cross-lamellar structure. Data provided for the family Pectinidae. Outer shell layer: calcite (prismatic). Inner shell layer: aragonite (cross-lamellar).

Genus INDOPECTEN Douglas, 1929, p. 632

Type species.—*Pecten clignetti* Krumbeck, 1913, p. 36.

Stratigraphic range.—Upper Triassic (Norian–Rhaetian) (Hautmann, 2001b). Cox and others (1969) assigned it an upper Norian range. New records expanded the range of this genus (see paleogeographic distribution).

Paleogeographic distribution.—Tethys (Fig. 36).

Tethys domain: Late Triassic: Norian of western Carpathians (Ruban, 2006a), China (Wen & others, 1976; J. Chen & Yang, 1983), Oman (R. Hudson & Jefferies, 1961), Armenia (Hautmann, 2001b), Timor (Indonesia) (Krumbeck, 1924), Himalayas (Kutassy, 1931), Thailand (Vu Khuc & Huyen, 1998); Norian–Rhaetian of Iran (Hautmann, 2001b); Rhaetian of Tibet (China) (Hautmann & others, 2005), Pamira (Afghanistan) (Polubotko, Payevskaya, & Repin, 2001).

Paleoautoecology.—B, E, S, Epi-Un, FaM; By-R-Sw. Some of *Indopecten* species, like *I. glaber* Douglas, 1929, could swim, as suggested by their ligament type (so-called alivincular-alate according to Hautmann, 2004), which would be fit enough for the constant opening and closing of the valves required by a swimming activity (Hautmann, 2004). The external morphology is also compatible with a swimming habit, according to S. M. Stanley (1972). It probably lived mostly reclined, but it could swim occasionally. However, other species have a byssal notch, and their shell morphology is not suitable for swimming, so these were probably epibyssate (see Hautmann, 2001b).

Mineralogy.—Aragonitic (Hautmann, 2006a). According to Waller (2006), the *Indopecten* inner shell layers are usually recrystallized, so they were probably aragonitic. Although the microstructure of the outer shell layer is unknown, its mineralogy was calcitic. However, Hautmann (2006a) studied the microstructure of two species of *Indopecten* [*I. serraticostata* (Bittner, 1899) and *I. glaber* Douglas, 1929)] and he concluded that all the shell was composed of a single microstructure (probably cross-lamellar) and was entirely aragonitic.

Genus CAMPTONECTES Agassiz in Meek, 1864, p. 39

Type species.—*Pecten lens* J. Sowerby, 1818, p. 3.

Remarks.—Cox and others (1969) included three subgenera within *Camptonectes*: *C.* (*Camptonectes*), *C.* (*Camptochlamys*) Arkell, 1930 in 1929–1937, p. 102, and *C.* (*Boreionectes*) Zakharov, 1965, p. 72. Subsequently, Allasinaz (1972, p. 316) added a fourth, *C.* (*Annulinectes*), and Fürsich (1982, p. 50) another, *C.* (*Costicamptonectes*). Kelly (1984) regarded *Boreionectes* as a junior synonym of *Mclearnia* Crickmay, 1930b, p. 45. According to Waller and Marincovich (1992), *Costicamptonectes* is unnecessary, and they raised *Camptochlamys* to generic level. We only consider two subgenera in our study interval: *C.* (*Camptonectes*) and *C.* (*Annulinectes*).

Stratigraphic range.—Middle Triassic (Anisian)–Upper Cretaceous (Maastrichtian) (Cox & others, 1969; Allasinaz, 1972). Cox and others

(1969) assigned a Jurassic–Upper Cretaceous (Maastrichtian) range to *C. (Camptonectes)*, but some Tertiary and Holocene species are now also referred to this genus by some authors (see Damborenea, 2002a, p. 56). Allasinaz (1972) assigned to *C. (Annulinectes)* an Anisian–Jurassic range, although the species he included in this subgenus were recorded only in Anisian, Ladinian, and Carnian beds. As we could not see the papers that recognize post-Cretaceous *Camptonectes*, we provisionally follow Cox and others (1969) for the end of the range.

Paleogeographic distribution.—Cosmopolitan (Fig. 36).

Tethys domain: Middle Triassic: Anisian of Slovakia (Kochanová, 1985), Romania and Yugoslavia (Allasinaz, 1972); Ladinian of Slovakia (Kochanová, Mello, & Siblík, 1975), Bosnia (Allasinaz, 1972); Late Triassic: Carnian of Slovenia (Jelen, 1988), Hungary and Italy (Allasinaz, 1972); Rhaetian of ?England (Johnson, 1984; Ivimey-Cook & others, 1999); Early Jurassic: Hettangian of England (Johnson, 1984; Liu, 1995), Germany and Switzerland (Johnson, 1984); Sinemurian of England and Portugal (Liu, 1995).

Circumpacific domain: Late Triassic: Carnian of Japan (Nakazawa, 1952; Hayami, 1975); Early Jurassic: Hettangian of Japan (Hayami, 1959; Hayami, 1975; Johnson, 1984); Sinemurian of western Canada (Poulton, 1991; Aberhan, 1998a).

Austral domain: Early Jurassic: Hettangian–Sinemurian of Argentina (Damborenea, 2002a; Damborenea & Manceñido, 2005b).

Boreal domain: Late Triassic: Norian–Rhaetian of northeastern Russia (Milova, 1976).

Paleoautoecology.—B, E, S, Epi, FaM; By-Sw. All species described by Johnson (1984) have a byssal notch and were epibyssate. However, he interpreted that they could swim to escape from predators, on the basis of the analysis of external shell morphology (shell thin, low convexity, and wide umbonal angle). According to Sha (2003), *Camptonectes* had planktotrophic larvae that facilitated its global distribution.

Mineralogy.—Bimineralic (Johnson, 1984; Carter, 1990b, p. 381). Outer shell layer: calcite (foliated-prismatic). Inner shell layer: aragonite (?).

Genus CRENAMUSSIUM

Newton in Newton & others, 1987, p. 46

Type species.—*Crenamussium concentricum* Newton in Newton & others, 1987, p. 50.

Remarks.—Newton (in Newton & others, 1987) included *Crenamussium* in the family Pectinidae. Later, Waller (in Waller & Stanley, 2005) included it in the Entoliidae, and a year later, Waller (2006) suggested that *Crenamussium* is a junior synonym of *Calvaentolium* Romanov, 1985, but he did not justify it. *Calvaentolium* is not included in this paper (see discussion in Genera not Included, p. 158). Newton (in Newton & others, 1987) included the type species in *Crenamussium* and, tentatively, *C. balatonicus* (Bittner, 1901b) (species included in *Pleuronectites* and *Chlamys* by other authors).

Stratigraphic range.—Upper Triassic (Carnian–Norian) (Newton in Newton & others, 1987). According to the species assigned by Newton (in Newton & others, 1987), the stratigraphic range of *Crenamussium* is Carnian–Norian.

Paleogeographic distribution.—Tethys and Circumpacific (Fig. 36).

Tethys domain: Late Triassic: Carnian of Italy (Allasinaz, 1972), Hungary (Bittner, 1912), Carpathians (Kiparisova, 1954).

Circumpacific domain: Late Triassic: Norian of Oregon (United States) (Newton in Newton & others, 1987).

Paleoautoecology.—B, E, S, Epi, Sed; By. According to the diagnosis given by Newton (in Newton & others, 1987), the shell is subcircular, the auricles are unequal, and a deep byssal notch is observed in the right anterior auricle, thus it probably lived as an epibyssate.

Mineralogy.—Bimineralic (Newton in Newton & others, 1987, p. 50). *Crenamussium* shell microstructure is not well known, but the mineralogy of the shell, as a member of the family Pectinidae, should have at least a calcitic outer layer. In the specimens described by Newton (in Newton & others, 1987), there is evidence of original fibrous calcite in the form of siliceous pseudomorphs.

Genus AVICHLAMYS Allasinaz, 1972, p. 368

Type species.—*Pecten csopakensis* Frech, 1905, p. 4.

Stratigraphic range.—Lower Triassic (Olenekian) (Posenato, 2008a). Allasinaz (1972) proposed *Avichlamys* and included two species: *Pecten csopakensis* Frech, 1905, and *Pecten nicolensis* Ogilvie Gordon, 1927, both from the Triassic. Subsequently, Neri and Posenato (1985) and Broglio-Loriga and others (1990) also included *Chlamys tellinii* Tommasi, 1896, which was reported from the Italian Triassic by Leonardi (1935) and Boni (1943).

Paleogeographic distribution.—Eastern Tethys (Fig. 36).

Tethys domain: Early Triassic: Italy (Allasinaz, 1972; Neri & Posenato, 1985; Broglio-Loriga & others, 1990), Hungary (Allasinaz, 1972).

Paleoautoecology.—B, E, S, Epi, Sed; By. According to the generic diagnosis provided by Allasinaz (1972), *Avichlamys* is characterized by a subequivalve shell, with different valve convexity, subequal auricles, and a wide byssal gape in the right auricle. It was probably an epibyssate bivalve.

Mineralogy.—Bimineralic (Carter, 1990a). No data are known about *Avichlamys* shell microstructure. We assume a bimineralic shell, as in the other pectinids, following Carter (1990a).

Genus PSEUDOPECTEN Bayle, 1878, explanation pl. 121

Type species.—*Pecten equivalvis* J. Sowerby, 1816, p. 83.

Remarks.—Although *Pseudopecten* lacks a ctenolium and should be excluded from the Pectinidae (Damborenea, 2002a), we list it here until it is assigned to another family according to its features.

Stratigraphic range.—Lower Jurassic (Hettangian)–Middle Jurassic (Bajocian) (Johnson, 1984). Cox and others (1969) distinguished two subgenera within *Pseudopecten*: *P. (Pseudopecten)* and *P. (Echinopecten)* Brasil, 1895. Both were reported from Hettangian beds. However, following Johnson (1984), we regard *P. (Pseudopecten)* as Hettangian and *P. (Echinopecten)* as Toarcian. Therefore, only *P. (Pseudopecten)* is included in our study interval.

Paleogeographic distribution.—western Tethys (Fig. 36). During our study interval, *Pseudopecten* was only distributed in the western Tethys, but from the Pliensbachian onward, it was also reported from South America (Damborenea, 2002a) and Australia (Grant-Mackie, 1994). In addition, Damborenea (2002a) suggested that its presence in the Early Jurassic of Japan and Siberia is also possible.

Tethys domain: Early Jurassic: Hettangian of Spain (Liu, 1995), France, Italy, and Germany (Johnson, 1984); Sinemurian of Spain,

Portugal, and Morocco (Liu, 1995), England (Johnson, 1984; Liu, 1995), Italy, France, and Germany (Johnson, 1984).

Paleoautoecology.—B, E, S, Un, FaM; R-Sw. Species attributed to *P. (Pseudopecten)* had a byssal gape at juvenile stages, but it disappeared in adult stages; they lived byssate when young but were later recliners on the substrate, and they could swim actively (see Johnson, 1984, for a complete interpretation of the various species).

Mineralogy.—Bimineralic (Carter, 1990b, p. 388). Outer shell layer: calcite (prismatic + foliated). Inner shell layer: aragonite (cross-lamellar).

Genus AGERCHLAMYS Damborenea, 1993, p. 119

Type species.—*Chlamys (Camptochlamys) wunschae* Marwick, 1953, p. 98.

Stratigraphic range.—Upper Triassic (Carnian)–Lower Jurassic (Toarcian) (Damborenea, 1993, 2002a). Damborenea (1993) proposed *Agerchlamys*, including several previously described species referred to other genera (see Damborenea, 1993, p. 120, and Damborenea, 2002a, p. 66, for species listed). These species were recorded from the Carnian to the Toarcian, and the author indicated the possibility that the genus may be present up to the Middle Jurassic.

Paleogeographic distribution.—Circumpacific, Austral, and Boreal (Fig. 36). *Agerchlamys* was distributed through the Austral and Boreal domains and also in the Circumpacific, but always at high latitudes. In the Austral domain (Argentina and New Zealand), it was reported primarily from Pliensbachian beds (Marwick, 1953; Damborenea, 1993, 2002a).

Circumpacific domain: Early Jurassic: Hettangian of Chile (Aberhan, 1994a), Oregon (United States) (D. G. Taylor & Guex, 2002), British Columbia (western Canada) (Wignall & others, 2007); Hettangian–Sinemurian of Canada (Aberhan, 1998a, 1998b), Sonora (Mexico) (Scholz, Aberhan, & González-León, 2008).

Austral domain: Early Jurassic: Hettangian–Sinemurian of Argentina (Damborenea, 2002b; Damborenea & Manceñido, 2005b).

Boreal domain: Late Triassic: Carnian–Norian of Siberia (Kiparisova, Bychkov, & Polubotko, 1966).

Paleoautoecology.—B, E, S, Epi, Sed; By. Due to the presence of a deep byssal gape below the right anterior auricle and a strong ctenolium, it was epibyssate (Damborenea, 1993, 2002a). Although it has a wide umbonal angle, the auricles are of different sizes, so it is not believed that it could swim.

Agerchlamys is usually found in low-energy and well-oxygenated environments, and associated with sponges and other bivalves, especially limids (Damborenea, 2002a).

Mineralogy.—Bimineralic (Carter, 1990a, p. 260). There are no data about *Agerchlamys* shell. We assume bimineralic mineralogy, as in the other members of the family Pectinidae (Carter, 1990a).

Genus CANADONECTITES Aberhan, 1998a, p. 110

Type species.—*Canadonectites paucicostatus* Aberhan, 1998a, p. 110.

Remarks.—Aberhan (1998a) proposed the genus *Canadonectites* to accommodate specimens with intermediate morphology between *Pleuronectites* Schlotheim, 1820, and *Radulonectites* Hayami, 1957c, and differing from both of them by ornamentation features.

Stratigraphic range.—Lower Jurassic (Sinemurian–Pliensbachian) (Aberhan, 1998a). It was only reported from Sinemurian and Pliensbachian beds of western Canada (Aberhan, 1998a).

Paleogeographic distribution.—Circumpacific (Fig. 36).

Circumpacific domain: Early Jurassic: Sinemurian of western Canada (Aberhan, 1998a, 2001).

Paleoautoecology.—B, E, S, Epi, Se; By. The mode of life of *Canadonectites* was probably very similar to *Agerchlamys*, since both have a deep byssal notch and ctenolium in the right valve.

Mineralogy.—Bimineralic (Carter, 1990a, p. 260). There are no data on *Canadonectites* shell microstructure. We assume bimineralic mineralogy, as in the other members of the family Pectinidae (Carter, 1990a).

Genus EOPECTEN Douvillé, 1897, p. 203

Type species.—*Hinnites tuberculatus* Goldfuss (*errore pro Spondylus tuberculosus* Goldfuss), 1835 in 1833–1841, p. 93.

Remarks.—See Johnson (1984, p. 149) and Damborenea (1987b, p. 198) for a discussion about synonymy and the problems related to this genus since its proposal.

Stratigraphic range.—Upper Triassic (Carnian)–Lower Cretaceous (Albian) (Hayami, 1975; Johnson, 1984). Cox and others (1969) assigned it a Jurassic–Lower Cretaceous (Albian) range. Although it seems fairly accepted that it appeared in the Early Jurassic, according to the literature, there are several records from the Carnian of Japan (Kobayashi & Ichikawa, 1949b; Nakazawa, 1952; Hayami, 1975) and from the Norian of Chile (Hayami, Maeda, & Ruiz-Fuller, 1977) that no other author except Hallam (1981) considered. Middle Triassic specimens assigned by Allasinaz (1972) to *Radulonectites* should be allocated to *Eopecten* instead (Damborenea, 2002a, p. 61). If *Radulonectites? flagellum* (Stoppani, 1858 in 1858–1860), described by Allasinaz (1972, p. 331), is assigned to *Eopecten*, the genus was present from Ladinian times. Another species that was referred to *Eopecten*, originally proposed as *Monotis albertii* Goldfuss, 1835 in 1833–1841 (Diener, 1923), was reported from the Lower and Middle Triassic of Europe, but it is currently included in *Lep-tochondria* (Waller & Stanley, 2005, p. 34).

Paleogeographic distribution.—Tethys, Circumpacific, and Austral (Fig. 36). According to the published records, it seems that *Eopecten* originated in the Late Triassic of Japan, and then it migrated to the western Tethys (Europe) and eastern Paleopacific.

Tethys domain: Early Jurassic: Hettangian of England (Liu, 1995), Belgium and Germany (Johnson, 1984); Sinemurian of Portugal and Spain (Liu, 1995), Germany (Johnson, 1984).

Circumpacific domain: Late Triassic: Carnian of Japan (Kobayashi & Ichikawa, 1949b; Nakazawa, 1952; Hayami, 1975); Early Jurassic: Hettangian of Chile (Aberhan, 1994a); Hettangian–Sinemurian of Canada (Aberhan, 1998a); Sinemurian of Canada (Poulton, 1991).

Austral domain: Early Jurassic: Hettangian–Sinemurian of Argentina (Riccardi & others, 1991; Damborenea, 2002a; Damborenea & Manceñido, 2005b).

Paleoautoecology.—B, E, S, Epi-C, Sed; By-C. Johnson (1984) and Harper and Palmer (1993) analyzed the mode of life of different species of *Eopecten*. The last authors concluded that some species could live cemented to the substrate, while others were epibyssate during most of their life.

Mineralogy.—Bimineralic (Carter, 1990b, p. 388; Harper & Palmer, 1993, p. 67). The shell of *Eopecten* had a foliated outer shell layer, both in the left valve (Carter, 1990a) and in the right one (Harper & Palmer, 1993), and aragonitic middle and inner shell layers with cross-lamellar microstructure (Carter, 1990a).

Genus JANOPECTEN Arkhipov & Trushchelev, 1980, p. 10

Type species.—*Janopecten kularensis* Arkhipov & Trushchelev, 1980, p. 10.

Stratigraphic range.—Middle Triassic (Anisian)—Upper Triassic (lower Carnian) (Waller in Waller & Stanley, 2005). *Janopecten* was reported from Anisian and Ladinian beds (Dagys & Kurushin, 1985) and from the lower Carnian of the Boreal area (Waller in Waller & Stanley, 2005).

Paleogeographic distribution.—Boreal (Fig. 36).

Boreal domain: Middle Triassic: Anisian of Yakutia (Russia) (Konstantinov, Sobolev, & Yadernkin, 2007); Anisian–Ladinian of Siberia (Arkhipov & Trushchelev, 1980; Dagys & Kurushin, 1985). Late Triassic: early Carnian of Siberia (Arkhipov & Trushchelev, 1980).

Paleoautoecology.—B, E, S, Epi, FaM; By-Sw? At least the type species (Dagys & Kurushin, 1985, pl. 21, 13a, 13b) had an equivalve shell, nearly equal auricles, and an umbonal angle large enough to be an occasional swimmer. The shells had a byssal notch throughout their ontogeny (Waller in Waller & Stanley, 2005), and they likely lived epibyssate and occasionally could perform swimming cycles. This is probably true only for the Anisian forms, since, according to Waller (in Waller & Stanley, 2005), Ladinian and Carnian species of *Janopecten* began to develop strongly inequilateral shells.

Mineralogy.—Bimineralic (Carter, 1990a, p. 260). There are no data on *Janopecten* shell microstructure. Bimineralic mineralogy is assumed, as in the other members of the family Pectinidae.

Genus OCHOTOCHLAMYS

Milova & Polubotko in Milova, 1976, p. 61

Type species.—*Chlamys* (*Ochotochlamys*) *gizhigensis* Polubotko in Milova, 1976, p. 61.

Remarks.—*Ochotochlamys* was erected as subgenus of *Chlamys* (Milova & Polubotko in Milova, 1976), but it was subsequently raised to genus level (Polubotko & Milova, 1986), which was followed by all later authors.

Stratigraphic range.—Upper Triassic (Norian)—Lower Jurassic (Toarcian) (Milova & Polubotko in Milova, 1976; Aberhan, 1998a). For a long time, *Ochotochlamys* was only reported from Late Triassic of northeastern Asia, but it was later recorded from the Pliensbachian (Polubotko & Milova, 1986; Aberhan 1998a; Damborenea, 2002a) and from the Toarcian (Aberhan, 1998a).

Paleogeographic distribution.—Boreal (Fig. 36). It was originally believed that the genus was restricted to northeastern Asia, but new records from the Pacific margin (Canada and Argentina) (Aberhan, 1998a; Damborenea, 2002b) extended its paleogeographic distribution; but it is only known from high paleolatitudes. The Austral record is Pliensbachian and thus outside our study range (Damborenea, 2002a). It was also mentioned from the Triassic–Jurassic boundary beds of British Columbia (Wignall & others, 2007) and eastern Alberta (Asgar-Deen & others, 2003).

Boreal domain: Late Triassic: Carnian–Norian of northeastern Asia (Polubotko & Milova in Milova, 1976); Early Jurassic: Hettangian of northeastern Russia (Milova, 1988); Hettangian–Sinemurian of western Canada (Aberhan, 1998a, 1998b, 2001); Sinemurian of northeastern Russia (Polubotko & Milova, 1986).

Paleoautoecology.—B, E, S, Epi, Sed; By. According to Aberhan (1998a), a typical feature of the genus is that the right anterior auricle had a byssal notch; a byssal sinus is observed in the left valve, but it is not distinguishable in all specimens. *Ochotochlamys* was probably an epibyssate bivalve.

Mineralogy.—Bimineralic (Carter, 1990a, p. 260). There are no data on *Ochotochlamys* shell microstructure. Bimineralic mineralogy is assumed, as in the other members of the family Pectinidae (Carter, 1990a).

Genus TOSAPECTEN Kobayashi & Ichikawa, 1949b, p. 166

Type species.—*Pecten* (*Velopecten*) *suzukii* Kobayashi, 1931, p. 258.

Remarks.—Although Kobayashi and Ichikawa (1949b) proposed *Tosapecten* within the family Pectinidae, Cox and others (1969) considered it to be a subgenus of *Weyla* Böhm, 1922. Currently, almost all authors (Hayami, 1975; Milova, 1976; J. Chen, 1982a; Okuneva, 1985; Damborenea, 1987b; Tanaka, 1989; Waller in Waller & Stanley, 2005; Waller, 2006) regard it as a distinct genus, separate from *Weyla*.

According to Waller (in Waller & Stanley, 2005), *Tosapecten* includes two subgenera, *T.* (*Tosapecten*) and *T.* (*Indigiropecten*) Trushchelev, 1984.

Stratigraphic range.—Upper Triassic (Carnian–Rhaetian) (Kobayashi & Ichikawa, 1949b; Milova, 1976). Cox and others (1969) stated that the genus was known from the Upper Triassic of Japan. Subsequently, it was also reported from Siberia (Kobayashi & Tamura, 1983b). It was known throughout the Carnian and Norian in Japan (see paleogeographic distribution, below). We lack information on the Siberian records; we could only check the Norian occurrence in Okuneva (1985). Milova (1976) reported *Tosapecten subhiemalis wittnburgi* n. subsp. from upper Norian–Rhaetian beds. Some biostratigraphic papers mentioned the presence of *Tosapecten* from latest Triassic times (Kurushin, 1990; Polubotko & Repin, 1990; Zakharov & others, 1997), referring to *Tosapecten efimovae* Polubotko, 1966.

Paleogeographic distribution.—Circumpacific and Boreal (Fig. 36). *Tosapecten* was mainly distributed through the northern Circumpacific and Boreal domains.

Circumpacific domain: Late Triassic: Carnian of Japan (Nakazawa, 1952; Ando, 1988); Carnian–Norian of Japan (Kobayashi & Ichikawa, 1949b; Tokuyama, 1959b; Hayami, 1975; Tanaka, 1989; Onoue & Tanaka, 2005); Norian of Japan (Nakazawa, 1963), ?Oregon (United States) (Newton in Newton & others, 1987; Newton, 1988).

Boreal domain: Late Triassic: Carnian of northeastern Russia (Bychkov & others, 1976), Primorie (Kiparisova, 1972); Norian of Siberia (Okuneva, 1985); Norian–Rhaetian of northeastern Russia (Milova, 1976); Rhaetian of northeastern of Siberia (Bychkov & others, 1976; McRoberts, 2010).

Paleoautoecology.—B, E, S, Epi, Sed; By. In all species assigned to *Tosapecten*, a byssal notch is observed, and they have unequal auricles (see description and figures in the published literature, listed above). Like most pectinids, they lived epibyssate.

Mineralogy.—Bimineralic (Carter, 1990a, p. 260). There are no data on *Tosapecten* shell microstructure. Bimineralic mineralogy is assumed, as in the other members of the family Pectinidae.

Genus NEVADAPECTEN

Waller in Waller & Stanley, 2005, p. 46

Type species.—*Nevadapecten lynnae* Waller in Waller & Stanley, 2005, p. 46.

Remarks.—Waller (in Waller & Stanley, 2005) included *Nevadapecten* in the subfamily Tosapectininae and related it with *Tosapecten* and *Janopecten*, considering it to be intermediate between these two genera in several aspects.

Stratigraphic range.—Middle Triassic (upper Ladinian) (Waller in Waller & Stanley, 2005). According to Waller (in Waller & Stanley, 2005), *Nevadapecten* was reported from the upper Ladinian of New Pass Range in Nevada.

Paleogeographic distribution.—Circumpacific (Fig. 36).

Circumpacific domain: Middle Triassic: Ladinian of Nevada (United States) (Waller in Waller & Stanley, 2005).

Paleoautoecology.—B, E, S, Epi, Sed; By. *Nevadapecten* had some features related to a swimming mode of life, such as circular shape, an almost equilateral shell, and a wide umbonal angle, but it had unequal auricles and a byssal gape, which indicates it was an epibyssate bivalve.

Mineralogy.—Bimineralic (Waller in Waller & Stanley, 2005). Outer shell layer: calcite (antimarginal fibrous). Inner shell layer: aragonite.

Genus LOXOCHLAMYS

Waller in Waller & Stanley, 2005, p. 40

Type species.—*Loxochlamys corallina* Waller in Waller & Stanley, 2005, p. 43.

Stratigraphic range.—Middle Triassic (Ladinian)—Upper Triassic (Carnian) (Waller in Waller & Stanley, 2005). Waller (in Waller & Stanley, 2005) included the type species within *Loxochlamys*, from the upper Ladinian, and two other species: *Pecten chiwanae* McLearn, 1941, and *Pecten sasuchan* McLearn, 1941, both from Carnian beds.

Paleogeographic distribution.—Circumpacific (Fig. 36).

Circumpacific domain: Middle Triassic: Ladinian of Nevada (United States) (Waller in Waller & Stanley, 2005); Late Triassic: Carnian of British Columbia (Canada) (McLearn, 1941; Waller in Waller & Stanley, 2005).

Paleoautoecology.—B, E, S, Epi, Sed; By. *Loxochlamys* had a byssal notch and ctenolium throughout its ontogeny; it probably lived epibyssate among corals with which it was usually associated (Waller in Waller & Stanley, 2005).

Mineralogy.—Bimineralic (Waller in Waller & Stanley, 2005). Outer shell layer: calcite (antimarginal fibrous). Inner shell layer: aragonite.

Genus PLEURONECTITES von Schlotheim, 1820, p. 217

Type species.—*Pleuronectites laevigatus* von Schlotheim, 1820, p. 217.

Stratigraphic range.—Middle Triassic (Anisian)—Upper Triassic (Carnian) (Hayami, 1975; Waller, 2006). Newell and Boyd (1995) extended the range of *Pleuronectites* to the Lower Triassic, with the

species *Pleuronectites meeki* Newell & Boyd, 1995, but Waller (in Waller & Stanley, 2005) regarded this species as an entoliid rather than a pectinid, because it lacks a ctenolium. Waller (2006) indicated that the oldest undoubted *Pleuronectites* is *P. laevigata* Schlotheim, 1820, from the Anisian (see Waller in Waller & Stanley, 2005 and Waller, 2006, for records mentioned from the Lower Triassic that are not taken into account). The youngest record of the genus is from the Carnian with *P. hirabarensis* Amano (Hayami, 1975). Newton (in Newton & others, 1987) mentioned it from the Norian, but this reference is questionable.

Hautmann (2010) considered most species attributed to *Pleuronectites* to be synonyms of *P. laevigatus* (previously referred by Waller in Waller & Stanley, 2005, to *Pecten laterestriatus* Philippi, 1899, and *Pecten schmiederi* Giebel, 1856) or as erroneously assigned to the genus, so *Pleuronectites* would be a monospecific genus. The author, and previously Waller (in Waller & Stanley, 2005), mentioned *P. balatonicus* (Bittner, 1901c), figured by Allasinaz (1972), and regarded it as entoliid. *Pleuronectites newelli* Waller in Waller & Stanley, 2005, was also regarded as an entoliid by Hautmann (2010). He assigned an Anisian–Ladinian range to *Pleuronectites*, but he did not mention Amano's Carnian species.

Paleogeographic distribution.—Tethys and Circumpacific (Fig. 36). The paleogeographic distribution agrees with Waller (in Waller & Stanley, 2005) and Waller (2006). Although *Pleuronectites* is often quoted as being from China, the specimens are uncertainly or erroneously assigned (Waller in Waller & Stanley, 2005).

Tethys domain: Middle Triassic: Anisian of Germany (Hagdorn, 1982, 1991, 1995); Anisian–Ladinian of Israel (Lerman, 1960), Germany, Hungary, Sardinia (Italy), Afghanistan, and China (Hautmann, 2010); Ladinian of Italy (Allasinaz, 1972), Spain (Márquez-Aliaga, 1983, 1985), Afghanistan (Farsan, 1972).

Circumpacific domain: Middle Triassic: Anisian of Japan (Hayami, 1975); Ladinian of Nevada (United States) (Waller in Waller & Stanley, 2005); Late Triassic: Carnian of Japan (Hayami, 1975).

Paleoautoecology.—B, E, S, Epi, Sed; By. According to the diagnosis offered by Waller (in Waller & Stanley, 2005), *Pleuronectites* probably lived epibyssate, and it had a deep byssal notch below the right anterior auricle, and a ctenolium throughout ontogeny.

Mineralogy.—Bimineralic (Waller in Waller & Stanley, 2005, p. 40). *Pleuronectites newelli* Waller in Waller & Stanley, 2005, shows an originally aragonitic inner shell layer and a calcitic outer shell layer (Waller in Waller & Stanley, 2005), and the same mineralogy was found in *Pleuronectites laevigatus* Schlotheim, 1820 (Hautmann, 2010; Carter & Hautmann, 2011); the microstructure of inner and middle shell layers was probably cross-lamellar, and the outer shell layer was prismatic.

Genus PERICLARAIA J. Li & Ding, 1981, p. 327, 330

Type species.—*Periclararaia circularis* J. Li & Ding, 1981, p. 327.

Remarks.—*Periclararaia* was proposed by J. Li and Ding (1981) from deposits of Anhui Province (China). These authors included three species: *Periclararaia circularis* J. Li & Ding, 1981, *Periclararaia reticulata* J. Li & Ding, 1981, and *Periclararaia chaonianensis* J. Li & Ding, 1981. Subsequently, J. Chen and Komatsu (2002) added a new species, *Periclararaia jinyaensis* Chen & Komatsu, 2002, and they considered that the three species proposed by J. Li and Ding (1981)

are variants of the same, as J. Li and Ding (1981) used differences in ornamentation and size of the right anterior auricle to separate them. These variations are regarded as intraspecific by J. Chen and Komatsu (2002). J. Li and Ding (1981) included *Periclararaia* in the family Pectinidae, but other authors (H. Yin, 1985, 1990; Gavrilova, 1995, 1996), based on its external resemblance to the clariids, referred it to the Pteropectinidae. However, J. Chen and Komatsu (2002) argued that since *Periclararaia* had a right valve ctenolium, a diagnostic character of the family Pectinidae, it should be included in this family.

Stratigraphic range.—Lower Triassic (upper Olenekian)—Middle Triassic (lower Anisian) (J. Li & Ding, 1981; J. Chen & Komatsu, 2002). J. Li and Ding (1981) reported *Periclararaia* from upper Olenekian beds of Anhui Province (China). Subsequently, J. Chen and Komatsu (2002) mentioned it from lower Anisian deposits of Guangxi province (China) and doubted the age assignment given by J. Li and Ding (1981). However, *Periclararaia* was quoted in several biostratigraphic papers in Anhui province in beds attributed to the Olenekian (Tong & others, 2004, 2006; Tong, 2005; S. Wu & others, 2005). Curiously, these papers considered *Periclararaia* as endemic to Anhui province, not mentioning J. Chen and Komatsu (2002).

Paleogeographic distribution.—Eastern Tethys (Fig. 36).

Tethys domain: Early Triassic: late Olenekian of Anhui province (China) (J. Li & Ding, 1981); Middle Triassic: early Anisian of Guangxi province (China) (J. Chen & Komatsu, 2002; J. Chen & Stiller, 2007).

Paleoautoecology.—B, E, S, Epi, Sed; By. The features of *Periclararaia* shells, which are inequivalve and inequilateral and had a deep byssal notch, indicate it was probably an epibyssate bivalve.

Mineralogy.—Bimineralic (Carter, Barrera, & Tevesz, 1998). Mineralogical data provided for the family Pectinidae by Carter, Barrera, and Tevesz (1998). Outer shell layer: calcite. Middle and inner shell layers: calcite-aragonite.

Genus RADULONECTITES Hayami, 1957c, p. 89

Type species.—*Radulonectites japonicus* Hayami, 1957c, p. 90.

Remarks.—*Hunanonectes* Z. Fang, 1978, p. 465, is considered to be a synonym of *Radulonectites* (see discussion for *Hunanonectes* in Genera not Included, p. 162).

Stratigraphic range.—Lower Jurassic (Hettangian—Pliensbachian) (Stiller, 2006; Hayami, 1975). Hayami (1957c) proposed the genus from the Japanese Pliensbachian (see also Hayami, 1985) and included the type species and *Pecten (Pleuronectites) laterestriatus* Philippi, 1899, from the German lower Muschelkalk, and also specimens referred by A. F. Leanza (1942) to *Pecten (Camptonectes) lens* Sowerby from the Pliensbachian of Argentina. He also provisionally included *Chlamys kakanuia* Marwick (1956, fig. 1) from the Upper Triassic of New Zealand, a species based on too poorly preserved material to discuss its affinities (Damborenea, 1993, 2002a). Later, Hayami (1975) disregarded these Triassic records and assigned the genus a Pliensbachian range. Cox and others (1969) referred it to the ?Triassic, Lower Jurassic. On the other hand, Sepkoski (2002) assigned it a Triassic (Anisian)—Jurassic (?Pliensbachian) range, mentioning Hayami (1975) and H. Yin (1985) as his sources. H. Yin (1985) mentioned it during Anisian and Ladinian but did not list the original source. Allasinaz (1962,

1972) quoted *Radulonectites* from the European Triassic. The specimens from the Italian Rhaetian referred by Allasinaz (1962) to *Radulonectites* are very poorly preserved; these doubtful records are not taken into account here, since, according to Damborenea (2002a), they belong to *Eopecten* Douvillé, 1897. The same occurs with material from the Triassic of New Zealand, similarly referred by other authors (see Damborenea, 2002a, p. 61). Onoue and Tanaka (2005) mentioned *Radulonectites* sp. from the Japanese Upper Triassic, based on a single deformed specimen, and their incomplete description is not enough to extend the range of this taxon. The oldest solid records are Hettangian (J. Chen, 1982b; Stiller, 2006 [*Hunanonectes*]) and the youngest are Pliensbachian (Hayami, 1957c, 1975, 1985).

Paleogeographic distribution.—Eastern Tethys (Fig. 36). During the Pliensbachian, this genus had a wide distribution (e.g., Siberia, Argentina, Chile) (Hayami, 1975; Polubotko & Milova, 1986; Milova, 1988; Damborenea, 1993, 2002a; Aberhan, 1994a, 1998a; Aberhan & Fürsich, 1997), and during the study interval, it was only reported with certainty from China.

Tethys domain: Early Jurassic: Hettangian—Sinemurian of southern China (J. Chen, 1982b, 1988; Z. Fang, 1978; Stiller, 2006); ?Sinemurian of Canada (Poulton, 1991, according to Aberhan, 1998a).

Paleoautoecology.—B, E, S, Epi, Sed; By. Several morphological traits (shell shape, convexity of valves, and the presence of deep byssal notch) and the encrusted epizoic organisms in several specimens suggest an epibyssate mode of life (Damborenea, 2002a).

Mineralogy.—Bimineralic (Carter, Barrera, & Tevesz, 1998). Mineralogical data provided for the family Pectinidae by Carter, Barrera, and Tevesz (1998). Outer shell layer: calcite. Middle and inner shell layers: calcite-aragonite.

Family ENTOLIIDAE Teppner, 1922

Syncyclonemidae Waller, 1978

In recent years, various genera for different groups of species that were traditionally referred to *Entolium* were proposed. This is very similar to what happened to the family Halobiidae, but there is no consensus about which characters should be used to discriminate between different taxonomic levels (see Damborenea, 2002a, p. 42–44, for a full discussion on the subject). Features that are distinctive at species level, according to some authors (see Johnson, 1984), are used by others to discriminate at genus level (Damborenea, 2002a): the presence or absence of lateral internal ribs; the presence or absence of byssal notch; and dorsal projection of the auricles. Furthermore, some surface shell structures are used at genus level, even if they are strongly influenced by diagenetic processes (Johnson, 1984; Damborenea, 2002a). In the absence of a good review on the subject, we are not taking into account the genera listed below (see discussion for each of them in Genera not Included, p. 156), since their proposition was based, in most cases, on diagnostic characters that are used by most authors at species level, and they can all be grouped under Staesche's (1926) original concept of *Entolium*: *Costentolium* Freneix, 1980, p. 89; *Cingentolium* Yamani, 1983, p. 6; *Neoentolium* Romanov, 1985, p. 37; *Cornutoentolium* Romanov, 1985, p. 52 (Upper Jurassic); *Calvaentolium* Romanov, 1985, p. 35; and *Palaeentolium* Romanov, 1985, p. 35. All of these

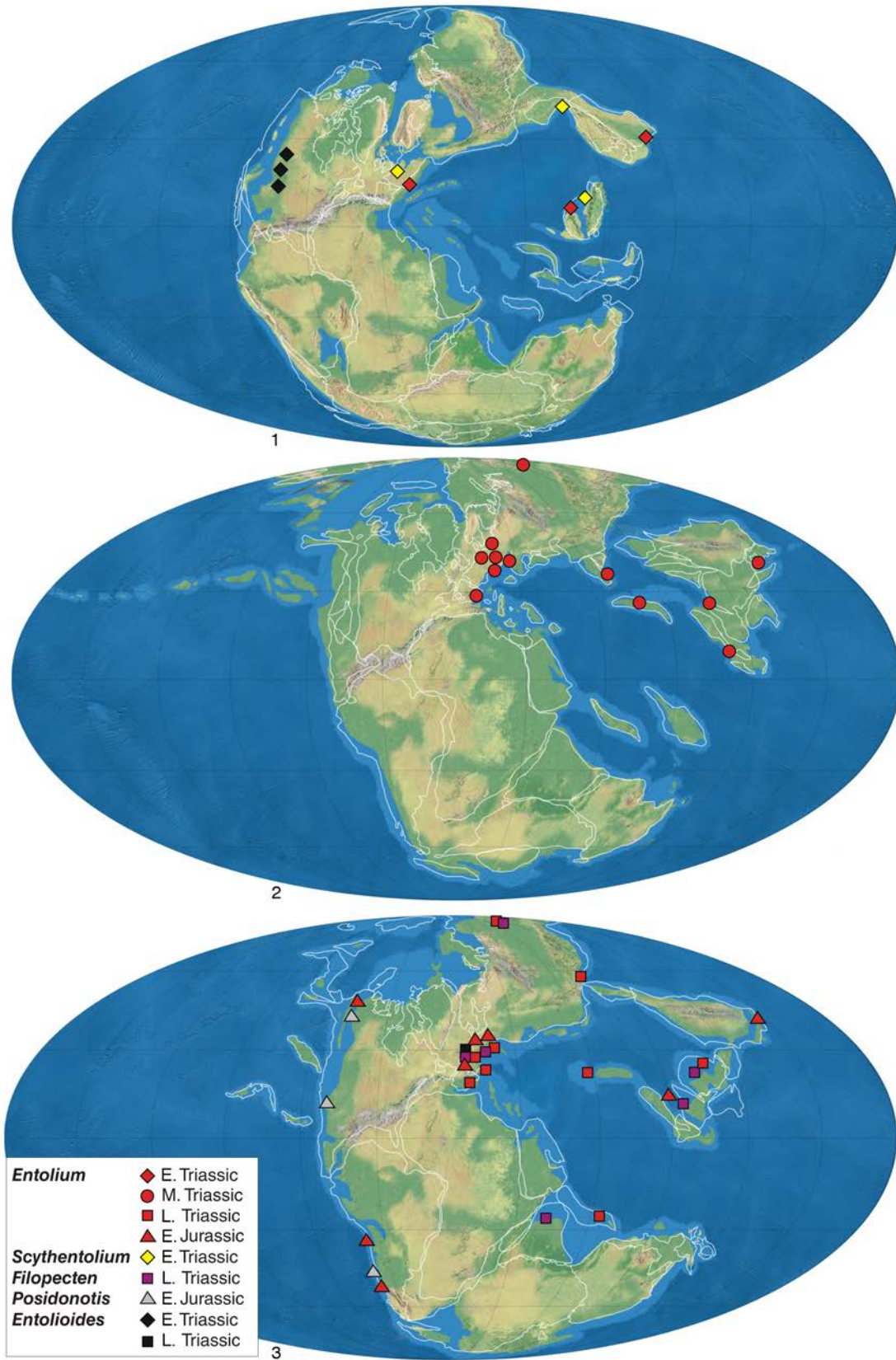


Figure 37. Paleogeographical distribution of Entoliidae (*Entolium*, *Scythentolium*, *Filopecten*, *Posidonotis*, *Entolioides*). 1, Early Triassic; 2, Middle Triassic; 3, Late Triassic–Early Jurassic.

nominal genera, except *Cornutoentolium*, were recorded as being in our study interval.

Waller (2006) proposed a new family, Entoliolidae Waller, 2006 and included within it the genera *Filopecten* Allasinaz, 1972, p. 301; *Entolioides* Allasinaz, 1972, p. 295; *Scythentolium* Allasinaz, 1972, p. 308; and *Calvaentolium* (= *Crenamussium* Newton in Newton & others, 1987, p. 46), thus grouping the old Triassic entoliids with filous structure and a deep byssal notch, and lacking internal ribs. Waller (2006) regarded this family as the link between *Pernopecten* and Mesozoic pectinids. On the other hand, other authors (H. Yin, 1983; Nakazawa, 1996) argued that the distinction between *Pernopecten* and *Entolium* is just a matter of convenience, using the first name for Paleozoic specimens and the second for Mesozoic ones. In fact, H. Yin (1983) reported *Entolium* from the upper Permian, like other authors, and Nakazawa (1996) reported *Pernopecten* from the Lower Triassic. This issue remains unresolved until future research is done. We provisionally follow Newell and Boyd (1995) in their suggestion that *Pernopecten* was a Paleozoic genus.

In view of the significant discrepancies between different authors, this discussion is beyond the purpose of this study, and, while there is no consensus on the diagnostic characters for each taxonomic level, we regard *Entolium* in its original sense (see Damborenea [2002a] for Staesche's concept [1926]).

Genus ENTOLIUM Meek, 1865, p. 478

Type species.—*Pecten demissus* Meek, 1865, p. 478.

Stratigraphic range.—Lower Triassic–Upper Cretaceous (Maastrichtian) (Allasinaz, 1972; Abdel-Gawad, 1986). Cox and others (1969) assigned it a Middle Triassic–Upper Cretaceous range. The youngest record is from the Maastrichtian (Abdel-Gawad, 1986) and the oldest one from the Lower Triassic (*E. discites* Schlothheim, 1820).

Paleogeographic distribution.—Cosmopolitan (Fig. 37). In the Boreal domain, in addition to the Triassic, it was also recorded in the Early Jurassic (Kurushin, 1990; Polubotko & Repin, 1990), but the specimens were not figured or discussed. Milova (1976) reported it from the Pliensbachian and Milova (1988) from the Toarcian of northeastern Russia.

Tethys domain: Early Triassic: Italy (Allasinaz, 1972; Neri & Posenato, 1985), China (C. Chen, 1982; S. Yang, Wang, & Hao, 1986); Middle Triassic: Hungary (Allasinaz, 1972; Szente, 1997), Germany (Bachmann, 1973; Hagdorn, 1995), Poland (Senkowitzowa, 1985); Anisian of Italy (Allasinaz, 1972; Posenato, 2008b), China (Gu & others, 1976; Sha, Chen, & Qi, 1990; J. Chen, 2003), Bulgaria (Tronkov & Damyanov, 1993), Bosnia and Yugoslavia (Allasinaz, 1972), northern Vietnam (Komatsu, Huyen, & Huu, 2010); Ladinian of Spain (Márquez-Aliaga, 1983, 1985; Márquez-Aliaga & Montoya, 1991; Budurov & others, 1991; López-Gómez & others, 1994), China (Gu & others, 1976), Malaysia (Tamura, 1973), Italy (Rossi Ronchetti, 1959; Allasinaz, 1972), northern Vietnam (Komatsu, Huyen, & Huu, 2010), Afghanistan (Farsan, 1972); Late Triassic: Carnian of the Alps (Allasinaz, 1966, 1972; Fürsich & Wendt, 1977; Hautmann, 2001b), Spain (Martín-Algarra, Solé de Porta, & Márquez-Aliaga, 1995), China (Gu & others, 1976; Sha, Chen, & Qi, 1990); Norian of China (Lu, 1981); Norian–Rhaetian of Iran (Hautmann, 2001b); Rhaetian of ?Tibet (“Lhasa Block”) (J.

Yin & Grant-Mackie, 2005), Alps (Vörös, 1981; Hautmann, 2001b), Hungary (Vörös, 1981; Hautmann, 2001b), Italy (Sirna, 1968); Early Jurassic: Hettangian of the Alps (Johnson, 1984), Germany and France (Vörös, 1971; Johnson, 1984), Vietnam (Vu Khuc & Huyen in Sato & Westermann, 1991).

Circumpacific domain: Early Triassic: Olenekian of Japan (Nakazawa, 1961; Hayami, 1975; Kashiyama & Oji, 2004); Middle Triassic: Japan (Hayami, 1975; Tamura & others, 1978); Early Jurassic: Hettangian of Chile (Hillebrandt, 1990); Hettangian–Sinemurian of Canada (Aberhan, 1998a; Aberhan, Hrudka, & Poulton, 1998), Chile (Aberhan, 1993, 1994a); Sinemurian of Japan (Hayami, 1975), Canada (Poulton, 1991).

Austral domain: Early Jurassic: Sinemurian of Argentina (Damborenea, 2002a; Damborenea & Manceñido, 2005b).

Boreal domain: Middle Triassic: Anisian of Siberia (Dagys & Kurushin, 1985); Late Triassic: Carnian of Primorie (Kiparisova, 1972); Norian of Siberia (Okuneva, 1985).

Paleoautoecology.—B, E, S, Un, FaM-Sed; R-Sw. Young specimens of *Entolium s.s.* had a byssal notch, but this was lost in adult stages. The life habit also probably changed from epibyssate in early stages to reclined in the upper ones. The low convexity of the shell, its reduced thickness, its circular outline, and the wide umbonal angle are characteristics that indicate it could have been a good swimmer, like some living pectinids (Johnson, 1984). However, in our provisional, broad concept of *Entolium*, there are some species that retained the byssal notch until the adult stages and therefore were epibyssate their entire lives.

Mineralogy.—Bimineralic (Carter, 1990a, p. 257). The family Entoliidae is characterized by bimineralic mineralogy (Carter, 1990a), with different microstructure types in juveniles and adults (homogeneous, simple prismatic, foliated, and fibrous prismatic), and a cross-lamellar inner shell layer (see Allasinaz, 1972; Waller, 1978; Johnson, 1984, among others, for more information).

Genus SCYTHENTOLIUM Allasinaz, 1972, p. 308

Type species.—*Pecten tirolicus* Wittenburg, 1908, p. 23.

Stratigraphic range.—Lower Triassic (Allasinaz, 1972). Allasinaz (1972) proposed the genus *Scythentolium*, including several Lower Triassic species: *S. eurasiaticum* (Wittenburg, 1908); *S. kokeni* (Wittenburg, 1909); *S. longauris* (Wittenburg, 1908); *S. rombergi* (Wittenburg, 1908); *S. sojale* (Wittenburg, 1908); *S. subtile* (Wittenburg, 1908); and *S. tirolicum* (Bittner, 1895).

Paleogeographic distribution.—Tethys (Fig. 37). Although Allasinaz (1972) assigned it a cosmopolitan distribution, the species included within *Scythentolium* were only reported from the southern Alps and Salt Range (Pakistan).

Tethys domain: Early Triassic: Alps (Diener, 1923; Allasinaz, 1972; Neri & Posenato, 1985; Broglio-Loriga & others, 1990; Fraiser & Bottjer, 2007a), China (Lu & Chen, 1986), Pakistan (Diener, 1923; Allasinaz, 1972; Nakazawa, 1996); Induan of southern China (Hautmann & others, 2011).

Paleoautoecology.—B, E, S, Epi, Sed; By. Its external morphology is similar to *Entolium*, but it had a byssal notch in the adult stage and had unequal auricles (Allasinaz, 1972), so we assume an epibyssate mode of life for *Scythentolium*.

Mineralogy.—Bimineralic (Carter, 1990a, p. 257). See mineralogy for *Entolium* (p. 105).

Genus FILOPECTEN Allasinaz, 1972, p. 301

Type species.—*Pecten filusus* Hauer, 1857, p. 30.

Remarks.—Allasinaz (1972) included in *Filopecten* the following species: *F. filusus* (Hauer); *F. schlosseri* (Woehrmann); *F. incognitus* (Bittner); *F. azzarolae* (Stoppani); *F. helii* (Emmrich); *F. aff. discites* (Cox); *F. fimbriatus* (Mansuy); *F. quotidianus* (Healey); *F. kolymaensis* (Kiparisova); and with doubts, *Pecten rosaliae* (Salomon, 1895). However, Waller (in Waller & Stanley, 2005) suggested that the last species should not be included, since, among other differences, it has a ctenolium, which is absent in all members of family Entoliidae. *Filopecten* is very similar to *Entolium* concerning the shape of the auricles, the general external form, and even the hinge, and they differ in the byssal notch and ornamentation (Allasinaz, 1972). According to Hautmann (2001b), these features should not be used for generic distinction within the family. In fact, Hautmann (2001b) included the species *incognitum* (Bittner, 1901c), which was transferred to *Filopecten* by Allasinaz (1972), into *Entolium* (*Entolium*).

Stratigraphic range.—Upper Triassic (Carnian–Rhaetian) (Allasinaz, 1972). According to the species listed by Allasinaz (1972), the genus had an Upper Triassic range.

Paleogeographic distribution.—Tethys and Boreal (Fig. 37).

Tethys domain: Late Triassic: China (Diener, 1923); Carnian of the Alps and Hungary (Allasinaz, 1972); Rhaetian of the Alps and Hungary (Allasinaz, 1972), Burma (Healey, 1908), Indochina (Allasinaz, 1972).

Boreal domain: Late Triassic: Siberia (Allasinaz, 1972).

Paleoautoecology.—B, E, S, Epi, Sed; By. Similar to *Scythentolium*.

Mineralogy.—Bimineralic (Carter, 1990a, p. 257). See mineralogy for *Entolium*.

Genus POSIDONOTIS Losacco, 1942, p. 11

Type species.—*Posidonotis dainelii* Losacco, 1942, p. 11.

Remarks.—Following Damborenea (1986, 1987b), we regard *Pectinula* A. F. Leanza, 1943, p. 241, as a junior synonym of *Posidonotis* (see discussion for *Pectinula* in Genera not Included, p. 167), and we include *Posidonotis* in the family Entoliidae, although not all authors agree with this (see Hayami, 1988; Aberhan, 1994a, 1998a; Monari, 1994; Waller, 2006). Cox and others (1969), as well as most mentioned authors, included it within the family Posidoniidae. *Pectinula* was assigned to Pectinidae by A. F. Leanza (1943), and this was followed by Cox and others (1969).

Stratigraphic range.—Lower Jurassic (Sinemurian–Toarcian) (Damborenea, 1987b). Cox and others (1969) assigned *Posidonotis* to the Middle Jurassic (Aalenian) and *Pectinula* to the Lower Jurassic. The range assigned by Cox and others (1969) to *Posidonotis* was taken from Losacco (1942), who reported it from Aalenian deposits, but these were later redated as Toarcian (see Damborenea, 1987b, p. 192–193).

Paleogeographic distribution.—Circumpacific (Fig. 37). During our study interval, it was only present on the eastern coast of the Paleopacific, but during the Pliensbachian its distribution was broader (see Damborenea, 1986, 1987b; Hayami, 1988; Monari, 1994).

Circumpacific domain: Early Jurassic: Sinemurian of Chile (Aberhan, 1994a, 1998a), California (United States) and British Columbia (Canada) (Damborenea, 1986, 1987b; Aberhan & Pálffy, 1996).

Paleoautoecology.—B, E, S, Un, Sed; R. Several authors (e.g., Hayami, 1969a, 1988; Hillebrandt, 1981) suggested a pseudoplanktonic mode of life for *Posidonotis*, because it is often found in black shales with no associated benthic fauna. This mode of life is unlikely, because byssal structures are not present in adult specimens, although juveniles had them. In addition, other modes of life have been suggested, as nektoplanktonic, benthic with chemosymbiotic organisms, or teleplanic larvae (see Aberhan & Pálffy, 1996). However, the most plausible mode of life during the adult stages is reclining on soft substrates; in young stages, it was a byssate bivalve (Aberhan & Pálffy, 1996). Some species are interpreted as opportunistic, as they were recorded in great abundance in facies poor in oxygen, where only ammonoids are found (Damborenea, 1987b; Aberhan & Pálffy, 1996).

Mineralogy.—Bimineralic (Carter, Barrera, & Tevesz, 1998). See mineralogy for *Entolium*.

Genus ENTOLIOIDES Allasinaz, 1972, p. 295

Type species.—*Pecten zitteli* Wöhrmann & Koken, 1892, p. 173.

Stratigraphic range.—Lower Triassic–Upper Triassic (Carnian) (Allasinaz, 1972; Newell & Boyd, 1995). Allasinaz (1972) assigned to *Entolioides* a Middle–Upper Triassic range, but all species he included were only recorded from Carnian deposits [*E. deeckei* (Parona, 1889); *E. lavaredanus* (Frech, 1904); *E. porschei* (Toula, 1913); *E. setinus* (Gortani, 1902); *E. subdemissus* (Münster, 1841); and *E. zitteli* (Wöhrmann & Koken, 1892)], according to the range listed on p. 222 of his monograph. Newell and Boyd (1995) reported the type species (*Pecten zitteli*) from the Middle Triassic of the Alps, but Allasinaz (1972) reported it from the Carnian of the southern Alps, and we only found it mentioned from this stage. Newell and Boyd (1995) reported the species *Entolioides utahensis* (Meek, 1877) from the Lower Triassic of the Thaynes Formation.

Paleogeographic distribution.—Tethys and Circumpacific (Fig. 37).

Tethys domain: Late Triassic: Carnian of the Alps (Allasinaz, 1972).

Circumpacific domain: Early Triassic: Idaho, Montana, and Nevada (United States) (Newell & Boyd, 1995).

Paleoautoecology.—B, E, S, Epi, FaM; By-Sw. Two groups can be distinguished within pectinoideans regarding their mode of life (S. M. Stanley, 1972): some are epibyssate, and they are characterized by different convexity in both valves, the anterior auricle being more developed, and a byssal sinus throughout their ontogeny; others, with more symmetrical shell with both valves similarly convex, have auricles of the same shape and size, and an umbonal angle greater than 90°, are also epibyssate but with the ability to swim. Both valves in *Entolioides* were nearly equally convex, with subequal auricles, an umbonal angle between 85° and 120°, and a small byssal notch (Allasinaz, 1972). According to these features, *Entolioides* belongs to the second group.

Mineralogy.—Bimineralic (Carter, Barrera, & Tevesz, 1998). See mineralogy for *Entolium* (see p. 105).

Superfamily KALENTEROIDEA Marwick, 1953

According to Z. Fang and Morris (1997) and Damborenea (2004), the classification of the superfamily Kalenteroidea Marwick, 1953, is modified with respect to Amler (1999); we consider the family Permophoridae Poel, 1959, as a synonym of Kalenteridae Marwick, 1953. Several genera assigned to this family are very similar to each other, both externally and internally (hinge details and muscle impressions) (Damborenea, 2004).

Family KALENTERIDAE Marwick, 1953

(=Permophoridae Poel, 1959)

Genus PERMOPHORUS Chavan, 1954, p. 200

nom. nov. pro Pleurophorus King, 1844, p. 313, *non* Mulsant, 1842, p. 312

Type species.—*Arca costata* Brown, 1844, p. 66.

Stratigraphic range.—Carboniferous (Mississippian)—Lower Triassic (Olenekian) (Hoare, Heaney, & Mapes, 1989; Newell & Boyd, 1999). Cox and others (1969) assigned it a Lower Carboniferous–Permian range. For a long time, it was regarded as an exclusively Paleozoic genus, but recently, it was also reported from the Triassic. We are only taking into account the Triassic record in Newell and Boyd (1999), since other records have some problems we cannot solve now. Newell and Boyd (1999) warned about the misunderstanding of the *Permophorus* hinge details in Cox and others (1969). Based on this interpretation, Waterhouse (1979b) described Lower Triassic specimens from New Zealand that were subsequently assigned to the Middle Triassic (H. J. Campbell, 1984). Although other species were reported from the Lower Triassic (see Newell & Boyd, 1999), they were based on poorly preserved material. In addition, *Permophorus* was also reported from the Upper Triassic (Rhaetian) by Ivimey-Cook and others (1999), but these authors pointed out that the assignment was doubtful, since they did not observe the hinge of their specimens. Skwarko (1967) referred his Carnian and Norian specimens from New Guinea to *Permophorus? hastatus*, but later, Skwarko (1983) designated this as type species of his new genus *Somareoides* Skwarko, 1983.

Paleogeographic distribution.—Circumpacific (Fig. 38). In our study interval, it was only known from the Circumpacific domain. Fraiser and Bottjer (2007a) also listed it from the Triassic of Italy, but they did not figure or describe the specimens.

Circumpacific domain: late Permian: Japan (Nakazawa & Newell, 1968; Hayami & Kase, 1977); Early Triassic: Olenekian of Utah, Wyoming, Idaho, and Montana (United States) (Newell & Boyd, 1999), ?Idaho (United States) (Ciriacks, 1963), western United States (Boyer, Bottjer, & Droser, 2004; Fraiser & Bottjer, 2007a).

Paleoautoecology.—B, Is, S, Endo-Un, Sed-SM; By-Sb. *Permophorus* had some characteristics that indicate a shallow burrowing habit. It had an equivalve, inequilateral, and elongated shell, with prosogyrous beaks, lunule, and escutcheon that, according to S. M. Stanley (1975), facilitates burial. No pallial sinus is observed, so if siphonate, siphons would have been very short. According to Quiroz-Barroso and Perrilliat (1998), *Permophorus* was an endobysate

bivalve, but none of the specimens described in the literature show a byssal notch or gape. However, S. M. Stanley (1972) noted that at least the type species had a reduced anterior part, which suggests the presence of a byssus.

Mineralogy.—Aragonitic (Carter, 1990a, p. 271). Outer shell layer: aragonite (fibrous-prismatic). Middle shell layer: aragonite (cross-lamellar). Inner shell layer: aragonite (homogeneous).

Genus CURIONIA Rossi Ronchetti in Rossi Ronchetti & Allasinaz, 1965, p. 366

Type species.—*Myoconcha curionii* Hauer, 1857, p. 561.

Stratigraphic range.—Lower Triassic (?)–Upper Triassic (Rhaetian) (Rossi Ronchetti & Allasinaz, 1965). Rossi Ronchetti (in Rossi Ronchetti & Allasinaz, 1965) proposed *Curionia* and assigned it a Triassic (Scythian–Rhaetian) range. When listing the included species, she first mentioned those that were contemporaneous with the type species (Carnian), and then the other Triassic species; so, in her list, the first recorded species is Carnian and the last is Rhaetian. Perhaps because of this arrangement, Cox and others (1969) considered the genus to be present only in the Late Triassic, or maybe they simply disagreed with the species listed by the author of the genus. We assign to *Curionia* the stratigraphic range given by its original authors.

Paleogeographic distribution.—Tethys (Fig. 38). *Curionia* was only known from the Tethys domain. It was reported from the Early Jurassic of Nevada (Laws, 1982), but Hallam and Wignall (2000) argued that Laws probably confused *Curionia* with *Modiolus*, which is very abundant in the area, since *Curionia* was a European genus that disappeared in the Late Triassic. However, Stiller and Chen (2006) reported it from the Anisian of China.

Tethys domain: Early Triassic: Olenekian of ?Bakony (Hungary) (Frech, 1907; Rossi Ronchetti & Allasinaz, 1965); Middle Triassic: Anisian of China (Stiller & Chen, 2006), Italy (Rossi Ronchetti & Allasinaz, 1965); Muschelkalk of Germany (Rossi Ronchetti & Allasinaz, 1965); Ladinian of Italy (Posenato, 2002); Late Triassic: Carnian of the Alps (Rossi Ronchetti & Allasinaz, 1965); Norian of Italy (Rossi Ronchetti & Allasinaz, 1965); Rhaetian of Italy (Stoppani, 1860–1865; Rossi Ronchetti & Allasinaz, 1965), Iran (Repin, 2001).

Paleoautoecology.—B, Is-Se, S, Endo-Un, Sed-SM; By-Sb. Like all Kalenteridae genera, the external morphology of *Curionia* indicates a shallow infaunal or semi-infaunal mode of life. By analogy with *Modiolus*, it could perhaps have been an endobysate bivalve.

Mineralogy.—Aragonitic (Schneider & Carter, 2001). Outer shell layer: aragonite (prismatic). Middle shell layer: aragonite (cross-lamellar). Inner shell layer: aragonite (prismatic).

Genus TRIAPHORUS Marwick, 1953, p. 69

Type species.—*Pleurophorus zealandicus* Trechmann, 1918, p. 212.

Stratigraphic range.—Upper Triassic (Carnian–Norian) (H. J. Campbell, 1984). Marwick (1953) proposed *Triaphorus* from Carnian deposits. Subsequently, Cox and others (1969) assigned it an Upper Triassic range. Grant-Mackie (1960) reported it from Otapirian (=Rhaetian) and Warepan (=Norian) of New Zealand, but he did not figure the specimens and based his record on a personal communication from J. D. Campbell. Moreover, H. J. Campbell

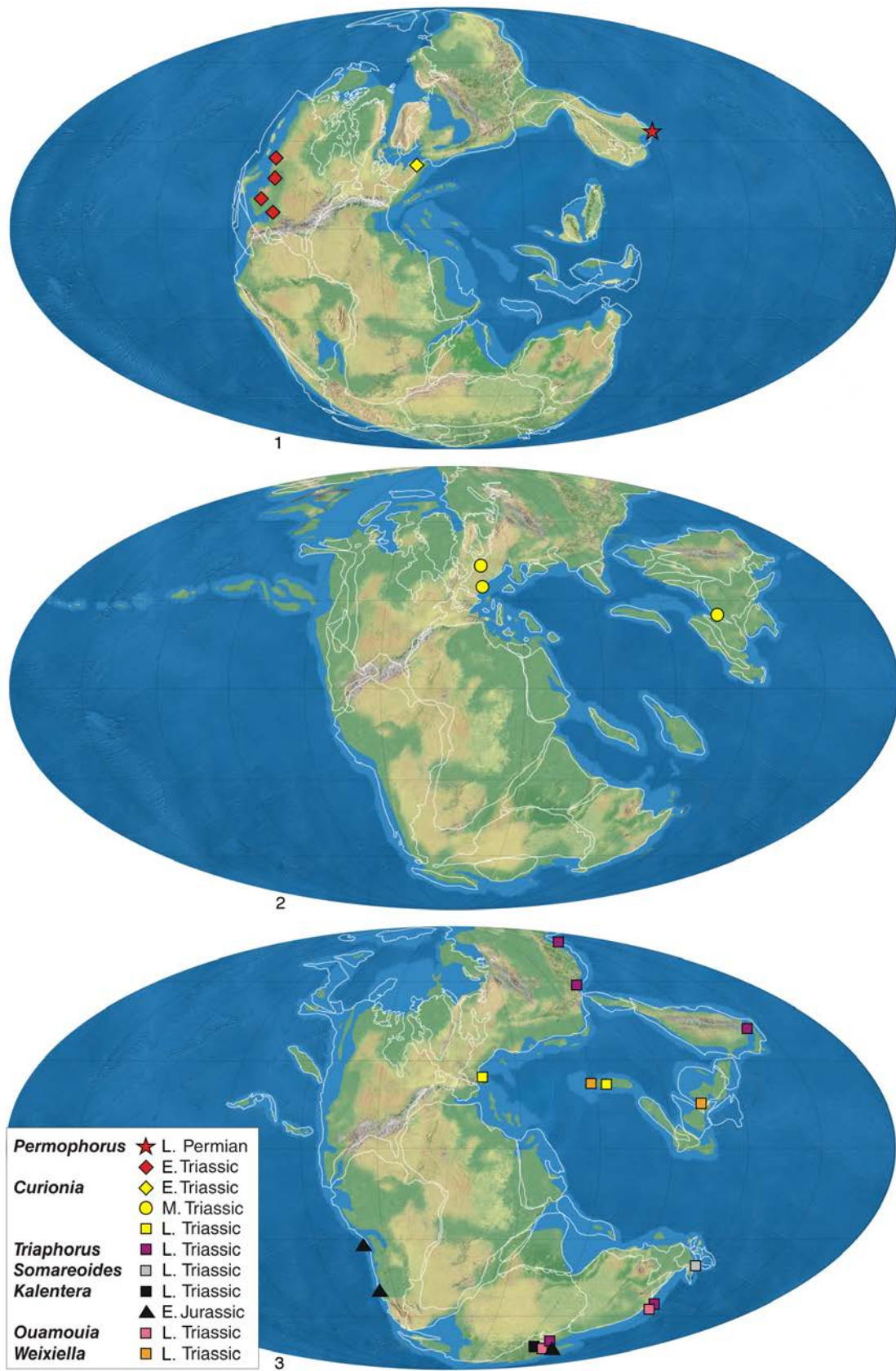


Figure 38. Paleogeographical distribution of Kalenteridae (*Permophorus*, *Curionia*, *Triaphorus*, *Somareooides*, *Kalentera*, *Ouanouia*, *Weixiella*). 1, Early Triassic; Middle Triassic; 3, Late Triassic–Early Jurassic.

(1984) mentioned the genus from the upper ?Carnian–Norian, but neither figured nor described the material, although he mentioned several references. Following H. J. Campbell (1984), we assign it a Carnian–Norian range.

Paleogeographic distribution.—Austral, Boreal, and Circumpacific (Fig. 38). *Triaphorus* was distributed in the Austral and Circumpacific domains and doubtfully in Boreal regions as well. When the specimens are not well preserved and the hinge is not seen, it is difficult to distinguish between *Triaphorus* and *Kalentera* (Damborenea, 2004). This latter genus had a bipolar distribution during the Jurassic, but during the Late Triassic, it was only known from the Austral domain. It is necessary to check if the Boreal records of *Triaphorus* can be confirmed and if the specimens show the diagnostic characters.

Austral domain: Late Triassic: Carnian of New Zealand (Trechmann, 1918; Marwick, 1953); Carnian–Norian of New Zealand and New Caledonia (H. J. Campbell, 1984).

Boreal domain: Late Triassic: northeastern Russia (Kiparisova, Bychkov, & Polubotko, 1966); Carnian of Primorie (Kiparisova, 1972).

Circumpacific domain: Late Triassic: Carnian of Japan (Kobayashi & Ichikawa, 1950; Hayami, 1975).

Paleoautoecology.—B, Is-Se, S, SM; Sb. *Triaphorus* is externally similar to *Permophorus* and *Kalentera*. It had a modioliform shell, and, in the genus diagnosis offered by Marwick (1953), the presence of a pedal muscle scar is pointed out. Since no pallial sinus and no evidence of byssate habit are listed, we assume that it was a shallow burrower belonging to the shallow infauna or semi-infauna (Grant-Mackie, 1960).

Mineralogy.—Aragonitic (Carter, 1990a, p. 270). According to Carter (1990a), although the shell mineralogy of *Triaphorus* and other members of the family Kalenteridae is unknown, its mode of preservation suggests an original aragonitic mineralogy.

Genus SOMAREOIDES Skwarko, 1983, p. 67

Type species.—*Permophorus? hastatus* Skwarko, 1967, p. 66.

Remarks.—Skwarko (1967) tentatively included the species *hastatus* Skwarko, 1967, in *Permophorus*, as only external structures could be observed in his specimens. The discovery of new material with well-preserved hinge confirmed that this species does not belong to *Permophorus* nor to any previously known genus (Skwarko, 1983).

Stratigraphic range.—Upper Triassic (Carnian) (Skwarko, 1983). Although Skwarko (1967) assigned a Carnian–Norian range to the type species, when he proposed *Somareoides* (Skwarko, 1983), he noted that the most likely age was Carnian.

Paleogeographic distribution.—Southern Tethys (Fig. 38).

Tethys domain: Late Triassic: Carnian of Papua New Guinea (Australian province according to Damborenea, 2002b) (Skwarko, 1967, 1983).

Paleoautoecology.—B, Se, S, Endo-Un, Sed-SM; Sb. According to Skwarko's (1983) description, *Somareoides* had an inequivalve and modioliform shell, with developed anterior part and elongated posterior one. With these characteristics, its mode of life should be similar to other family members. It was probably a semi-infaunal bivalve.

Mineralogy.—Aragonitic (Carter, 1990a, p. 270). See mineralogy for *Triaphorus* (p. 107).

Genus KALENTERA Marwick, 1953, p. 108

Type species.—*Kalentera mackayi* Marwick, 1953, p. 108.

Stratigraphic range.—Upper Triassic (Norian)–Lower Jurassic (Toarcian) (Grant-Mackie, 1960). Marwick (1953) proposed *Kalentera* and included two new species, *K. mackayi* from the Lower Jurassic and *K. flemingi* from the Temaikan (Bathonian). Later, Grant-Mackie (1960) indicated that the beds that Marwick (1953) referred to as Temaikan were Ururoan instead (= Pliensbachian–Toarcian), and he proposed another new species within the genus, *K. marwicki* from the Otapirian (=Rhaetian). He also mentioned the genus from Warepan (=Norian) as being associated with *Monotis calvata* Marwick, 1953. Cox and others (1969) assigned *Kalentera* a Lower Jurassic range and Sepkoski (2002) assigned it an Upper Triassic (upper Carnian)–Middle Jurassic (Bathonian) range, following Hallam (1977). Hallam mentioned the genus from the Middle Jurassic, but not in the Carnian. H. J. Campbell (1984) assigned it a Norian–Bathonian range. Following Grant-Mackie (1960), we assign it a Norian–Toarcian range.

Paleogeographic distribution.—Austral and Circumpacific (Fig. 38). Although originally thought to be endemic to the Austral domain, new records showed that *Kalentera* was endemic to the southern domain (Maorian Province) during the Late Triassic and had a bipolar distribution (at high latitudes) during the Early Jurassic (Damborenea, 2001, 2002b, 2004) (see also *Triaphorus* paleogeographic distribution, p. 107). Boreal records date from the Pliensbachian (Damborenea, 2004; Zakharov & others, 2006), and, therefore, they are not taken into account here. D. G. Taylor and Guex (2002) included their new species *K. lawsi* Taylor & Guex, 2002, from the Triassic–Jurassic boundary beds of Oregon in *Kalentera*, but this assignment is tentative, because their specimens did not show hinge details. Damborenea (2004) noticed that those specimens were previously allocated to *Curionia* sp. by Laws (1982), and, later, D. G. Taylor, Boelling, and Guex (2000) assigned them to *Kalentera?* sp. However, Hallam and Wignall (2000) considered that Laws's (1982) "*Curionia*" specimens could probably refer to *Modiolus*, a genus very abundant in the area. Laws (1982) did not figure the specimens, and those figured by D. G. Taylor and Guex (2002) are unconvincing.

Circumpacific domain: Early Jurassic: Sinemurian of northern Chile (Covacevich, Pérez, & Escobar, 1991).

Austral domain: Late Triassic: Norian–Rhaetian of New Zealand (Grant-Mackie, 1960; MacFarlan, 1998); Early Jurassic: Hettangian–Sinemurian of New Zealand (Marwick, 1953), Argentina (Damborenea, 2004).

Paleoautoecology.—B, Se-Is, S, SM; Sb. *Kalentera* shell morphology indicates that it was probably a shallow burrower that lived wholly or partly buried in the sediment (Grant-Mackie, 1960; H. J. Campbell, 1984; Damborenea, 2004). The inferred environment of the fossil-bearing beds indicates that stability and type of substrate limited the distribution of this genus (Damborenea, 2004) in nearshore deposits. According to Grant-Mackie (1960), the absence of excavated galleries in the sediment and of a pallial sinus suggests *Kalentera* lacked siphons (or perhaps they were too short), and therefore it would have been a very shallow burrower.

Mineralogy.—Aragonitic (Carter, 1990a, p. 270; Damborenea, 2004). In *Kalentera* (or other members of the family Kalenteridae), the shell mineralogy is unknown, although, according to Carter (1990a), its mode of preservation suggests an original aragonitic

mineralogy. Furthermore, Damborenea (2004, fig. 4b) showed a hexagonal dissolution pattern for one of her specimens, which can be interpreted as a relict aragonitic nacreous trace in the inner shell layer.

Genus OUAMOUIA H. J. Campbell, 1984, p. 158

Type species.—*Ouamouia grantmackiei* H. J. Campbell, 1984, p. 159.

Remarks.—H. J. Campbell (1984) included *Ouamouia* in the family Permophoridae (=Kalenteridae) and related it mainly to *Permophorus* and *Kalentera*. However, Damborenea (2004) argued that *Ouamouia* is quite different from *Kalentera*, and its massive hinge dentition and other characters indicate it was a cardiniid.

Stratigraphic range.—Upper Triassic (Norian–Rhaetian) (H. J. Campbell, 1984). This monospecific genus was described by H. J. Campbell (1984) from Norian–Rhaetian beds.

Paleogeographic distribution.—Austral (Fig. 38).

Austral domain: Late Triassic: Norian–Rhaetian of New Zealand and New Caledonia (H. J. Campbell, 1984).

Paleoautoecology.—B, Is, S, Endo-Un, Sed-SM; By-Sb. *Ouamouia grantmackiei* had a modioliform shell, undefined pallial sinus, lunule, and ornamented shell. These characteristics match well with a shallow burrower mode of life. Probably it lived buried near the surface and possessed short siphons (see H. J. Campbell, 1984, p. 162). Because it had a thick shell and a massive hinge, it probably lived in high-energy environments (H. J. Campbell, 1984). No structure suggesting it was a byssate bivalve is present, but its modioliform shape may indicate this life habit.

Mineralogy.—Aragonitic. There are no data about *Ouamouia* shell mineralogy or microstructure. The shell was probably entirely aragonitic.

Genus WEIXIELLA Guo & Chen in Guo, 1985, p. 187, 268

Type species.—*Weixiella diana* Guo & Chen in Guo, 1985, p. 187.

Remarks.—Guo and Chen (in Guo, 1985) included *Weixiella* in the family Pachycardiidae Cox, 1962, due its resemblance to *Cardiniodes* Kobayashi & Ichikawa, 1952, especially in hinge features. However, Hautmann (2001b) found more similarities with *Permophorus* Chavan, 1954, and included it in the family Permophoridae (=Kalenteridae), although he also indicated some resemblance to the family Unionidae Fleming, 1828. Z. Fang and others (2009) followed the original paper by Guo (1985) and referred it to the family Pachycardiidae.

Stratigraphic range.—Upper Triassic (Norian–Rhaetian) (Hautmann, 2001b). The genus was described from the Upper Triassic of Yunnan (China). Hautmann (2001b) reported it from the Norian–Rhaetian of Iran and also mentioned it from coeval beds in China, referring to the original description of the genus.

Paleogeographic distribution.—Tethys (Fig. 38).

Tethys domain: Late Triassic: Norian–Rhaetian of China (Guo & Chen in Guo, 1985; Hautmann, 2001b), Iran (Hautmann, 2001b).

Paleoautoecology.—B, Is, S, Endo-Un, Sed-SM; By-Sb. *Weixiella* was a suspensorious shallow burrower (Hautmann, 2001b). The external morphology is not very different from the other members of the family Kalenteridae, but the anterior is more lobed. Although structures indicating the presence of byssus were not observed, it might have been endobysate, as were other members of this family.

Mineralogy.—Aragonitic. There are no data about *Weixiella* shell structure. We assigned it aragonitic shell mineralogy, as in other members of the family Kalenteridae.

Family MYOCONCHIDAE Newell, 1957

Genus MYOCONCHA J. de C. Sowerby, 1824, p. 103

Type species.—*Myoconcha crassa* J. de C. Sowerby, 1824, p. 103.

Stratigraphic range.—Upper Triassic (Rhaetian)–Upper Cretaceous (Maastrichtian) (Hodges, 2000). With the inclusion of Triassic species previously assigned to *Myoconcha* into *Curionia* Rossi Ronchetti (in Rossi Ronchetti & Allasinaz, 1965, p. 366) and *Pseudomyoconcha* Rossi Ronchetti (in Rossi Ronchetti & Allasinaz, 1966, p. 1101), *Myoconcha* was restricted to Jurassic onward. Cox and others (1969) assigned it a Lower Jurassic–Upper Cretaceous range, with a doubtful record from the Permian. Even so, some authors maintained its range from the Upper Triassic. Hautmann (2001b) considered *Pseudomyoconcha* to be a subgenus of *Myoconcha* and mentioned it from the Norian and Rhaetian. Hodges (2000) assigned it an Upper Triassic–Upper Cretaceous range and doubtfully extended it to the Permian. Hodges (2000) reported *Myoconcha (Myoconcha) psilonoti* Quenstedt, 1856 in 1856–1858, from the Rhaetian of England, and it was also mentioned from the Rhaetian of the Apennines (Diener, 1923). Ivimey-Cook and others (1999) mentioned the same species from the Rhaetian of England, but the figured specimen does not show the hinge, a character critical to distinguish it from other Myoconchidae. Other authors (e.g., Zorn, 1971; Busse & Horn, 1978; Malinowskiej, 1979) mentioned Triassic species assigned to *Myoconcha* that were transferred to other genera by Rossi Ronchetti and Allasinaz (1965, 1966).

The Permian quotations appeared from the subjective synonymy proposed by Newell (1957), who considered *Labayophorus* Licharew, 1939, upper Permian genus of the Caucasus, as a junior synonym of *Myoconcha*. This seems to have been accepted with reservations by subsequent authors who indicated the doubtful presence of *Myoconcha* in the Permian. Rossi Ronchetti and Allasinaz (1966) noticed that the illustration of the right valve of *Myoconcha*, figured in Newell (1957) and prepared by Cox, is the only existing schematic representation of the right valves of *Myoconcha*. *Labayophorus* and *Myoconcha* are distinguished by the presence of one cardinal tooth in each valve in the former, while the latter has one on the right and two on the left valve. In addition, Rossi Ronchetti and Allasinaz (1966) listed some other differences that could separate the two genera, and they considered *Labayophorus* to be Paleozoic and *Myoconcha* to be Mesozoic, predominantly Jurassic. Some Permian records do not seem to be attributable to *Myoconcha*. Simões and Fittipaldi (1987) reported *Myoconcha* from the Permian, following Mendes (1944), who recorded a doubtful *Myoconcha* sp. from sediments originally dated as Triassic but later proved to be Permian (Simões & Fittipaldi, 1987). Later, Mendes (1945) reassigned these specimens to *Naiadopsis lamellosus* Mendes. Furthermore, Mendes (1944) noticed that Permian specimens attributed to *Myoconcha* are probably *Modiolopsis*. Another Permian record is found in Hayasaka (1967) from Japan, but the only available specimen is strongly deformed and incomplete, and its generic assignment is very doubtful.

Paleogeographic distribution.—Tethys and Austral (Fig. 39).

Tethys domain: Late Triassic: Rhaetian of England (Ivimey-Cook & others, 1999; Hodges, 2000); Early Jurassic: Hettangian–Sine-

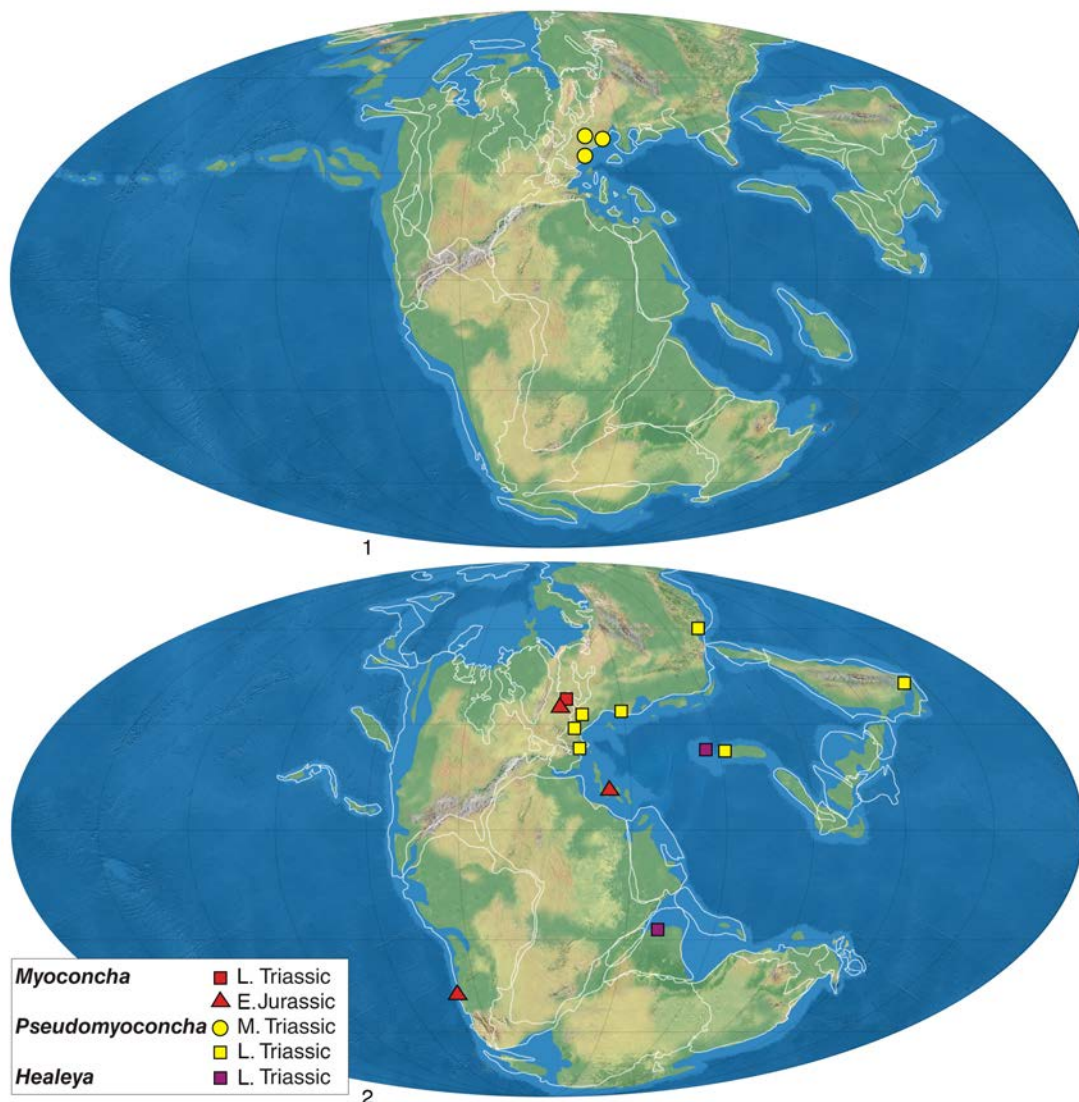


Figure 39. Paleogeographical distribution of Myoconchidae (*Myoconcha*, *Pseudomyoconcha*, *Healeyia*). 1, Middle Triassic; 2, Late Triassic–Early Jurassic.

murian of England (Hodges, 2000; Hallam, 1987); Sinemurian of England (Liu, 1995), Turkey (M. A. Conti & Monari, 1991).

Austral domain: Early Jurassic: Hettangian–Sinemurian of Argentina (Damborenea & Manceñido, 2005b).

Paleoautoecology.—B, Se, S, Endo, Sed; By. According to S. M. Stanley (1972), most species belonging to this genus have a modioliform external appearance, have elongated and prosocline shells, with a reduced anterior part and broad byssal gape, indicating an endobyssate semi-infaunal mode of life, similar to *Modiolus*. Other authors agreed with the attribution of this mode of life (Damborenea in Damborenea & González-León, 1997; Hodges, 2000; Delvene, 2001).

Mineralogy.—Aragonitic (Morris, 1978; Z. Fang & Morris, 1997). According to Morris (1978), *Myoconcha decorata* (Münster, 1837, in Goldfuss, 1833–1841) had a homogeneous shell microstructure, but he noticed that the lack of a prismatic outer shell layer may be due to erosion of the shell. Carter (1990a) suggested that the shell

should be reviewed to observe if there is cross-lamellar structure. Z. Fang and Morris (1997) found remains of cross-lamellar structure preserved in specimens of *Myoconcha saemanni* Loriol.

Genus PSEUDOMYOCONCHA

Rossi Ronchetti in Rossi Ronchetti & Allasinaz, 1966, p. 1101

Type species.—*Myoconcha lombardica* Hauer, 1857, p. 559.

Remarks.—Rossi Ronchetti (in Rossi Ronchetti & Allasinaz, 1966) transferred all Triassic species previously assigned to *Myoconcha* to *Pseudomyoconcha*, except for those she included in *Curionia* (see Rossi Ronchetti & Allasinaz, 1965). Some species were introduced in *Pseudomyoconcha* tentatively, because the hinge (a key character) was not observed. She separated these species into two groups: one containing the species that were consistent with the new genus diagnosis, and another with species that did not fit strictly there but were closer to *Pseudomyoconcha* than to *Myoconcha*.

She noticed that the latter group probably could be recognized as a new taxon but could not see details of the hinge and muscle scars. Hautmann (2001b) argued that differences between *Myoconcha* and *Pseudomyoconcha* are very subtle and decided to keep the second as a subgenus of the first.

Stratigraphic range.—Middle Triassic (Ladinian)—Upper Triassic (Rhaetian) (Rossi Ronchetti & Allasinaz, 1966; Hautmann, 2001b). The range assigned by Rossi Ronchetti (in Rossi Ronchetti & Allasinaz, 1966), according to the species included in the new genus, was Ladinian–Norian. Cox and others (1969) assigned it the same stratigraphic range. The genus was extinguished in the Late Triassic (Hallam, 1981, 2002).

Paleogeographic distribution.—Tethys, Boreal, and Circumpacific (Fig. 39). *Pseudomyoconcha* was reported from the Late Triassic of China (Wen & others, 1976; Lu, 1981; Gou, 1993), but the specimens figured in those papers do not seem convincing. In none is the hinge shown, and the external morphology of the members of the families Myoconchidae and Permophoridae are similar. J. Chen (2003, p. 658, fig. 4.4.2) recorded it from the Anisian and throughout the Late Triassic in southern China, but he did not figure it or indicate the original data source. The presence of *Pseudomyoconcha* in southern China is thus still doubtful.

Tethys domain: Middle Triassic: Ladinian of Hungary, Germany, and Italy (Rossi Ronchetti & Allasinaz, 1966); Late Triassic: Carnian of Italy (Rossi Ronchetti & Allasinaz, 1966), Germany (Linck, 1972), Slovenia and Yugoslavia (Jelen, 1988); Carnian–Norian of Hungary (Rossi Ronchetti & Allasinaz, 1966); Norian–Rhaetian of Iran (Hautmann, 2001b).

Circumpacific domain: Late Triassic: Carnian, ?Norian of Japan (Rossi Ronchetti & Allasinaz, 1966); Norian of western Carpathians (Kollarova & Kochanová, 1973).

Boreal domain: Late Triassic: Primorie (Kiparisova, 1972).

Paleoautoecology.—B, Se, S, Endo, Sed; By. According to the generic diagnosis by Rossi Ronchetti (in Rossi Ronchetti & Allasinaz, 1966), the *Pseudomyoconcha* shell is equivalve, strongly inequilateral, modioliform, and had a byssal notch. With these characteristics, it was most likely an endobysate semi-infaunal bivalve.

Mineralogy.—Aragonitic (Rossi Ronchetti & Allasinaz, 1966; Carter, 1990a, p. 271). Carter (1990a) interpreted the data provided by Rossi Ronchetti and Allasinaz (1966) slightly differently. He identified a fibrous prismatic outer shell layer and a middle shell layer of cross-lamellar structure.

Genus HEALEYA Hautmann, 2001b, p. 108

Type species.—*Modiolopsis gonoides* Healey, 1908, p. 51.

Remarks.—Hautmann (2001b) proposed the genus *Healeya* within the subfamily Myoconchinae. Subsequently, Hautmann (2008) proposed a new family, Healeyidae, to include *Healeya* and other genera. Given the objections with this new family proposition, we consider *Healeya* in its original allocation (see discussion for the family Mysidiellidae Cox, 1964, p. 22).

Stratigraphic range.—Upper Triassic (Norian–Rhaetian) (Hautmann, 2001b, 2008). *Healeya* is a Upper Triassic monospecific genus. Hautmann (2001b) reported from the Norian–Rhaetian of

Iran. The type species was originally described from the Rhaetian of Burma (India) by Healey (1908).

Paleogeographic distribution.—Tethys (Fig. 39). Apart from Iran and Burma, Hautmann (2001b) mentioned the possible occurrence of this genus from the Upper Triassic of Malaysia and Vietnam, due to the doubtful inclusion of two species recorded from that area, in the list of synonyms of the type species.

Tethys domain: Late Triassic: Norian–Rhaetian of Iran (Hautmann, 2001b); Rhaetian of Burma (India) (Healey, 1908).

Paleoautoecology.—B, Se, S, Endo, Sed; By. Hautmann (2001b) found specimens in life position that corroborate what their morphology indicated, i.e., *Healeya* lived semi-infaunally and it was probably an endobysate bivalve. In the anterior part of the shell, the muscle scar of probably a byssal retractor is observed; the byssus would have been strong and protruded from the anterior part of the shell (Hautmann, 2008).

Mineralogy.—Aragonitic (Hautmann, 2008). Although no studies of *Healeya* shell microstructure were performed, the type of recrystallization indicates an aragonitic mineralogy (Hautmann, 2008).

Family HIPPOPODIIDAE Cox in Cox and others, 1969

Genus HIPPOPODIUM J. Sowerby, 1819, p. 91

Type species.—*Hippopodium ponderosum* J. Sowerby, 1819, p. 91.

Stratigraphic range.—Upper Triassic (?Rhaetian)—Upper Jurassic (Tithonian). Cox and others (1969) assigned it a Lower Jurassic range (Hettangian–Pliensbachian) and also considered it to be from the Upper Jurassic (Tithonian). However, Zapfe (1967) suggested the origin of *Hippopodium* in the Rhaetian of the Alps. Hallam and El Shaarawy (1982) also reported it from the Rhaetian of the Alpine region of northwestern Europe, but they did not figure or describe the specimens, nor did Hallam (1981), who quoted it from the Upper Triassic of western Tethys.

Paleogeographic distribution.—Western Tethys and Boreal (Fig. 40). *Hippopodium* was a characteristic genus of the Boreal domain during the Early Jurassic (Sinemurian and Pliensbachian) (Liu, 1995). This author included England in the Boreal domain during this time. This area was on the boundary between the Boreal and Tethys domains, depending on whether their definition is based on bivalves or ammonoids. Hallam (1977) mentioned it from the European province, and, previously, he stated that although it was present in the Tethys domain, records were always from the north (Hallam, 1972).

Tethys domain: Late Triassic: Rhaetian of the ?Alps (Zapfe, 1967); Early Jurassic: Hettangian–Sinemurian of Germany (Arp, 2007).

Boreal domain: Early Jurassic: Sinemurian of England (Liu, 1995).

Paleoautoecology.—B, Se, S, Endo, Sed; By. *Hippopodium* had a lobate anterior part, thick shell, prosogyrous umbones, and a pallial line without sinus. No structures indicating the presence of byssus were observed. It probably lived semiburied.

Mineralogy.—Aragonitic (Morris, 1978; Carter, 1990a; Z. Fang & Morris, 1997). The species *H. ovale* Moore had a homogeneous microstructure in the whole shell (Morris, 1978). Carter (1990a) noticed the need for more careful studies of the shell of this species

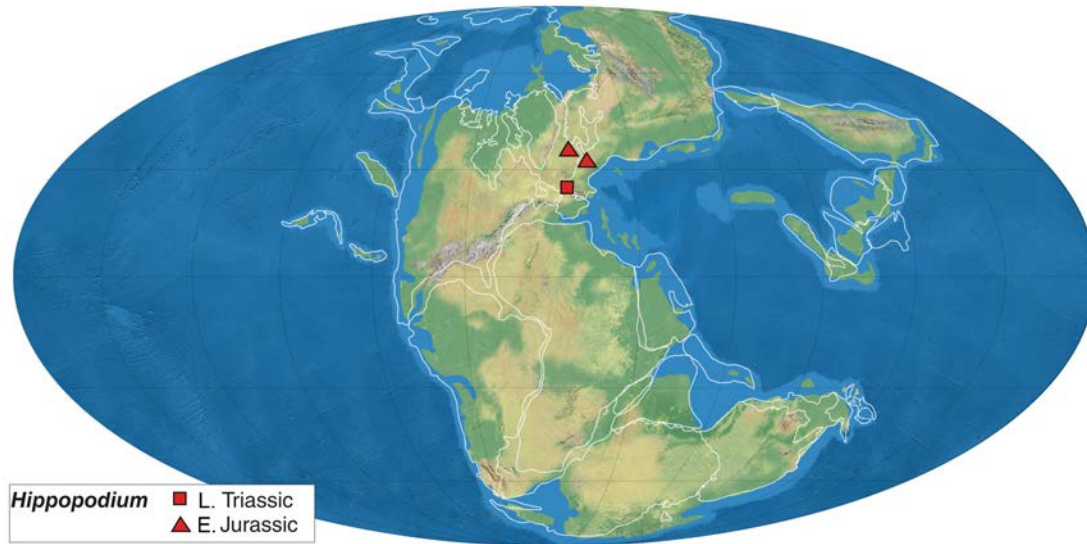


Figure 40. Paleogeographical distribution of Hippopodiidae (*Hippopodium*). Late Triassic–Early Jurassic.

to exclude the presence of cross-lamellar microstructure. Z. Fang and Morris (1997, p. 57) found, in a *H. ponderosum* Sowerby specimen, “patches of ill preserved but distinct crossed-lamellar structure;” but they did not find any trace of cross-lamellar structure in *H. ovale*, while in other species reported from the same beds, this microstructure was perfectly preserved.

Superfamily TRIGONIOIDEA Lamarck, 1819

For the location of genera in the Trigonioidea families, we mainly follow Cox and others (1969), except for families Minetrigoniidae and Myophoriidae, for which we follow Fleming (1987).

Family TRIGONIIDAE Lamarck, 1819

Genus TRIGONIA Bruguière, 1789 in 1789–1792, p. xiv

Type species.—*Venus sulcata* Hermann, 1781, p. 127.

Stratigraphic range.—Middle Triassic (Anisian)–Upper Cretaceous (Cenomanian) (H. A. Leanza, 1993). Cox and others (1969) assigned it a Middle Triassic–Upper Cretaceous range. The Anisian species *Trigonia tabacoensis* Barthel, 1958, is the earliest known species in this genus (Fleming, 1964, 1987; Pérez & Reyes, 1991; Francis & Hallam, 2003). It is difficult to establish the top of the range because, in recent years, many Cretaceous genera related to *Trigonia* were proposed, and many of them were based on type species previously referred to *Trigonia*. Of the subgenera considered by Cox and others (1969), only *T. (Trigonia)* is included here, since *Frenquelliella* A. F. Leanza, 1942, is here regarded as a distinct genus, with *Kumatrighonia* Tamura, 1959, p. 213, as its subgenus. We follow Cox and others (1969) for the top of the range (Cenomanian). *T. (Heslingtonia)* Fleming, 1987, p. 22, is also considered as a subgenus within *Trigonia* in our study interval.

Paleogeographic distribution.—Tethys, Circumpacific, and Austral (Fig. 41). Its distribution is limited during the Triassic to Barthel’s (1958) record from the Anisian. Pérez and Reyes (1991) also reported *Trigonia* from the Upper Triassic and the Early Jurassic of Peru. In

Europe, the family Trigoniidae appears in the Toarcian (Francis & Hallam, 2003). However, Hautmann (2001b) reported the type species of his new subgenus, *Trigonia (Modestella) zlambachensis* Haas, 1909, from the Alpine Rhaetian. Previously, this was reported by Fallahi, Gruber, and Tichy (1983) and Fleming (1987). Moreover, Hautmann (2001b) also quoted this species from the Norian of Vietnam and the Rhaetian of Burma (Malaysia).

Tethys domain: Late Triassic: Norian of Vietnam (Vu Khuc & Huyen, 1998; Hautmann, 2001b; Guo, 1985); Norian–Rhaetian of Iran (Fallahi, Gruber, & Tichy, 1983; Hautmann, 2001b).

Circumpacific domain: Middle Triassic: Anisian of Chile (Barthel, 1958); Late Triassic: Norian of Peru (Pérez & Reyes, 1991); Early Jurassic: Hettangian of Japan (Kobayashi & Kaseno, 1947; Hayami, 1975; Sato & Westermann, 1991); Hettangian–Sinemurian of Peru (Ishikawa & others, 1983; Pérez & Reyes, 1991); Sinemurian of Nevada (United States) (Poulton, 1979).

Austral domain: Middle Triassic: Anisian–Ladinian of New Zealand (Fleming, 1964, 1987).

Paleoautoecology.—B, Is, S, FM; Sb. Many authors have dealt with the mode of life of trigoniids (Tevesz, 1975; S. M. Stanley, 1977, 1978; Kelly, 1995b; Villamil, Kauffman, & Leanza, 1998; Francis & Hallam, 2003). Currently, there is only one genus, *Neotrigonia*, that lives in Australian waters (Beesley, Ross, & Wells, 1998). *Neotrigonia* is infaunal, filtering, and a nonsiphonate, fast, shallow-burrowing bivalve, which lives partially buried near the surface of the sediment (Tevesz, 1975). Mesozoic trigoniids probably had this same way of life, by analogy with *Neotrigonia*. S. M. Stanley (1969, 1970) showed that prosogyrous umbos helped burrowing, but the trigoniids have mostly opisthogyrous or orthogyrous umbos (S. M. Stanley, 1977). However, the external morphology, the varied ornamentation, the strong foot, and the complex hinge teeth are adapted to this mode of life (S. M. Stanley, 1977). Thus, the life position of species of this group is interpreted as being similar to *Neotrigonia*, with the posterior

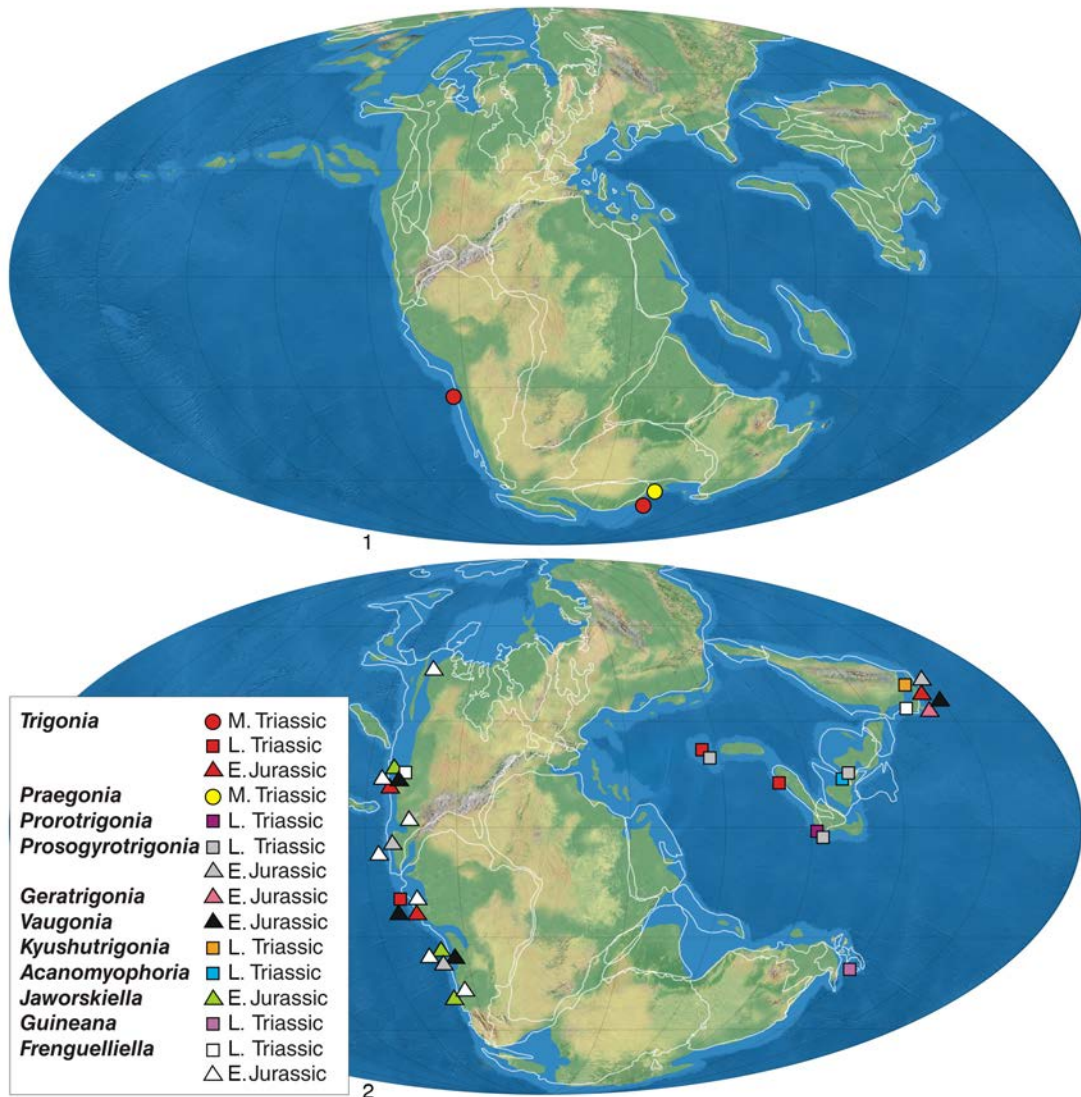


Figure 41. Paleogeographical distribution of Trigoniidae (*Trigonia*, *Praegonia*, *Prorotrigonia*, *Prosogyrotrigonia*, *Geratrigonia*, *Vaugonia*, *Kyushutrighonia*, *Acanomyophoria*, *Jaworskiella*, *Guineana*, *Frenguelliella*). 1, Middle Triassic; 2, Late Triassic–Early Jurassic.

part near the sediment surface. In many instances, the presence of epibionts on the posterior part was observed, adding to the assumption that some species lived with this part exposed, in a semi-infaunal position (Villamil, Kauffman, & Leanza, 1998). However, no epibionts were observed on the Triassic genera, perhaps due to their small size (as compared with Cretaceous forms). Cretaceous species are larger and tend to have had a more sedentary mode of life (Kelly, 1995b).

We assign an infaunal shallow-burrowing mode of life to all members of the superfamily, although some may live with the posterior part slightly exposed. For more information about the mode of life of this interesting group of burrowers, see Tevesz (1975), S. M. Stanley (1977, 1978), Kelly (1995b), Villamil, Kauffman, and Leanza (1998), or Francis and Hallam (2003), among others.

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1969). The shells of all members of the superfamily Trigonioidae probably were entirely aragonitic, with a prismatic outer shell layer and a nacreous inner shell layer, as in the living species of *Neotrigonia* (J. D. Taylor, Kennedy, & Hall, 1969; Newell & Boyd, 1975).

Genus PRAEGONIA Fleming, 1962, p. 2

Type species.—*Praegonia coombsi* Fleming, 1962, p. 2.

Stratigraphic range.—Middle Triassic (Ladinian). Fleming (1962) proposed *Praegonia* from the Ladinian of New Zealand. It was only recorded from that time and area (Fleming, 1964, 1987; Cox & others, 1969).

Paleogeographic distribution.—Austral (Fig. 41). *Praegonia* is monospecific and endemic to the Austral domain.

Austral domain: Middle Triassic: Ladinian of New Zealand (Fleming, 1962, 1964, 1987).

Paleoautoecology.—B, Is, S, FM; Sb. See discussion under *Trigonia* (p. 113).

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1969). No details are known about *Praegonia* shell microstructure. See discussion under *Trigonia* (p. 113).

Genus PROROTRIGONIA Cox, 1952, p. 57

Type species.—*Trigonia seranensis* Krumbeck, 1923a, p. 211.

Stratigraphic range.—Upper Triassic (Norian) (Kutassy, 1931). Cox (1952) erected *Prorotrigonia* and reported it from the Upper Triassic. Cox and others (1969) assigned it an Upper Triassic range. Krumbeck (1923a) described the type species from the Norian of Seram (Indonesia).

Paleogeographic distribution.—Tethys (Fig. 41). Hautmann (2001b) mentioned it from the Himalayas, as well as from southern Indonesia, but he did not refer to the original source. In addition, Tamura and Nishimura (1994) reported *Prorotrigonia* sp. from the Upper Triassic of Japan, but the figure of their specimen is of poor quality and it cannot be assigned with certainty to the genus. In fact, later, Tamura (1996) doubtfully recorded it as *Prorotrigonia* (?) sp. from the Upper Triassic of Japan.

Tethys domain: Late Triassic: Norian of Seram (Indonesia) (Krumbeck, 1923a; Sepm; Cox, 1952).

Paleoautoecology.—B, Is, S, FM; Sb. See mode of life for *Trigonia* (p. 113).

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1969). No details are known about *Prorotrigonia* shell microstructure. See discussion under *Trigonia* (p. 113).

Genus PROSOGYROTRIGONIA Krumbeck, 1924, p. 244

Type species.—*Trigonia (Prosogyrotrigonia) timorensis* Krumbeck, 1924, p. 245.

Stratigraphic range.—Upper Triassic (Norian)—Lower Jurassic (Sinemurian) (Hayami, 1975; Hautmann, 2001b). Cox and others (1969) assigned it an Upper Triassic range. Subsequent records extended the stratigraphic range of this genus to the Lower Jurassic (Hayami, 1975).

Paleogeographic distribution.—Tethys and Circumpacific (Fig. 41). *Prosogyrotrigonia* was also mentioned (*Prosogyrotrigonia?* sp.) from the Hettangian of northern Yukon (Canada) (Friebold & Poulton, 1977; Poulton, 1979), and new species were described from the Hettangian–Sinemurian of Chile (Pérez & others, 2008). It was also reported from Tibet (Kobayashi & Tamura, 1983a; Hautmann, 2001b), but these papers did not indicate the original source reference.

Tethys domain: Late Triassic: Norian–Rhaetian of Iran (Fallahi, Gruber, & Tichy, 1983; Hautmann, 2001b), Yunnan (China) (Guo, 1985); Rhaetian of Timor (Indonesia) (Krumbeck, 1924; Kobayashi & Mori, 1954a).

Circumpacific domain: Early Jurassic: Hettangian–Sinemurian of Chile (Pérez & others, 2008); Sinemurian of Japan (Yehara, 1921; Kobayashi & Mori, 1954a; Hayami, 1975; Sato & Westermann, 1991), Sonora (Mexico) (Scholz, Aberhan, & González-León, 2008).

Paleoautoecology.—B, Is, S, FM; Sb. See mode of life for *Trigonia* (p. 113).

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1969). No details are known about *Prosogyrotrigonia* shell microstructure. See discussion under *Trigonia* (p. 113).

Genus GERATRIGONIA Kobayashi in Kobayashi & Mori, 1954a, p. 171

Type species.—*Trigonia hosourensis* Yokoyama, 1904, p. 11.

Stratigraphic range.—Lower Jurassic (Hettangian–Toarcian) (Hayami, 1975). Cox and others (1969) assigned it a Lower Jurassic (lower Lower Jurassic) range, but *Geratrigrigonia* had been reported from the Toarcian (Kobayashi, 1957). The genus was quite common in the Hettangian of Japan (Hayami, 1959, 1975).

Paleogeographic distribution.—Circumpacific (Fig. 41). Although we consider *Geratrigrigonia* to be a Japanese endemic genus, it was also mentioned from South America (Pérez & Reyes, 1991), specifically the species *Trigonia (Geratrigrigonia) kurumensis* Kobayashi, 1954, from the Bata Formation (Colombia), then dated as Lower Jurassic. The specimens were later reassigned to *Vaugonia niranohamensis santamariae* Geyer, 1973, and, moreover, the Bata Formation was redated as Cretaceous (Etayo Serna & others, 2003).

Circumpacific domain: Early Jurassic: Hettangian of Japan (Kobayashi & Mori, 1954a; Hayami, 1959, 1975; Sato & Westermann, 1991; Sugawara & Kondo, 2004; Kondo & others, 2006).

Paleoautoecology.—B, Is, S, FM; Sb. See mode of life for *Trigonia* (p. 113).

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1969). No details are known about *Geratrigrigonia* shell microstructure. See discussion under *Trigonia* (p. 113).

Genus VAUGONIA Crickmay, 1930a, p. 53

Type species.—*Vaugonia veronica* Crickmay, 1930a, p. 53.

Stratigraphic range.—Lower Jurassic (Hettangian)—Upper Jurassic (Oxfordian) (Hayami, 1975). Crickmay (1932) mentioned *Vaugonia* from the Middle Jurassic. Subsequently, Kobayashi and Mori (1954b) proposed the new subgenus *Hijitrigonia* Kobayashi, 1954, from the Jurassic of Japan and indicated that *Vaugonia* had its origin during the Hettangian in Japan, and later it had a cosmopolitan distribution, probably extending to the Early Cretaceous. Cox and others (1969) considered *V. (Hijitrigonia)* as a junior synonym of *V. (Vaugonia)* and assigned a Jurassic range to the genus, including two subgenera: *V. (Vaugonia)* and *V. (Orthotrigonia)* Cox, 1952. No evidence of *Vaugonia* is found after the Jurassic. The youngest record is Oxfordian (Hayami, 1975).

Paleogeographic distribution.—Circumpacific (Fig. 41). *Vaugonia* originated in Japan during the Hettangian, and later it extended to the rest of the world. However, Francis and Hallam (2003) assumed a South American origin during the Sinemurian. Although during our study interval it was only recorded from the Circumpacific domain, since Pliensbachian times and throughout the Middle Jurassic, it had a cosmopolitan distribution (Fleming, 1964, 1987; Hallam, 1976; Poulton, 1976, 1979, 1991; Ishikawa & others, 1983; Pugaczewska, 1986; H. A. Leanza & Garate Zubilaga, 1987; H. A. Leanza, 1993; H. J. Campbell & Grant-Mackie, 1995; Kelly, 1995a).

Circumpacific domain: Early Jurassic: Hettangian–Sinemurian of Japan (Kobayashi & Mori, 1954b; Hayami, 1975; Sato & Westermann, 1991; Sugawara & Kondo, 2004); Sinemurian of Nevada (United States) (Poulton, 1979), Peru (Pérez & Reyes, 1991), Chile (Pérez & others, 2008).

Paleoautoecology.—B, Is, S, FM; Sb. See mode of life for *Trigonia*.

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1969). No details are known about *Vaugonia* shell microstructure. See discussion under *Trigonia* (p. 113).

Genus KYUSHUTRIGONIA

Tamura & Nishimura, 1994, p. 15

Type species.—*Kyushutrigonia hachibarensis* Tamura & Nishimura, 1994, p. 18.

Stratigraphic range.—Upper Triassic (Carnian–Norian) (Tamura & Nishimura, 1994; see Onoue & Tanaka, 2005). *Kyushutrigonia* was proposed by Tamura and Nishimura (1994) from Japan (Sambosan Terrane). They indicated it was recorded in the Upper Triassic, but they did not provide the exact age of the association. Onoue and Tanaka (2005) reported an association from the same locality, with bivalves in common, and assigned it a Carnian–Norian age.

Paleogeographic distribution.—Circumpacific (Fig. 41).

Circumpacific domain: Late Triassic: Japan (Tamura & Nishimura, 1994; Tamura, 1996).

Paleoautoecology.—B, Is, S, FM; Sb. See mode of life for *Trigonia*.

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1969). No details are known about *Kyushutrigonia* shell microstructure. See discussion under *Trigonia* (p. 113).

Genus ACANOMYPHORIA Guo, 1985, p. 203, 269

Type species.—*Acanomyphoria tuberosa* Guo, 1985, p. 203.

Remarks.—*Sichuantrigonia* Gou, 1993, was placed in synonymy with *Acanomyphoria* by Z. Fang and others (2009).

Stratigraphic range.—Upper Triassic (Carnian) (Guo, 1985). Guo (1985) proposed *Acanomyphoria* from Carnian beds of the Weiyuanjiang Formation of Guanfangnabang in Yunnan (China). Gou (1993) proposed *Sichuantrigonia* for material from the upper member of Hanwang Formation of Maantang area in Jiangyou, Sichuan (China), which was dated as Carnian.

Paleogeographic distribution.—Eastern Tethys (Fig. 41).

Tethys domain: Late Triassic: Carnian of southwestern China (Guo, 1985; Gou, 1993).

Paleoautoecology.—B, Is, S, FM; Sb. See mode of life for *Trigonia* (p. 113).

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1969). No details are known about *Acanomyphoria* shell microstructure. See discussion under *Trigonia* (p. 113).

Genus JAWORSKIELLA A. F. Leanza, 1942, p. 144, 166

Type species.—*Trigonia burckhardtii* Jaworski, 1914, p. 299.

Remarks.—Although A. F. Leanza (1942) proposed it as a subgenus of *Trigonia*, Cox and others (1969) and subsequent authors regarded *Jaworskiella* as a separate genus. Later, Reyes and Pérez (1980) proposed a new subgenus, *Quadratojaworskiella* Reyes & Pérez, 1980, and subsequently raised it to generic rank (Pérez & others, 2008).

Stratigraphic range.—Lower Jurassic (Hettangian–Pliensbachian) (H. A. Leanza, 1993; Pérez & others, 2008). Cox and others (1969) assigned it a Lower Jurassic (middle Liassic)–Upper Jurassic range, but we only found it recorded from the Lower Jurassic. Poulton (1979) already doubted that the genus was present in the Upper Jurassic, and H. A. Leanza (1993) restricted its range to the Lower Jurassic. It is especially abundant during the Pliensbachian (A. F. Leanza, 1942; H. A. Leanza, 1993; Poulton, 1979; H. A. Leanza & Garate Zubillaga, 1987).

Paleogeographic distribution.—Circumpacific and Austral (Fig. 41).

Circumpacific domain: Early Jurassic: Hettangian–Sinemurian of Chile (Pérez & Reyes, 1991; Pérez & others, 2008); Sinemurian of Nevada (United States) (Poulton, 1979).

Austral domain: Early Jurassic: Sinemurian of Argentina (Pérez & Reyes, 1991; Damborenea & Manceñido, 2005b).

Paleoautoecology.—B, Is, S, FM; Sb. See mode of life for *Trigonia*.

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1969). No details are known about *Jaworskiella* shell microstructure. See discussion under *Trigonia* (p. 113).

Genus GUINEANA Skwarko, 1967, p. 59

Type species.—*Guineana jimienensis* Skwarko, 1967, p. 60.

Stratigraphic range.—Upper Triassic (Carnian–Norian) (Skwarko, 1967). When Skwarko (1967) proposed *Guineana*, he tentatively included in this genus other species distributed throughout the Norian and Rhaetian of western Europe, Asia, and Nevada. We are not taking them into account, as Skwarko simply indicated they were externally similar, but he did not study the hinge details of any of them.

Paleogeographic distribution.—Austral (Fig. 41). According to Damborenea (2002b), *Guineana* was endemic to the Australian province of the South Pacific domain.

Austral domain: Late Triassic: Carnian–Norian of New Guinea (Skwarko, 1967).

Paleoautoecology.—B, Is, S, FM; Sb. See mode of life for *Trigonia* (p. 113).

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1969). No details are known about *Guineana* shell microstructure. See discussion under *Trigonia* (p. 113).

Genus FRENGUELLIELLA A. F. Leanza, 1942, p. 164

Type species.—*Trigonia inexpectata* Jaworski, 1915, p. 377.

Remarks.—A. F. Leanza (1942) proposed *Frenguelliella* as a subgenus of *Trigonia*, and this status was maintained by Cox and others (1969). Poulton (1979) decided to separate it from *Trigonia* and considered it to be a different genus due to the absence of radial ribs in the area. Furthermore, this author regarded *Kumatrigonia* Tamura, 1959, as a subgenus of *Frenguelliella*, as it was originally proposed. Cox and others (1969) considered *Kumatrigonia* as a subgenus of *Trigonia*. We follow Poulton (1979).

Stratigraphic range.—Upper Triassic (Carnian)–Middle Jurassic (Bajocian) (Hayami, 1975; H. A. Leanza, 1996). Cox and others (1969) assigned a Jurassic–Upper Cretaceous and Upper Triassic range to *Trigonia* (*Frenguelliella*) and *Trigonia* (*Kumatrigonia*), respectively. The last refers to *Frenguelliella* (*Kumatrigonia*) *tanourensis* Tamura, 1959, from the Carnian of Japan (Hayami, 1975). *Frenguelliella* was

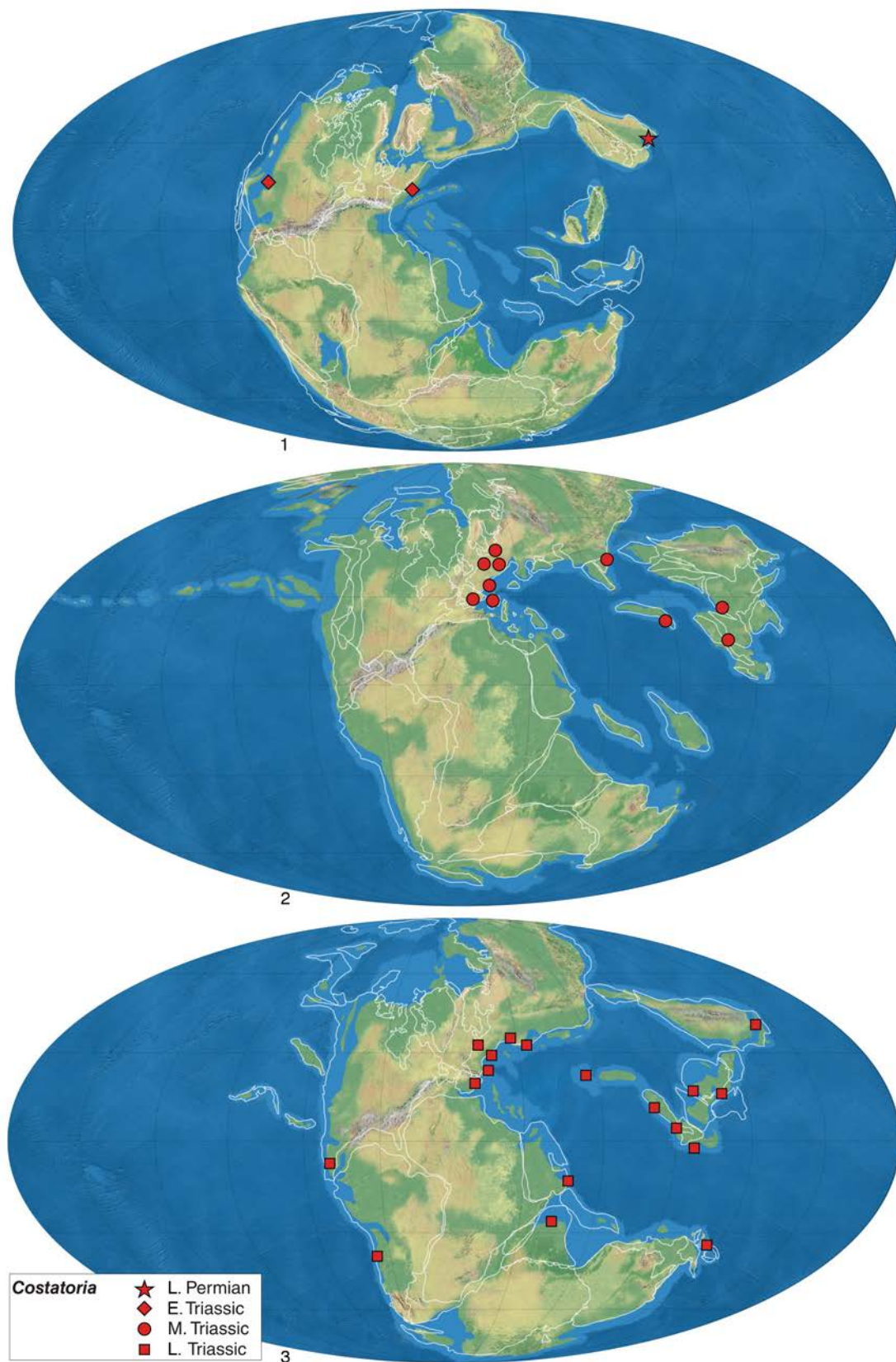


Figure 42. Paleogeographical distribution of Costatoriidae (*Costatoria*). 1, late Permian–Early Triassic; 2, Middle Triassic; 3, Late Triassic–Early Jurassic.

well distributed during the Jurassic, especially in the Pliensbachian (A. F. Leanza, 1942; Poulton, 1979; Ishikawa & others, 1983; H. A. Leanza & Garate Zubillaga, 1987; Pérez & Reyes, 1991; H. A. Leanza, 1993; Kelly, 1995a; Liu, 1995), but, although it was also recorded from the Upper Cretaceous in several papers (Cox & others, 1969; Poulton 1979; H. A. Leanza, 1993), we did not locate any species from deposits of that age. H. A. Leanza (1996) indicated that *Frenguelliella* was extinct by the Middle Jurassic (Bajocian), and its last species was *F. perezreyesi* H. A. Leanza 1993.

Paleogeographic distribution.—Circumpacific and Austral (Fig. 41). Although Cox and others (1969) considered it to be a cosmopolitan genus, the genus is primarily distributed on the Paleopacific margins. Pérez and Reyes (1991) recorded its presence in Europe, but no record from this area was found.

Circumpacific domain: Late Triassic: Carnian of Japan (Hayami, 1975); Norian of ?Oregon (United States) (Newton in Newton & others, 1987); Early Jurassic: Hettangian–Sinemurian of Texas (United States) (Liu, 1995); Sinemurian of northern Canada and Nevada (United States) (Poulton, 1979), Sonora (Mexico) (Scholz, Aberhan, & González-León, 2008), Peru (Pérez & Reyes, 1991), Chile (Pérez & others, 2008).

Austral domain: Early Jurassic: Sinemurian of Argentina (H. A. Leanza, 1993, 1996; Damborenea, 1996a; Damborenea & Manceñido, 2005b; Damborenea & Lanés, 2007).

Paleoautoecology.—B, Is, S, FM; Sb. See mode of life for *Trigonia* (p. 113).

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1969). No details are known about *Frenguelliella* shell microstructure. See discussion under *Trigonia* (p. 113).

Family COSTATORIIDAE Newell & Boyd, 1995

Genus COSTATORIA Waagen, 1907, p. 149

Type species.—*Donax costata* Zenker, 1833, p. 55.

Stratigraphic range.—upper Permian–Upper Triassic (Rhaetian) (Nakazawa & Newell, 1968; Hautmann, 2001b). Cox and others (1969) reported it from lower Permian of Texas and Wyoming, from the upper Permian of Japan, and assigned it a Triassic cosmopolitan distribution. The lower Permian records are from Ciriacks (1963), with *Costatoria sexraditata* (Branson, 1930), which is the type species of *Procostatoria* Newell & Boyd, 1975. The genus is recorded from the upper Permian, with the species *C. katsurensis* Nakazawa, 1967 (Nakazawa & Newell, 1968; Hayami & Kase, 1977) and *C. kobayasii* (Kambe, 1957) (Nakazawa, 1960; Hayami, 1975; Hayami & Kase, 1977). Throughout the Triassic, it was recorded from various localities, from the Lower Triassic (Broglia-Loriga & Posenato, 1986) to the Rhaetian (Hautmann, 2001b). Many different species were recorded from the Tethys domain, sometimes based on biostratigraphic criteria; a revision and an evolutionary analysis of the group would be most interesting.

Paleogeographic distribution.—Tethys, Circumpacific, and Austral (Fig. 42). Although Cox and others (1969) regarded *Costatoria* as cosmopolitan during the Triassic, we did not find records from the Boreal domain.

Tethys domain: Early Triassic: Olenekian of Italy (Neri & Posenato, 1985; Broglia-Loriga & Posenato, 1986; Neri, Pasini, & Posenato, 1986; Posenato, 1989; Broglia-Loriga & others, 1990;

Fraiser & Bottjer, 2007a); Middle Triassic: Germany (Hagdorn & Simon, 1985; Mahler & Sell, 1991), Poland (Senkowiczowa, 1985), Malaysia (Kobayashi & Tamura, 1968b); Anisian of southern China (Sha, Chen, & Qi, 1990; Tong & Liu, 2000; Komatsu, Chen, & others, 2004), Hungary (Szente, 1997), northern Vietnam (Komatsu, Huyen, & Huu, 2010); Ladinian of Italy (Márquez-Aliaga & Ros, 2002; Posenato, 2002; Márquez-Aliaga & others, 2004), Spain (Márquez-Aliaga, 1983, 1985; Márquez-Aliaga, Hirsch, & López-Garrido, 1986; Budurov & others, 1991; Márquez-Aliaga & Montoya, 1991; López-Gómez & others, 1994; Freneix, 1999; Márquez-Aliaga, García-Forner, & Plasencia, 2002; Márquez-Aliaga & Ros, 2003), northern Vietnam (Komatsu, Huyen, & Huu, 2010), Afghanistan (Farsan, 1972); Late Triassic: Malaysia (Tamura, 1996), China (Sha, Chen, & Qi, 1990; Gou, 1993), Oman (R. Hudson & Jefferies, 1961); Carnian of Italy (Bittner, 1895; Allasinaz, 1966; Márquez-Aliaga & Ros, 2002; Márquez-Aliaga & others, 2004), Spain (Martín-Algarra, Solé de Porta, & Márquez-Aliaga, 1995); Norian of Vietnam (Vu Khuc & Huyen, 1998; Hautmann, 2001b), Germany (Tichy & Schramm, 1983), Austria (Tichy, 1975), Armenia and northern Caucasus (Hautmann, 2001b); Norian–Rhaetian of Iran (Hautmann, 2001b); Rhaetian of Tibet (Hautmann & others, 2005), Myanmar and Sumatra (Hautmann, 2001b).

Circumpacific domain: late Permian: Japan (Nakazawa, 1960; Nakazawa & Newell, 1968; Hayami, 1975; Newell & Boyd, 1975; Hayami & Kase, 1977); Early Triassic: Olenekian of western United States (Fraiser & Bottjer, 2007a); Late Triassic: Carnian–Norian of Japan (Onoue & Tanaka, 2005); Norian of ?Sonora (Mexico) (Damborenea in Damborenea & González-León, 1997); Norian–Rhaetian of Chile (Chong & Hillebrandt, 1985; Hillebrandt, 1990; Pérez & Reyes, 1991).

Austral domain: Late Triassic: Carnian–Norian of New Guinea (Skwarko, 1967).

Paleoautoecology.—B, Is, S, SM; Sb. See mode of life for *Trigonia* (p. 113). Hautmann (2001b) attributed a mode of life similar to the rest of trigonoioids, but he argued that it would be a slow burrower due to the radial ornamentation and an undeveloped foot.

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1969). The shells of all members of the superfamily Trigonoidea were probably entirely aragonitic, with a prismatic outer shell layer and a nacreous inner shell layer, as in the living species of *Neotrigonia* (J. D. Taylor, Kennedy, & Hall, 1969; Newell & Boyd, 1975). The last authors noted that *Costatoria harpa* (Münster) may have also had a cross-lamellar structure (see Newell & Boyd, 1975, fig. 8–9).

Family MYOPHORIIDAE Bronn, 1849 in 1848–1849

Genus MYOPHORIA Bronn, 1834 in 1834–1838, p. 54

Type species.—*Trigonellites vulgaris* Schlotheim, 1822 in 1822–1823, p. 192.

Stratigraphic range.—Middle Triassic (Anisian)–Upper Triassic (Rhaetian) (Newell & Boyd, 1975). Although Cox and others (1969) assigned it a Lower–Upper Triassic range, subsequently Newell and Boyd (1975) reported it only from the Middle and Upper Triassic. No reliable records were found from the Lower Triassic, and we follow Newell and Boyd (1975) in the range assigned. Many Trigonoidea genera were based on species originally described under *Myophoria*,

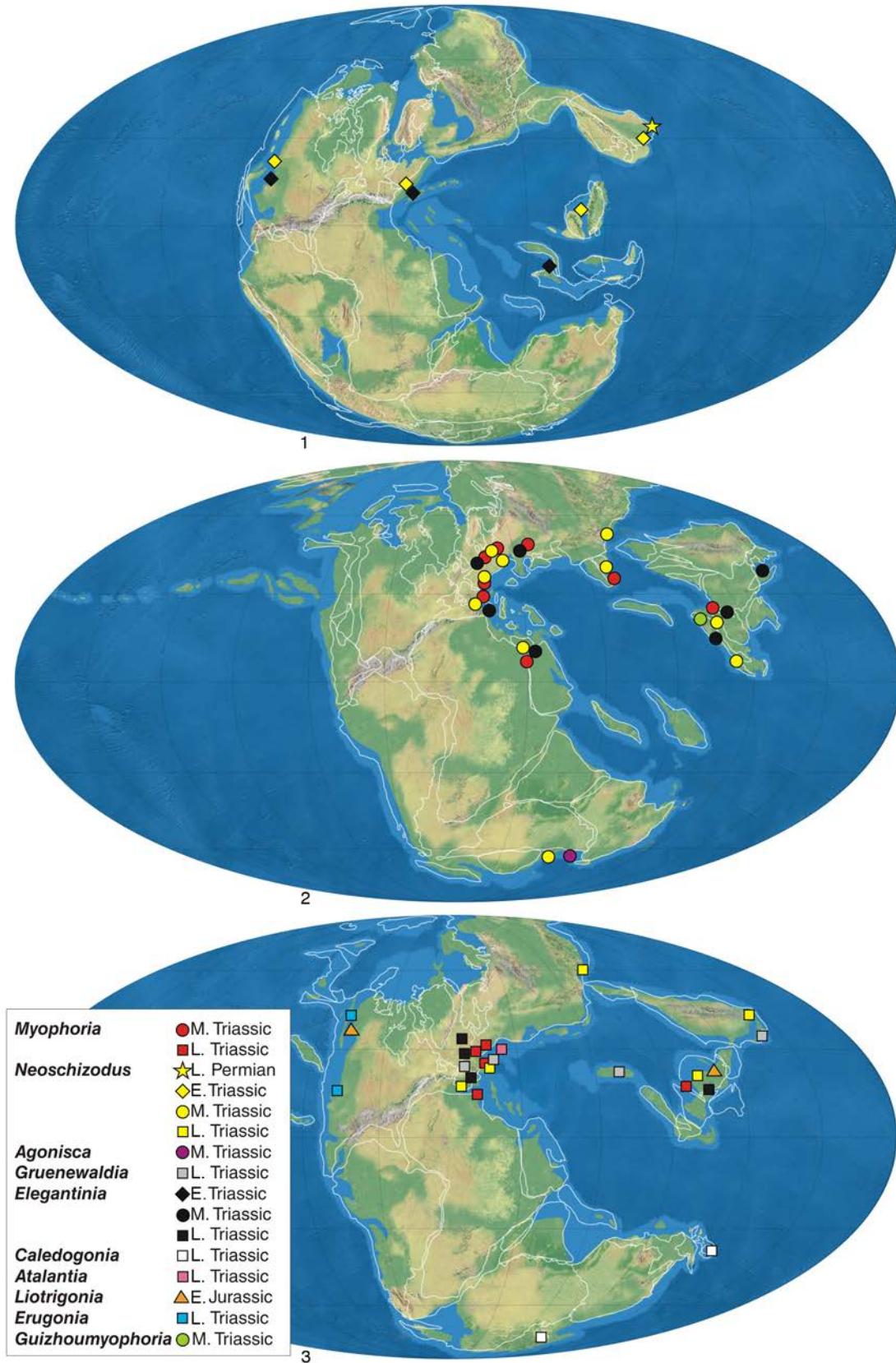


Figure 43. Paleogeographical distribution of Myophoriidae (*Myophoria*, *Neoschizodus*, *Agonisca*, *Gruenewaldia*, *Elegantinia*, *Caledogonia*, *Atalantia*, *Liotrigonia*, *Erugonia*, *Guizhoumyophoria*). 1, late Permian–Early Triassic; 2, Middle Triassic; 3, Late Triassic–Early Jurassic.

so the stratigraphic and paleogeographic ranges of *Myophoria* may seem larger if a thorough revision of the species is not performed. *Myophoria* does not pass through the Triassic–Jurassic boundary (Hallam, 1981, 1990; Hallam & Wignall, 1997, 2000; Tanner, Lucas, & Chapman, 2004); it is a characteristic Triassic genus.

Paleogeographic distribution.—Tethys (Fig. 43).

Tethys domain: Middle Triassic: Germany (Bachmann, 1973; Baumgarte, 1975; Newell & Boyd, 1975; Fuchs & Mader, 1980; Hagdorn & Simon, 1983; Mahler & Sell, 1991), Poland (Senkowiczowa, 1985), Israel (Lerman, 1960); Anisian of Germany (Klug, Hagdorn, & Monterani, 2005), Spain (Budurov & others, 1991), China (Lu & Chen, 1986), Bulgaria (Encheva, 1969); Ladinian of Germany (Ürlich, 1978; Hagdorn, 1982; Klug, Hagdorn, & Monterani, 2005), Spain (Márquez-Aliaga, 1983, 1985; López-Gómez & others, 1994; Márquez-Aliaga & Martínez, 1996; Márquez-Aliaga & others, 2001, 2002), Italy (Fantini Sestini, 1966; Ürlich & Tichy, 1998), Afghanistan (Farsan, 1972); Late Triassic: China (Gou, 1993), Yugoslavia (Newell & Boyd, 1975); Carnian of Italy (Fürsich & Wendt, 1977; Ürlich & Tichy, 1998), Slovenia (Boué, 1835, as *Cryptina*; Jelen, 1988; Jurkovsek, 1978, 1993); Carnian–Rhaetian of Tunisia (Desio, Rossi Ronchetti, & Vigano, 1960), the Alps (Kutassy, 1931); Rhaetian of Europe (Guérin-Franiette, 1990).

Paleoautoecology.—B, Is, S, FM; Sb. See mode of life for *Trigonia* (p. 113).

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1969). No details are known about *Myophoria* shell microstructure. See discussion under *Trigonia* (p. 113).

Genus NEOSCHIZODUS Giebel, 1855, p. 35

Type species.—*Lyrodon laevigatum* Goldfuss, 1837 in 1833–1841, p. 197.

Remarks.—Only one subgenus is considered in the study interval within *Neoschizodus*: *Okunominetania* Ichikawa, 1949.

Stratigraphic range.—middle Permian (Guadalupian)–Upper Triassic (Rhaetian) (Newell & Boyd, 1995; Márquez-Aliaga, Plasencia, & Ros, 2005). Cox and others (1969) assigned it a Permian–Upper Triassic range. Subsequently, Newell and Boyd (1975) and Boyd and Newell (1997) reported it from the middle and upper Permian of Japan, the Lower Triassic of Utah (United States), and the German Middle Triassic (Muschelkalk facies). However, *Neoschizodus* probably had a wider range, both stratigraphic and paleogeographic (see paleogeographic distribution). The youngest record is Rhaetian (Márquez-Aliaga, Plasencia, & Ros, 2005).

Paleogeographic distribution.—Cosmopolitan (Fig. 43).

Tethys domain: Early Triassic: China (S. Yang, Wang, & Hao, 1986); Induan of Italy (Fraiser & Bottjer, 2007a), southern China (Hautmann & others, 2011); Olenekian of Italy (Broglio-Loriga, Masetti, & Neri, 1982; Neri & Posenato, 1985; Posenato, 1989; Broglio-Loriga & others, 1990; Fraiser & Bottjer, 2007a); Middle Triassic: China (Ling, 1988), Poland (Senkowiczowa, 1985), Malaysia (Kobayashi & Tamura, 1968b), Israel (Lerman, 1960); lower Muschelkalk (?Anisian) of Germany (Newell & Boyd, 1975); Anisian of Germany (Klug, Hagdorn, & Monterani, 2005), Hungary (Szente, 1997), China (Sha, Chen, & Qi, 1990), northern Vietnam (Komatsu, Huyen, & Huu, 2010); Ladinian of Afghanistan (Farsan, 1972,

1975), Germany (Ürlich, 1992; Márquez-Aliaga & others, 2002; Klug, Hagdorn, & Monterani, 2005), Spain (Márquez-Aliaga, 1983, 1985; Márquez-Aliaga & Montoya, 1991; Calvet & others, 1994; López-Gómez & others, 1994; Freneix, 1999; Márquez-Aliaga & Ros, 2003), China (Sha, Chen, & Qi, 1990), Italy (Rossi Ronchetti, 1959), northern Vietnam (Komatsu, Huyen, & Huu, 2010); Late Triassic: Carnian of China (Sha, Chen, & Qi, 1990), Italy (Allasinaz, 1962, 1966; Gelati & Allasinaz, 1964); Rhaetian of Italy (Pozzi, Gelati, & Allasinaz, 1962; Sirna, 1968), Spain (Márquez-Aliaga, Plasencia, & Ros, 2005).

Circumpacific domain: late Permian: Japan (Nakazawa, 1960; Nakazawa & Newell, 1968; Hayami & Kase, 1977); Early Triassic: Induan of western United States (Fraiser & Bottjer, 2007a); Olenekian of western United States (Newell & Boyd, 1975; Boyd & Newell, 1997; Schubert, 1993; Fraiser & Bottjer, 2007a), Japan (Nakazawa, 1961; Hayami, 1975; Kashiya & Oji, 2004; Fraiser & Bottjer, 2007a); Late Triassic: Japan (Nakazawa, 1956; Tamura, 1990); Carnian of Japan (Hayami, 1975).

Austral domain: Middle Triassic: Anisian–Ladinian of New Zealand (Fleming, 1987).

Boreal domain: Middle Triassic: Ladinian of Primorie (Kiparisova, 1972); Late Triassic: of Primorie (Kiparisova, 1972).

Paleoautoecology.—B, Is, S, FM; Sb. See mode of life for *Trigonia* (p. 113).

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1969). No details are known about *Neoschizodus* shell microstructure. See discussion under *Trigonia* (p. 113).

Genus AGONISCA Fleming, 1963, p. 843

Type species.—*Agonisca corbiensis* Fleming, 1963, p. 844.

Stratigraphic range.—Middle Triassic (Ladinian) (Fleming, 1987). Fleming (1963) proposed *Agonisca* from the Kaihikuan (=Ladinian–Carnian). Cox and others (1969) assigned it the same range. Although originally introduced into the family Trigoniidae, later Fleming (1987) included it in Myophoriidae and indicated its possible occurrence from Etalian (=Anisian–Ladinian) beds (?*Agonisca* aff. *corbiensis* Fleming), although the hinge of these specimens was incomplete, and the author pointed out the need for more material to indicate the correct relationships of this taxon.

Paleogeographic distribution.—Austral (Fig. 43).

Austral domain: Middle Triassic: Ladinian of New Zealand (Fleming, 1963, 1964, 1987).

Paleoautoecology.—B, Is, S, FM; Sb. See mode of life for *Trigonia* (p. 113).

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1969). No details are known about *Agonisca* shell microstructure. See discussion under *Trigonia* (p. 113).

Genus GRUENEWALDIA Wöhrmann, 1889, p. 215

Type species.—*Myophoria woehrmanni* Bittner, 1895, p. 106.

Remarks.—Wöhrmann (1889) designated *Cardita decussata* Münster, 1837, in Goldfuss, 1833–1841, p. 185, as type species of *Gruenewaldia*. Bittner (1895) indicated that the identification of Wöhrmann's specimens was incorrect and gave a new name to them: *Myophoria woehrmanni* Bittner, 1895. Cox and others (1969) failed

to take this into account, but Hautmann (2001b, 2003) pointed it out and, according to ICZN Article 70 (1999), he designated *Myophoria woehrmanni* Bittner as type species of *Gruenewaldia*, which he included within the family Myophoriidae. Although Cox and others (1969) regarded *Elegantinia* Waagen, 1907, as junior synonym of *Gruenewaldia*, *Elegantinia* is treated here as a valid genus (see discussion under *Elegantinia* below).

Stratigraphic range.—Upper Triassic (Carnian–Rhaetian). Cox and others (1969) assigned it a Middle–Upper Triassic range, but, as mentioned above, the type species designated by Wöhrmann (1889) was not *Cardita decussata* Münster, 1837, in Goldfuss, 1833–1841, from the Ladinian (Diener, 1923; Kutassy, 1931), but *Myophoria woehrmanni* Bittner, 1895, only reported from the Upper Triassic. Newell and Boyd (1975) mentioned the genus from the Middle Triassic of the Cassian Formation, which is currently considered to be Carnian in age (see Fürsich & Wendt, 1977).

Paleogeographic distribution.—Tethys and Circumpacific (Fig. 43). Hautmann (2001b) reported *Gruenewaldia* from Iran and also mentioned it from Yunnan, Tibet, and the Himalayas. Hallam (1981) listed it from the Arctic region, but we did not find any reference from that area.

Tethys domain: Late Triassic: Carnian of the Alps (Laube, 1865; Wöhrmann, 1889; Bittner, 1895; Allasinaz, 1966; Newell & Boyd, 1975; Fürsich & Wendt, 1977), Slovenia (Jelen, 1988); Norian de Iran (Repin, 2001); Norian–Rhaetian of Iran (Hautmann, 2001b, 2003).

Circumpacific domain: Late Triassic: Carnian of Japan (Hayami, 1975; Tamura & others, 1978); Carnian–Norian of Japan (Tamura & Nishimura, 1994; Onoue & Tanaka, 2002, 2005).

Paleoautoecology.—B, Is, S, FM; Sb. See mode of life for *Trigonia*.

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1969). No details are known about *Gruenewaldia* shell microstructure. See discussion under *Trigonia* (p. 113).

Genus ELEGANTINIA Waagen, 1907, p. 149

Type species.—*Lyrodon elegans* Dunker, 1851, p. 300.

Remarks.—Cox and others (1969) treated *Elegantinia* as a junior synonym of *Gruenewaldia* Wöhrmann, 1889. However, a year earlier, Kobayashi and Tamura (1968b) had considered both valid and regarded *Lyriomyophoria* Kobayashi, 1954, as a junior synonym of *Elegantinia*, since both genera had the same type species. For years, the vast majority of western authors followed Cox and others (1969), without paying attention to the paper by Kobayashi and Tamura (1968b), until Boyd and Newell (1999) exposed the situation. Subsequently, Hautmann (2003) suggested the separation of *Elegantinia* and *Gruenewaldia* on the basis of hinge and ornamentation differences.

Stratigraphic range.—Lower Triassic (Olenekian)–Upper Triassic (Rhaetian) (Kobayashi & Tamura, 1968b). Kobayashi and Tamura (1968b) indicated a Lower–Upper Triassic (Rhaetian) range for *Elegantinia*, dismissing the Permian records as not belonging to *Elegantinia* (see Kobayashi & Tamura, 1968b, p. 104–105). Nevertheless, they were taken into account by Cox and others (1969) to assign the stratigraphic range to *Lyriomyophoria* [= *Elegantinia*]. Subsequently, several authors (Newell & Boyd, 1975; Boyd & Newell, 1997) regarded *Lyriomyophoria* [= *Elegantinia*] as an exclusively Triassic genus.

Paleogeographic distribution.—Tethys and Circumpacific (Fig. 43).

Tethys domain: Early Triassic: Tonkin (Vietnam) (Patte, 1926), Italy (Leonardi, 1935); Middle Triassic: Israel (Lerman, 1960); Anisian of southern China (Komatsu, Chen, & others, 2004); lower Muschelkalk (=Anisian) of Germany (Brinkmann, 1966; Busse, 1972; Baumgarte, 1975; Newell & Boyd, 1975), Hungary (Szente, 1997); Ladinian of Spain (Márquez-Aliaga, 1983, 1985; Pérez-López, 1991; López-Gómez & others, 1994), Vietnam (Vu Khuc & Huyen, 1998), Sinai (Awad, 1945), Alps (Arthaber, 1908); Late Triassic: Carnian of China (Wen & others, 1976; Sha, Chen, & Qi, 1990; Gou, 1993), Spain (Martín-Algarra & others, 1993; Márquez-Aliaga & Ros, 2002; Márquez-Aliaga & others, 2004); Rhaetian of England (Castell & Cox, 1975; Warrington & Ivimey-Cook, 1990; Ivimey-Cook & others, 1999), Hungary (Vörös, 1981).

Circumpacific domain: Early Triassic: Olenekian of Nevada (United States) (Boyd & Newell, 1997; Fraiser & Bottjer, 2007a); Middle Triassic: Ladinian or Carnian of Japan (Hayami, 1975).

Paleoautoecology.—B, Is, S, FM; Sb. See mode of life for *Trigonia* (p. 113).

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1969). No details are known about *Elegantinia* shell microstructure. See discussion under *Trigonia* (p. 113).

Genus CALEDONIA Freneix & Avias, 1977, p. 282

Type species.—*Caledonia globosa* Freneix & Avias, 1977, p. 286.

Stratigraphic range.—Upper Triassic (upper Carnian–lower Norian) (Freneix & Avias, 1977). *Caledonia* was reported from the Otamitan (=upper Carnian–lower Norian, according to Freneix & Avias, 1977; now Norian, see H. J. Campbell & Raine in Cooper, 2004) Later, Fleming (1987) treated it as a subgenus of *Neoschizodus* and reported it from the Norian of New Zealand.

Paleogeographic distribution.—Austral (Fig. 43). *Caledonia* was endemic to the Maorian province (Freneix & Avias, 1977; Damborenea, 2002b).

Austral domain: Late Triassic: Carnian–Norian of New Caledonia (Freneix & Avias, 1977); Norian of New Zealand (Fleming, 1987).

Paleoautoecology.—B, Is, S, FM; Sb. See mode of life for *Trigonia* (p. 113). More specific information on the mode of life of *Caledonia* is provided by Freneix and Avias (1977).

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1969). No details are known about *Caledonia* shell microstructure. See discussion under *Trigonia* (p. 113).

Genus ATALANTIA Termier & Verriez, 1974, p. 158

Type species.—*Atalantia trigonioides* Termier in Termier & Verriez, 1974, p. 158.

Stratigraphic range.—Upper Triassic (lower Carnian) (Termier & Verriez, 1974). Termier (in Termier & Verriez, 1974) proposed the monospecific genus *Atalantia* from the lower Carnian of southern Atalanti (Greece).

Paleogeographic distribution.—western Tethys (Fig. 43). *Atalantia* is a genus endemic to Greece.

Tethys domain: Late Triassic: early Carnian of Greece (Termier & Verriez, 1974).

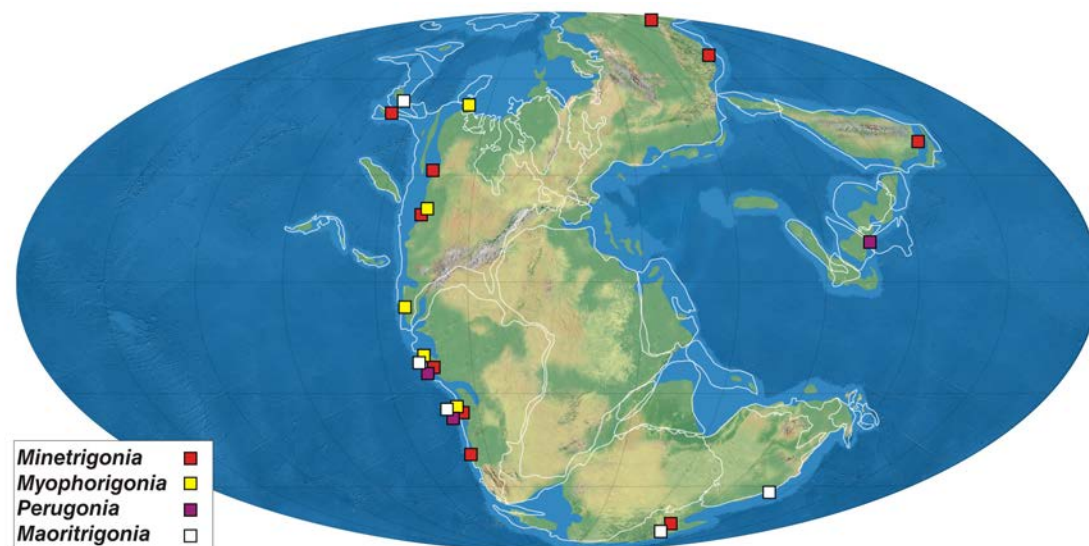


Figure 44. Paleogeographical distribution of Minetrioniidae (*Minetrigonia*, *Myophorigonia*, *Perugonia*, *Maoritrigonia*). Late Triassic.

Paleoautoecology.—B, Is, S, FM; Sb. See mode of life for *Trigonia* (p. 113).

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1969). No details are known about *Atalantia* shell microstructure. See discussion under *Trigonia* (p. 113).

Genus LIOTRIGONIA Cox, 1952, p. 53

Type species.—*Trigonia lingonensis* Dumortier, 1869 in 1864–1874, p. 275.

Stratigraphic range.—Lower Jurassic (?Hettangian, Sinemurian–Pliensbachian). Cox (1952) reported it from middle Lias of France and England. Cox and others (1969) assigned it an Lower Jurassic (middle Lower Jurassic) range. Subsequently, new records expanded the range of this genus, since it was quoted from ?Hettangian (Poulton, 1991), Sinemurian (Poulton, 1991; Stiller, 2006), and Pliensbachian (Hallam, 1976, 1977, 1987; Zakharov & others, 2006).

Paleogeographic distribution.—Tethys and Circumpacific (Fig. 43). Although during our study interval it was only known from China and Canada, during the Pliensbachian it was also present in France, England, and Siberia (Cox & others, 1969).

Tethys domain: Early Jurassic: Sinemurian of China (Stiller, 2006).

Circumpacific domain: Early Jurassic: ?Hettangian–Sinemurian of Yukon (northwestern Canada) (Poulton, 1991).

Paleoautoecology.—B, Is, S, FM; Sb. See mode of life for *Trigonia* (p. 113).

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1969). No details are known about *Liotrigonia* shell microstructure. See discussion under *Trigonia* (p. 113).

Genus ERUGONIA Newton in Newton & others, 1987, p. 63

Type species.—*Erugonia canyonensis* Newton in Newton & others, 1987, p. 65.

Stratigraphic range.—Upper Triassic (Norian) (Newton in Newton & others, 1987). *Erugonia* was only quoted from the Norian (Newton in Newton & others, 1987). In PBDB, it is also mentioned from the Rhaetian of Canada, but the review of the original source is pending.

Paleogeographic distribution.—Circumpacific (Fig. 43).

Circumpacific domain: Late Triassic: Norian of Oregon (United States) and British Columbia (western Canada) (Newton in Newton & others, 1987).

Paleoautoecology.—B, Is, S, FM; Sb. See mode of life for *Trigonia* (p. 113).

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1969). No details are known about *Erugonia* shell microstructure. See discussion under *Trigonia* (p. 113).

Genus GUIZHOU MYOPHORIA Z. Fang, 2009, p. 998

Type species.—*Quadratia quadrata* H. Yin, 1974, p. 25.

Remarks.—*Guizhoumyophoria* was proposed by Z. Fang (2009) as a new name for *Quadratia* H. Yin, 1974, homonym of *Quadratia* Muir-Wood & Cooper, 1960, p. 161 (Brachiopoda: Productellidae). According to Z. Fang and others (2009, p. 56), “This genus is not very well established and all the material is poor.”

Stratigraphic range.—Middle Triassic (Anisian) (H. Yin, 1974). *Quadratia* [*Guizhoumyophoria*] was erected by H. Yin (1974) from the Anisian of China, and only the type species was included. The description was made in a restricted publication and in H. Yin in Gan and Yin (1978) was published again. Later, it was reported from the same stage by Komatsu, Chen, and others (2004). Kobayashi and Tamura (1983a) mentioned *Quadrata* H. Yin, 1974, by mistake and assigned a Middle–Upper Triassic range, but no original source of Upper Triassic records was given, so we are not taking it into account.

Paleogeographic distribution.—Eastern Tethys (Fig. 43).

Tethys domain: Middle Triassic: Anisian of southwestern China (Ghizou province) (H. Yin, 1974; Yin in Gan & Yin, 1978; Komatsu, Chen, & others, 2004; Z. Fang, 2009; Z. Fang & others, 2009).

Paleoautoecology.—B, Is, S, FM; Sb. See mode of life for *Trigonia* (p. 113).

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1969). No details are known about *Guizhoumyophoria* shell microstructure. See discussion under *Trigonia* (p. 113).

Family MINETRIGONIIDAE Kobayashi, 1954

Genus MINETRIGONIA Kobayashi & Katayama, 1938, p. 187

Type species.—*Trigonia hegiensis* Saeki, 1925, p. 35.

Stratigraphic range.—Upper Triassic (Carnian–Rhaetian). Cox and others (1969) assigned it an Upper Triassic range. It is recorded from Carnian (Hayami, 1975) to Rhaetian (Fleming, 1987).

Paleogeographic distribution.—Circumpacific, Austral, and Boreal (Fig. 44). Kobayashi and Tamura (1968b, p. 108–109; 1983b) noticed that many Late Triassic species attributed to *Trigonia* and *Myophoria* actually belonged to *Minetrigonia*; these species were distributed through China, Peru, British Columbia, and New Zealand. Fleming (1987) documented the same situation for some of them known from the boreal area and Nevada (United States). *Minetrigonia* may also have been present in Malaysia (Kobayashi & Tamura, 1968b; Tamura & others, 1975).

Circumpacific domain: Late Triassic: Peru (Rangel, 1978); Carnian of Japan (Nakazawa, 1956; Hayami, 1975), Oregon (United States) (Tamura & McRoberts, 1993); Norian of British Columbia (Canada) (McLearn, 1946), Oregon (United States) (Newton in Newton & others, 1987); Norian or Rhaetian of Chile (Chong & Hillebrandt, 1985).

Austral domain: Late Triassic: Carnian of New Zealand (Trechmann, 1918); ?Norian, Rhaetian of New Zealand (Fleming, 1987); Rhaetian of ?Argentina (Riccardi & others, 1997, 2004; Damborenea & Manceñido, 2012).

Boreal domain: Late Triassic: Norian–Rhaetian of Siberia (Kiparisova, Bychkov, & Polubotko, 1966), northeastern Asia (Kurushin, 1990), Alaska (United States) (McRoberts & Blodgett, 2000).

Paleoautoecology.—B, Is, S, FM; Sb. See mode of life of *Trigonia* (p. 113).

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1969). No details are known about *Minetrigonia* shell microstructure. See discussion under *Trigonia* (p. 113).

Genus MYOPHORIGONIA Cox, 1952, p. 52

Type species.—*Myophoria paucicostata* Jaworski, 1922, p. 126.

Stratigraphic range.—Upper Triassic (Carnian–Rhaetian). Cox (1952) included several species in his new genus and reported it from Upper Triassic of Peru and Bear Islands, Inferior Oolite of England, and doubtfully from the Oxfordian of Syria. Cox and others (1969) assigned it a Upper Triassic–Middle Jurassic (Bajocian) range. Hallam (1981, 1990) indicated *Myophorigonia* did not survive the Triassic–Jurassic boundary, although Newton (1989) considered it to be a survivor of the Triassic–Jurassic extinction event. The oldest record during the Upper Triassic is from the Carnian in the Santa Clara Formation, Sonora (Mexico) (Alencaster de Cserna, 1961). According to Kobayashi and Tamura (1968b), Jurassic records of

the genus refer to various species included by Cox (1952), but these need to be better studied to establish their relations. However, Kelly (1995a, p. 80, fig. 17) accepted *Myophorigonia* from Hettangian to Pliensbachian and Bathonian of South America, though these records are now referred to *Groeberella* (see Pérez, Reyes, & Damborenea, 1995). Since we cannot confirm the Lower Jurassic records of the genus, we accept the Rhaetian as the earliest solid record.

Paleogeographic distribution.—Circumpacific (Fig. 44). Although Hallam (1981) mentioned *Myophorigonia* from the Upper Triassic of the Arctic, we did not locate any earlier record from this area. However, Tamura and McRoberts (1993) transferred several Arctic species to *Myophorigonia*. Pérez and Reyes (1994) indicated its presence in the Upper Triassic of Singapore, referring to Kobayashi and Tamura (1968b), but, in this last paper, *Maoritrigonia* is recorded from that area but not *Myophorigonia*. G. D. Stanley and others (1994) and McRoberts (1997a) recorded *Myophorigonia jaworskii* (Steinmann, 1929) from the Norian of Peru, but this is the type species of *Perugonia* Kobayashi & Tamura, 1968a, and they made no comment in this respect.

Circumpacific domain: Late Triassic: Carnian of Sonora (Mexico), Oregon (United States) (Tamura & McRoberts, 1993), Bear Island (Cox, 1952; Kobayashi & Tamura, 1968b); Carnian–Norian of Peru (Körner, 1937); Norian of Chile (Hayami, Maeda, & Ruiz-Fuller, 1977), Sonora (Mexico) (G. D. Stanley & others, 1994; McRoberts, 1997a); Norian–Rhaetian of Peru (Cox, 1949, 1952; Pérez & Reyes, 1991), Chile (Chong & Hillebrandt, 1985; Pérez & Reyes, 1991).

Paleoautoecology.—B, Is, S, FM; Sb. See mode of life for *Trigonia* (p. 113).

Mineralogy.—Aragonitic (Hayami, Maeda, & Ruiz-Fuller, 1977). Hayami, Maeda, and Ruiz-Fuller (1977) described two aragonitic shell layers for *Myophorigonia* sp. aff. *M. paucicostata* (Jaworski, 1922): a prismatic outer layer and an alleged nacreous inner layer.

Genus PERUGONIA Kobayashi & Tamura, 1968a, p. 112

Type species.—*Myophoria jaworskii* Steinmann, 1929, p. 57.

Remarks.—*Myophoria baertli* Boit (1966, p. 10), from the same age and region as *M. jaworskii*, is the type species of *Albitrigonia* Prado-Velazco, 1991, p. 444. The relationships within this group of Norian Peruvian species are not well known, and a thorough systematic revision is needed. In the meantime, we regard *Albitrigonia* as a subgenus of *Perugonia*.

Stratigraphic range.—Upper Triassic (?Carnian–?Rhaetian). *Perugonia* was mainly reported from the Norian, and there are some doubts about whether its range extends to the Carnian (Kobayashi & Tamura, 1968b) or to the Rhaetian (Chong & Hillebrandt, 1985). Pérez and Reyes (1991) recorded *Perugonia* from all the three Upper Triassic stages of Peru and also from the Norian of Chile and Colombia.

Paleogeographic distribution.—Circumpacific (Fig. 44). G. D. Stanley and others (1994) and McRoberts (1997a) reported the type species of *Perugonia* (as *Myophorigonia jaworskii*) from the Norian of Peru. Pérez and Reyes (1991) recorded it from the Carnian, Norian, and Rhaetian of Peru, but we have not located original information for the Carnian and Rhaetian.

Circumpacific domain: Late Triassic: Carnian or Norian of Malaysia (Kobayashi & Tamura, 1968b); Norian of Peru (Jaworski, 1922; Steinmann, 1929; Cox, 1949; Rangel, 1978; Maeda & oth-

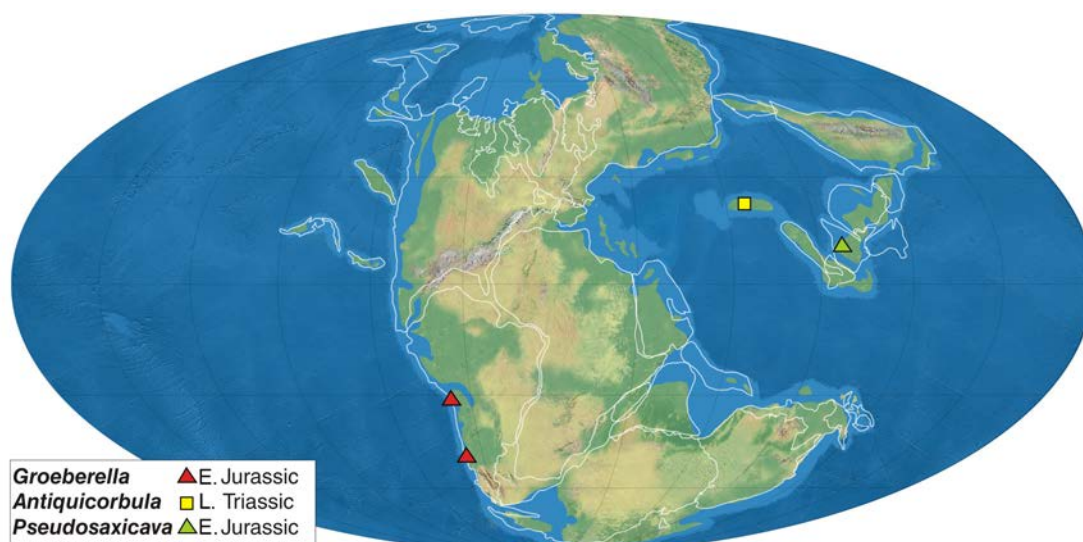


Figure 45. Paleogeographical distribution of Groeberellidae (*Groerberella*), Corbulidae (*Antiquicorbula*) and Hiattellidae (*Pseudosaxicava*). Late Triassic–Early Jurassic.

ers, 1983); Norian or Rhaetian of Chile (Jaworski, 1922; Chong & Hillebrandt, 1985; Hillebrandt, 1990).

Paleoautoecology.—B, Is, S, FM; Sb. See mode of life for *Trigonia* (p. 113).

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1969). No details are known about *Perugonia* shell microstructure. See discussion under *Trigonia* (p. 113).

Genus MAORITRIGONIA Fleming, 1962, p. 3

Type species.—*Myophoria nuggetensis* Trechmann, 1918, p. 210.

Stratigraphic range.—Upper Triassic (Carnian–Rhaetian) (Fleming, 1987). Cox and others (1969) assigned it a Carnian–Norian range, as did Fleming (1962), who also noticed possible records of *Maoritrigonia* from the Ladinian. Later, Fleming (1987) reported it from the Rhaetian.

Paleogeographic distribution.—Austral and Circumpacific (Fig. 44). Kobayashi and Tamura (1968b) recorded a possible record of the genus from the Upper Triassic of Malaysia, although they only doubtfully included *Myophoria bittneri* Newton, 1906, into *Maoritrigonia*. Fleming (1962, 1964) and Freneix and Avias (1977) considered *Maoritrigonia* to be endemic to the Maorian province, but later, Fleming (1987) and Pérez and Reyes (1994) reported it from the Upper Triassic of Chile. Damborenea (2002b) indicated that *Maoritrigonia* had a bipolar distribution. The only references we found from northern high latitudes are Polubotko and Repin (1990), who neither described nor illustrated the specimens, and McRoberts and Blodgett (2000).

Austral domain: Late Triassic: Carnian of New Zealand (Trechmann, 1918; Fleming, 1962, 1964, 1987), New Caledonia (Fleming, 1962); Carnian–Norian of New Caledonia (Freneix & Avias, 1977); Norian of New Zealand (Fleming, 1962, 1964, 1987), ?New Caledonia (Fleming, 1987); Rhaetian of New Zealand (Fleming, 1987).

Circumpacific domain: Late Triassic: ?Peru (Ishikawa & others, 1983; Maeda & others, 1983); Norian of southwestern Alaska

(McRoberts & Blodgett, 2000); Norian–Rhaetian of Chile (Fleming, 1987; Pérez & Reyes, 1991, 1994).

Paleoautoecology.—B, Is, S, FM; Sb. See mode of life for *Trigonia* (p. 113).

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1969). No details are known about *Maoritrigonia* shell microstructure. See discussion under *Trigonia* (p. 113).

Family GROEBERELLIDAE

Pérez, Reyes, & Damborenea, 1995

Genus GROEBERELLA H. A. Leanza, 1993, p. 18

Type species.—*Myophoria neuquensis* Groeber, 1924, p. 92.

Stratigraphic range.—Lower Jurassic (Sinemurian)–Middle Jurassic (Bajocian) (Pérez, Reyes, & Damborenea, 1995). H. A. Leanza (1993) proposed *Groerberella* and assigned it a Pliensbachian–Bajocian range, tentatively including it in the subfamily Minetrigoniinae. Subsequently, the genus was reported from the Sinemurian and referred to a new family, Groeberellidae, because although it had similarities with both Myophoriidae and Minetrigoniidae, it did not fit into any of them (Pérez, Reyes, & Damborenea, 1995). The genus was especially abundant during the Pliensbachian (H. A. Leanza, 1993, 1996; Pérez, Reyes, & Damborenea, 1995; Scholz, Aberhan, & González-León, 2008).

Paleogeographic distribution.—Austral and Circumpacific (Fig. 45).

Austral domain: Early Jurassic: Sinemurian of Argentina (Pérez, Reyes, & Damborenea, 1995; Damborenea & Manceñido, 2005b; Damborenea & Lanés, 2007).

Circumpacific domain: Early Jurassic: Sinemurian of Chile (Pérez, Reyes, & Damborenea, 1995; Pérez & others, 2008).

Paleoautoecology.—B, Is, S, FM; Sb. See mode of life for *Trigonia* (p. 113).

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1969). No details are known about *Groerberella* shell microstructure. See discussion under *Trigonia* (p. 113).

Superfamily MYOIDEA Lamarck, 1809**Family CORBULIDAE Lamarck, 1819****Genus ANTIQUICORBULA Hautmann, 2001b, p. 148**

Type species.—*Antiquicorbula concentrica* Hautmann, 2001b, p. 150.

Stratigraphic range.—Upper Triassic (Norian–Rhaetian) (Hautmann, 2001b). *Antiquicorbula* was a monospecific genus only reported from the Upper Triassic of central Iran (Hautmann, 2001b).

Paleogeographic distribution.—Tethys (Fig. 45).

Tethys domain: Late Triassic: Norian–Rhaetian of Iran (Hautmann, 2001b).

Paleoautoecology.—B, Is, S, SM; Sb. Hautmann (2001b) compared the external morphology of *Antiquicorbula* with the living genus *Corbula* Bruguière, 1797, assigning it the same mode of life. S. M. Stanley (1970) studied the behavior of *Corbula caribaea* d'Orbigny, proving that it is a slow, shallow burrower with very short siphons.

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1973). There are no data about *Antiquicorbula* mineralogy and shell microstructure. The family Corbulidae is characterized by an entirely aragonitic shell with an outer shell layer of cross-lamellar structure and a complex cross-lamellar inner shell layer (J. D. Taylor, Kennedy, & Hall, 1973; Harper, Palmer, & Hudson, 2002).

Superfamily HIATELLOIDEA Gray, 1824**Family HIATELLIDAE Gray, 1824****Genus PSEUDOSAXICAVA Chavan, 1952, p. 119**

Type species.—*Pseudosaxicava bernardi* Chavan, 1952, p. 119.

Remarks.—Chavan (1952) proposed *Pseudosaxicava* as genus, but later Cox and others (1969) regarded it as a subgenus under *Hiatella* Bosc, 1801, and assigned it an Upper Jurassic range. Many authors (e.g., Kelly, 1980; Vokes, 1980; Pisera, 1987; Fürsich, Palmer & Goodyear, 1994; Schneider & Kaim, 2012) followed Cox and others (1969), but Stiller (2006) regarded it as a genus after studying a rich hiatellid fauna from the Lower Jurassic of China.

Stratigraphic range.—Lower Jurassic (Hettangian)–Upper Jurassic (Tithonian) (Fürsich, Palmer, & Goodyear, 1994; Stiller, 2006). Chavan (1952) described the genus from the lower Kimmeridgian of Normandy (France), and, for a long time, *Pseudosaxicava* was thought to be restricted to the Upper Jurassic (Chavan, 1952; Cox & others, 1969; Kelly, 1980; Pisera, 1987; Wignall, 1990; Fürsich, Palmer, & Goodyear, 1994). However, Sepkoski (2002) assigned it a Middle–Upper Jurassic (upper Tithonian) range, following Fürsich, Palmer, and Goodyear (1994), who only mentioned it from the Tithonian. The Chinese specimens studied by Stiller (2006) show that it was already present in the earliest Jurassic. The top of its range is Tithonian (Portlandian; Fürsich, Palmer, & Goodyear, 1994).

Paleogeographic distribution.—Eastern Tethys (Fig. 45). Although during other times (mainly Late Jurassic), *Pseudosaxicava* was also known from the western Tethys (Chavan, 1952; Kelly, 1980; Pisera, 1987; Fürsich, Palmer, & Goodyear, 1994); during our study interval, it was only reported from the Eastern Tethys.

Tethys domain: Early Jurassic: Hettangian of southern China (Guangdong province) (Gu & others, 1976; J. Chen, 1982b; Stiller, 2006, and references therein); Hettangian–Sinemurian of southern China (Hunan province) (Stiller, 2006).

Paleoautoecology.—B, E, S, Epi, Sed; By–N. Holocene species of *Hiatella* are chemical borers or byssate nestlers and are characterized by highly variable shell morphology, due to these life habits, with a high percentage of malformed shells. They can actively bore or reoccupy vacant borings built by other organisms or live epibyssate on several substrates, such as rocks, shells, and vegetation (Stiller, 2006). The same habits were suggested for Jurassic species (Kelly, 1980; Fürsich, Palmer, & Goodyear, 1994), although no evidence of boring activity was detected. The Lower Jurassic specimens from China do not show evidence of malformations or boring capacity, and they likely had an epibyssate or nestling mode of life (Stiller, 2006).

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1973). There are no data about *Pseudosaxicava* mineralogy and shell microstructure. The Recent genus *Hiatella* is characterized by an entirely aragonitic shell with two shell layers of homogeneous microstructure (J. D. Taylor, Kennedy, & Hall, 1973; Brand & McCarthy, 2005).

Superfamily MEGALODONTOIDEA**Morris & Lycett, 1853 in 1851–1855****Family MEGALODONTIDAE****Morris & Lycett, 1853 in 1851–1855****Genus CONCHODON Stoppani, 1865 in 1860–1865, p. 246**

Lycodus Schafhäütl, 1863, p. 375, *non* Quenstedt, 1856, p. 240

Type species.—*Conchodon infraliassicus* Stoppani, 1865 in 1860–1865, p. 246 (= *Lycodus cor* Schafhäütl, 1863, p. 375).

Stratigraphic range.—Upper Triassic (?upper Norian, Rhaetian) (Mensink & Tichy, 1977). Cox and others (1969) assigned a Rhaetian range. Mensink and Tichy (1977) reported it from the Norian (=Sevastian) and Rhaetian, but these authors only described material from the Spanish Rhaetian and did not give any specific data from the Norian. Most authors considered *Conchodon* a typical Rhaetian genus, but Véghe-Neubrandt (1982) indicated that *Conchodon hungaricus* (Hoernes) had a Norian range, although she expressed some doubts about the reliability of this age.

Paleogeographic distribution.—western Tethys (Fig. 46).

Tethys domain: Late Triassic: ?Norian of Hungary and Bakony (Véghe-Neubrandt, 1982); Rhaetian of Poland, Hungary, Bakony, Bavaria, Italy, and Romania (Véghe-Neubrandt, 1982), Austria (Véghe-Neubrandt, 1982; Hallam & El Shaarawy, 1982), Spain (Mensink & Tichy, 1977; Véghe-Neubrandt, 1982), Alps (Italy) (McRoberts, Newton, & Allasinaz, 1995).

Paleoautoecology.—B, E–Se, S, Un, Sed; R. Most megalodontids had very thick, heavy, large, and globose shells with peculiar morphologies. They tended to have the umbonal region thickened; in living position, this area was probably buried into the soft sediment (Posenato & Ietto, 1995). According to Skelton (1978), they may have been byssate in the earlier stages, but adults were reclined on the substrate, probably with part of the shell buried. Pedal muscle scars are present in earlier stages, but the foot was probably atrophied in adulthood. Many megalodontids had a gregarious mode of life. They diversified mainly in tropical environments in shallow, high-energy waters during the Late Triassic (Tichy, 1974; Allasinaz & Zardini, 1977; Freitas, Brunton, & Bernecker, 1993).

The possibility that megalodontids established symbiotic relationships with microorganisms was also postulated, but this is difficult to prove (Seilacher, 1990; Freitas, Brunton, & Bernecker,

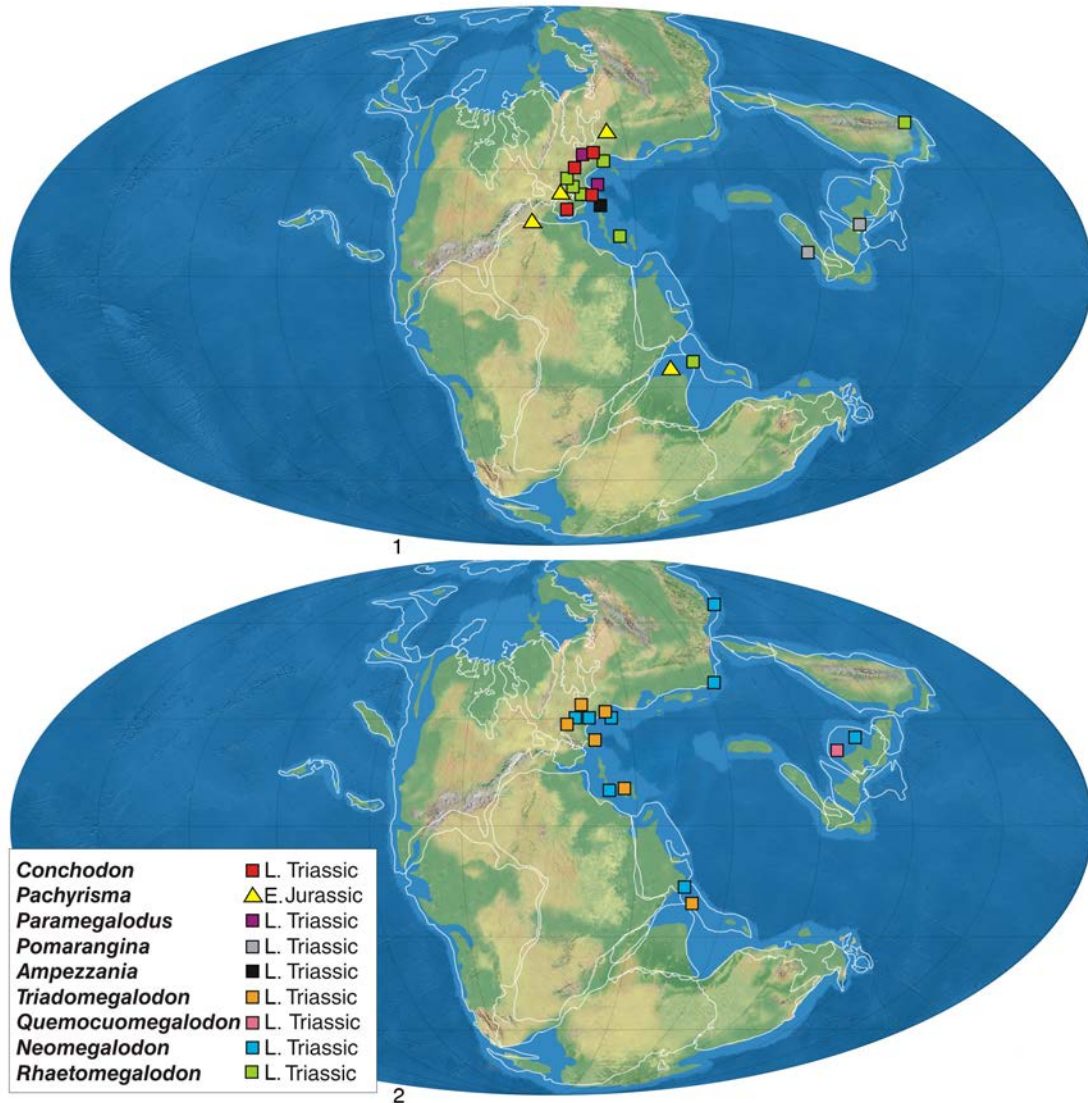


Figure 46. Paleogeographical distribution of Megalodontidae. Late Triassic–Early Jurassic. 1, *Conchodon*, *Pachyrisma*, *Paramegalodus*, *Pomarangina*, *Ampezzania*, *Rhaetomegalodon*; 2, *Triadomegalodon*, *Quemocuomegalodon*, *Neomegalodon*.

1993). The main criteria (see Seilacher, 1990, and Jones & Jacobs, 1992) are the following: they lived in tropical environments; their shells were abnormally large; they showed aberrant morphologies; they had epifaunal habits while coexisting with other infaunal bivalves; and many were gregarious. Although there is no isotopic data to support these relationships, photosymbiosis cannot be rejected (see discussion in Freitas, Brunton, & Bernecker, 1993).

Mineralogy.—Aragonitic (Carter, Barrera, & Tevesz, 1998). No details are known about *Conchodon* shell microstructure. Members of the superfamily Megalodontoidea usually appear as molds or with recrystallized shells, which were interpreted as entirely aragonitic (Carter, Barrera, & Tevesz, 1998; Hautmann, 2006a).

Genus PACHYRISMA Morris & Lycett, 1850, p. 399

Type species.—*Pachyrisma grande* Morris & Lycett, 1850, p. 401.

Remarks.—*Pachyrisma* Morris & Lycett, 1850, along with *Protodicerias* G. Böhm, 1892 (see discussion in Genera not Included, p. 126), represented the recovery of megalodontids during the Early Jurassic, after extinction of all Triassic genera at the Rhaetian–Hettangian boundary. Some authors (e.g., Végh-Neubrandt, 1982) considered *Pachymegalodon* Gümbel, 1862, at generic level and left *Pachyrisma* as a Middle Jurassic genus. According to Végh-Neubrandt (1982, p. 134), *Protodicerias* arose from the *Dicerocardium* lineage and *Pachymegalodon* from *Triadomegalodon*.

Stratigraphic range.—Lower Jurassic (Sinemurian)–Upper Jurassic (Tithonian) (Cox & others, 1969). Cox and others (1969) considered three subgenera within *Pachyrisma*: *P.* (*Pachyrisma*) from the Middle and Upper Jurassic, *P.* (*Durga*) and *P.* (*Pachymegalodon*) from the Lower Jurassic (lower Lower Jurassic). After the interval considered in this paper, the genus was particularly abundant in the Pliensbachian (Hallam 1972, 1977; Tichy, 1974;

Buser & Debeljak, 1994; Liu, 1999; Fraser, Bottjer, & Fischer, 2004). However, it was also reported from the Sinemurian: *P.* (*Pachymegalodon*) from Morocco (Liu, 1995); *P.* (*Durga*) *nicolisi* Böhm, and *P.* (*Pachymegalodon*) *chamaeformis* (Schlotheim) from Europe (Hallam, 1976); *Pachyrisma* aff. *chamaeformis* Schlotheim from Pamir (Melnikova, 2006); *Pachymegalodon crassus* Böhm from the lower Lower Jurassic of Italy (Kennedy, Morris, & Taylor, 1970). None of these papers included Sinemurian specimens, but as we lack information about this genus, we provisionally accept them.

Paleogeographic distribution.—Tethys (Fig. 46).

Tethys domain: Early Jurassic: Sinemurian of Morocco (Liu, 1995), Europe (Kennedy, Morris, & Taylor, 1970; Hallam, 1976), Pamir (Melnikova, 2006).

Paleoautoecology.—B, E-Se, S, Un, Sed; R. See mode of life for *Conchodon*.

Mineralogy.—Aragonitic (Kennedy, Morris, & Taylor, 1970). Kennedy, Morris, and Taylor (1970) studied the shell microstructure of two species attributed to *Pachyrisma*: *Pachymegalodon crassus* (Böhm, 1884) and *Durga trigonalis* Böhm, 1884. The first shows two aragonitic layers: a homogeneous outer layer, and an inner layer with homogeneous to cross-lamellar structure. The second species has a fully recrystallized shell, but they described two aragonitic homogeneous layers.

Genus PARAMEGALODUS Cox in Cox and others, 1969, p. 746

Type species.—*Dicerocardium eupalliatum* Frech, 1904, p. 51.

Remarks.—Végh-Neubrandt (1982) attributed *Paramegalodus* to Kutassy, 1953. This will not be followed here, as Kutassy's manuscript about megalodontids was never published (Végh-Neubrandt, 1969), and, although Kutassy (1934) designated a type species, he did not provide a diagnosis. The first diagnosis was done by Cox in Cox and others (1969, p. 746–747), and therefore he is considered to be the author of the genus. Végh-Neubrandt (1982) noticed that the figures in Cox and others (1969, p. 747, fig. E218a–c) belong to *Dicerocardium eupalliatum* (Vigh, 1914) and not to *Dicerocardium eupalliatum* Frech, 1904, as indicated in the diagnosis of *Paramegalodus*. Therefore, the figured specimens belong, in fact, to the type species of *Rhaetomegalodon* Végh-Neubrandt, 1969 (*R. bajotensis* Végh-Neubrandt, 1969 [= *Megalodus?* *eupalliatum* Vigh, 1914]) rather than to the type species of *Paramegalodus* [*P. eupalliatum* (Frech, 1904)].

Allasinaz in Allasinaz and Zardini (1977) found a great number of well-preserved specimens of *Paramegalodus* and offered a new generic diagnosis with clear diagnostic morphological characteristics and clarified the differences between this genus and *Rhaetomegalodon* Végh-Neubrandt, 1969. Indeed, Allasinaz (in Allasinaz & Zardini, 1977) included two new species in *Paramegalodus*: *P. prolatus* Allasinaz (in Allasinaz & Zardini, 1977), and *P. travenanzensis* Allasinaz (in Allasinaz & Zardini, 1977).

Stratigraphic range.—Upper Triassic (Norian) (Allasinaz & Zardini, 1977). Cox in Cox and others (1969) assigned it a Rhaetian range. Subsequently, Allasinaz in Allasinaz and Zardini (1977) extended its range back to the Norian. However, Végh-Neubrandt (1982)

discussed that the Rhaetian specimens referred to *Paramegalodus* actually belong to *Rhaetomegalodon*. This genus was proposed by Végh-Neubrandt (1969) to group the species formerly included in *Paramegalodus* but which are really different from *P. eupalliatum* Frech, 1904 (see discussion in Végh-Neubrandt, 1969, or Végh-Neubrandt, 1982, p. 357). Following this author, records such as *P. belcheri* from the Rhaetian of Japan (Tamura, 1981) should be included in *Rhaetomegalodon*.

Allasinaz (in Allasinaz & Zardini, 1977) assigned a Norian–Rhaetian range to the type species of *Paramegalodus*. This Rhaetian record is based on Végh-Neubrandt (1960, fig. 34), but, later, Végh-Neubrandt (1982) included this specimen in the synonymy of *Rhaetomegalodon bajotensis bajotensis* Végh-Neubrandt, 1969 [= *Megalodus* (?) *eupalliatum* sensu Vigh (1914), non Frech (1904)], which is the type species of *Rhaetomegalodon*.

Paleogeographic distribution.—Tethys (Fig. 46).

Tethys domain: Late Triassic: Norian of Hungary (Frech, 1904), Italy (Frech, 1904; Allasinaz & Zardini, 1977; Végh-Neubrandt, 1982).

Paleoautoecology.—B, E-Se, S, Un, Sed; R. See mode of life for *Conchodon* (p. 125).

Mineralogy.—Aragonitic (Carter, Barrera, & Tevesz, 1998). No details are known about *Paramegalodus* shell microstructure. See discussion under *Conchodon* (p. 125).

Genus POMARANGINA Diener, 1908, p. 64

Type species.—*Pomarangina haydeni* Diener, 1908, p. 66.

Remarks.—Krumbeck (1914) described some specimens he referred to *P. haydeni*, including this species in the family Lucinidae, since he regarded it as being close to *Gonodon* Schafhüttl, 1863. He also figured the hinge of one specimen (plate XVII, fig. 37), which is very similar to the type species of *Schafhaeutlia* Cossman, 1897 (*pro Gonodon* Schafhüttl, 1863). Diener (1915) argued that Krumbeck (1914) misidentified his specimens and referred them to *Krumbeckia tambangensis* Diener, 1915, type species of *Krumbeckia* Diener, 1915, which is considered a synonym of *Schafhaeutlia* by Hautmann (2001b). Cox in Cox and others (1969) included *Pomarangina* in the family Megalodontidae with doubts and indicated that the hinge and muscles of this genus were unknown. Végh-Neubrandt (1982) did not refer to *Pomarangina* in her monograph of Triassic megalodontids, and no other systematic discussion was published.

Stratigraphic range.—Upper Triassic (Carnian). Cox and others (1969) assigned it a Upper Triassic range. The genus was reported from the Carnian (Diener, 1908; Krumbeck, 1914). Kobayashi and Tamura (1983a) mentioned it from the Upper Triassic of Sichuan, but they did not specify the stage.

Paleogeographic distribution.—Eastern Tethys (Fig. 46).

Tethys domain: Late Triassic: Sichuan (China) (Kobayashi & Tamura, 1983a); Carnian of the Himalayas (Diener, 1908).

Paleoautoecology.—B, E-Se, S, Un, Sed; R. The diagnosis offered by Cox and others (1969) indicates that *Pomarangina* was externally similar to other megalodontids. See mode of life for *Conchodon* (p. 125).

Mineralogy.—Aragonitic (Carter, Barrera, & Tevesz, 1998). No details are known about *Pomarangina* shell microstructure. See discussion under *Conchodon* (p. 125).

Genus AMPEZZANIA

Allasinaz in Allasinaz & Zardini, 1977, p. 121

Type species.—*Ampezzania zardini* Allasinaz in Allasinaz & Zardini, 1977, p. 122.

Stratigraphic range.—Upper Triassic (Norian) (Allasinaz & Zardini, 1977). The genus was proposed by Allasinaz (in Allasinaz & Zardini, 1977), including two species, *A. zardini* Allasinaz (in Allasinaz & Zardini, 1977), and *A. subovata* Allasinaz (in Allasinaz & Zardini, 1977), both reported from the Norian.

Paleogeographic distribution.—western Tethys (Fig. 46).

Tethys domain: Late Triassic: Norian of Cortina d'Ampezzo (Italy) (Allasinaz in Allasinaz & Zardini, 1977).

Paleoautoecology.—B, E-Se, S, Un, Sed; R. See mode of life for *Conchodon* (p. 125).

Mineralogy.—Aragonitic (Carter, Barrera, & Tevesz, 1998). No details are known about *Ampezzania* shell microstructure. See discussion under *Conchodon* (p. 125).

Genus TRIADOMEGALODON Végh-Neubrandt, 1974, p. 10

Type species.—*Megalodus damesi* Hoernes, 1880, p. 121.

Stratigraphic range.—Upper Triassic (Carnian–Rhaetian) (Allasinaz & Zardini, 1977). According to Allasinaz (in Allasinaz & Zardini, 1977), *Triadomegalodon* had a Norian–Rhaetian range. Subsequently, Végh-Neubrandt (1982) reported the genus from Carnian deposits in several localities.

Paleogeographic distribution.—Tethys, ?Circumpacific (Fig. 46). *Triadomegalodon* was also reported from the Upper Triassic of Japan (Tamura, 1990), but the figured specimens are not conclusive. Yancey and Stanley (1999) reported it from the Norian of the western coast of North America, but this datum is dubious, since, according to these authors, the genus was mentioned by Végh-Neubrandt (1982, p. 204), where the species ?*Triadomegalodon canadensis* (Shimer, 1926), from the Norian of British Columbia (Canada), is referred to an uncertain genus.

Tethys domain: Late Triassic: Carnian of Italy, Slovenia, and Austria (Végh-Neubrandt, 1982); Norian of Italy (Végh-Neubrandt & others, 1976; Allasinaz & Zardini, 1977; Végh-Neubrandt, 1982), Austria (Végh-Neubrandt, 1982), Hungary and Turkey (Végh-Neubrandt & others, 1976), Yugoslavia, Hungary, Bulgaria, and Romania (Végh-Neubrandt, 1982); Rhaetian of Hungary and Turkey (Végh-Neubrandt, 1982), Italy (Végh-Neubrandt, 1982; McRoberts, Newton, & Allasinaz, 1995; Posenato & Ietto, 1995), Austria (Végh-Neubrandt & others, 1976; Végh-Neubrandt, 1982), ?India (Végh-Neubrandt, 1982).

Paleoautoecology.—B, Se, S-Ph, Un, Sed; R. The shell of *Triadomegalodon* is thick and heavy, especially in the dorsal region, and the ventral elongation increased during ontogeny (Posenato & Ietto, 1995). These features are interpreted as adaptations to a semi-infaunal mode of life, the shell resting with its umbonal region buried into the soft substrate and the ventral part exposed (Posenato & Ietto, 1995). In the adult stage, the foot was probably atrophied and the bivalve was sedentary. A symbiotic relationships with zooxanthellae is also very likely (Seilacher, 1990; McRoberts, Newton, & Allasinaz, 1995).

Mineralogy.—Aragonitic (Carter, Barrera, & Tevesz, 1998). No details are known about *Triadomegalodon* shell microstructure. See discussion under *Conchodon* (p. 125).

Genus QUEMOCUOMEGALODON H. Yao, Sha, & Zhang in H. Yao & others, 2003, p. 395, 399

Type species.—*Quemocuomegalodon orientus* H. Yao, Sha, & Zhang in H. Yao & others, 2003, p. 396.

Stratigraphic range.—Upper Triassic (Norian) (H. Yao & others, 2007). H. Yao and others (2003) proposed the genus from Upper Triassic beds of western China, associated with *Palaeocardita*, gastropods, and algae. Later, H. Yao and others (2007) described a richer associated fauna, which included other bivalves and ammonoids and allowed them to date the sediments where *Quemocuomegalodon* was found as Norian. *Quemocuomegalodon* includes three species: *Q. orientus* H. Yao, Sha, & Zhang in H. Yao & others, 2003, *Q. longitatus* H. Yao, Sha, & Zhang in H. Yao & others, 2003, and *Q. circularis* H. Yao & others, 2007.

Paleogeographic distribution.—Eastern Tethys (Fig. 46).

Tethys domain: Late Triassic: Norian of western China (H. Yao & others, 2003, 2007).

Paleoautoecology.—B, E-Se, S, Un, Sed; R. See mode of life for *Conchodon* (p. 125).

Mineralogy.—Aragonitic (Carter, Barrera, & Tevesz, 1998). No details are known about *Quemocuomegalodon* shell microstructure. See discussion under *Conchodon* (p. 125).

Genus NEOMEGALODON Gümbel, 1862, p. 362

Type species.—*Cardium triquetrum* Wulfen, 1793, p. 48.

Remarks.—Although Cox and others (1969) considered *Neomegalodon* as a subgenus of *Megalodon*, following Gümbel (1862), Allasinaz (1965) raised it to generic level and included three subgenera: *N. (Neomegalodon)*, *N. (Rossiodus)* Allasinaz, 1965, and *N. (Gemmellarodus)* Di Stefano, 1912. Subsequently, both *Gemmellarodus* and *Rossiodus* were raised to generic level by Allasinaz (in Allasinaz & Zardini, 1977), and followed by Végh-Neubrandt (1982). Neither of these two taxa are included in this study (see discussion in Genera not Included, p. 161, 170). Like most authors, we regard *Neomegalodon* as a distinct genus (Végh-Neubrandt & others, 1976; Allasinaz & Zardini, 1977; Tichy, 1980a, 1980b; Végh-Neubrandt, 1982; Tichy & Schramm, 1983).

Stratigraphic range.—Upper Triassic (Carnian–Rhaetian) (Cox & others, 1969; Allasinaz & Zardini, 1977). *Neomegalodon* was reported exclusively from the Upper Triassic (Cox & others, 1969). There is a record of the genus from Ladinian beds of western North America (Fraser, 1997), but the specimens were not described, and the figures provided are inconclusive.

Paleogeographic distribution.—Tethys and Boreal (Fig. 46). Cox and others (1969) regarded it a cosmopolitan genus, but we only found it recorded in the Tethys domain, the same distribution provided by Allasinaz and Zardini (1977). Damborenea (2002b) indicated that it was never found in South America.

Tethys domain: Late Triassic: Hungary (Frech, 1904); Carnian of the Alps (Austria) (Zapfe, 1972; Tichy, 1980a, 1980b; Végh-Neubrandt, 1982), Italy (Allasinaz, 1965; Allasinaz & Zardini, 1977; Végh-Neubrandt, 1982), Hungary, Bavaria, Slovenia, Slovakia, and India (Végh-Neubrandt, 1982); Carnian–Norian of Slovakia (Bujnovsky & Kochanová, 1973);

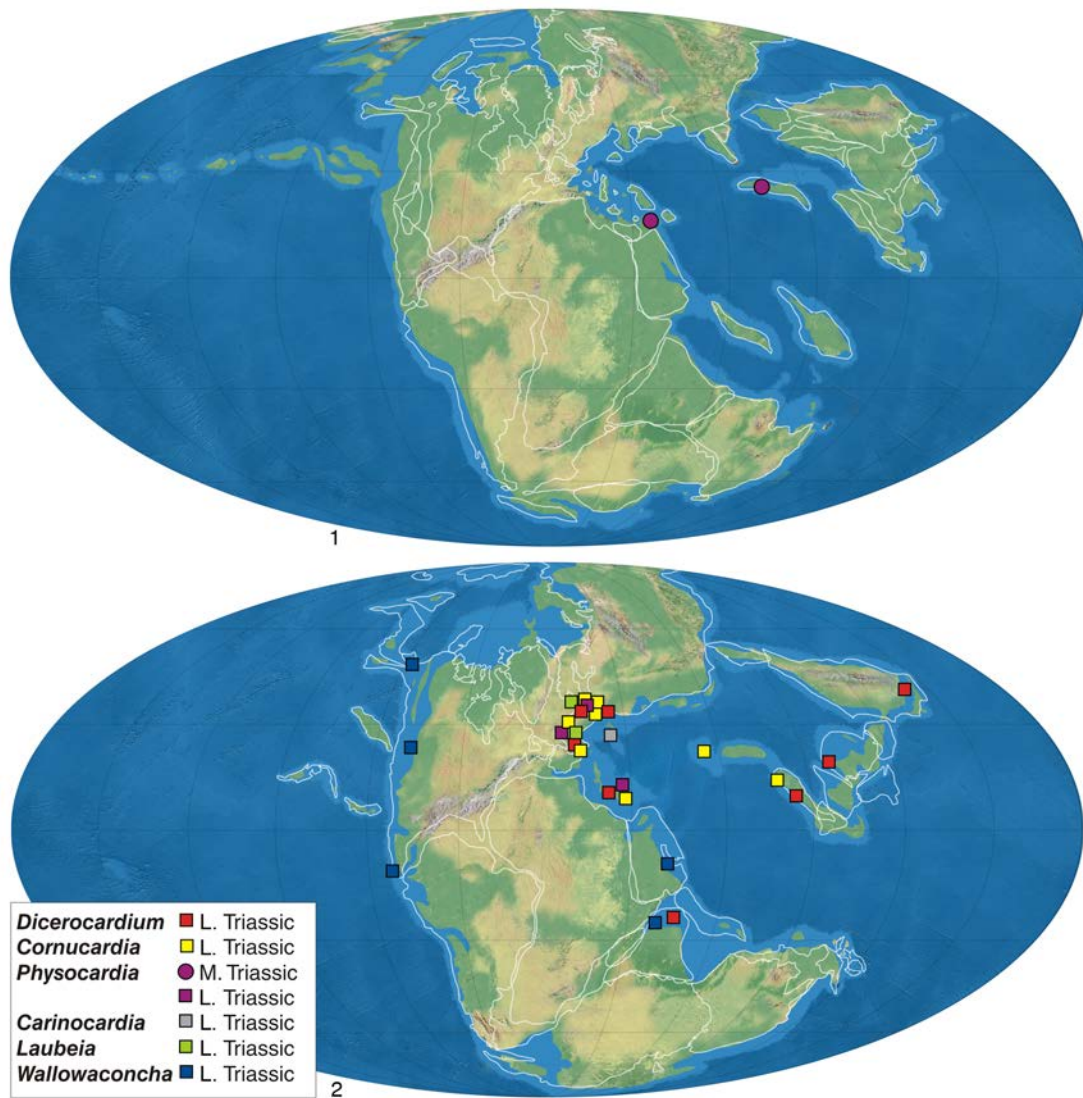


Figure 47. Paleogeographical distribution of Dicerocardiidae (*Dicerocardium*, *Cornucardia*, *Physocardia*, *Carinocardia*, *Laubeia*) and Wallowaonchidae (*Wallowaoncha*). 1, Middle Triassic; 2, Late Triassic.

Norian of western China (H. Yao & others, 2007), Afghanistan (Polubotko, Payevskaya, & Repin, 2001), Alps (Austria) (Tichy, 1975; Végh-Neubrandt, 1982; Tichy & Schramm, 1983), Italy (Allasinaz & Zardini, 1977; Végh-Neubrandt, 1982), Hungary, Slovenia, Albania, Turkey, Yugoslavia, and India (Végh-Neubrandt, 1982), Turkey (Végh-Neubrandt & others, 1976; Végh-Neubrandt 1982); Rhaetian of Austria (Cox & others, 1969; Végh-Neubrandt, 1982).

Boreal domain: Late Triassic: Carnian of Primorie (Kiparisova, 1972).

Paleoautoecology.—B, E-Se, S, Un, Sed; R. See mode of life for *Conchodon* (p. 125).

Mineralogy.—Aragonitic (Carter, Barrera, & Tevesz, 1998). No details are known about *Neomegalodon* shell microstructure. See discussion under *Conchodon* (p. 125).

Genus RHAETOMEGALODON Végh-Neubrandt, 1969, p. 121

Type species.—*Rhaetomegalodon bajotensis* Végh-Neubrandt, 1969, p. 123; =*Megalodus ? eupalliatius sensu* Vigh, 1914, p. 603, *non sensu* Frech, 1904.

Remarks.—Végh-Neubrandt (1969) proposed the genus *Rhaetomegalodon* to group many of the Rhaetian species formerly included in *Paramegalodus*, since she considered them to be different from the type species of *Paramegalodus* and useful biostratigraphically. Allasinaz and Zardini (1977) indicated that Végh-Neubrandt (1969) did not give a precise diagnosis and warned that, given the similarities between *Paramegalodus* and *Rhaetomegalodon*, this could be considered a subgenus of the first (see Allasinaz & Zardini, 1977, p. 46, 109, 117). However, these authors offered a number of differences to distinguish *Rhaetomegalodon* at generic level: “In realtà

questi due generi si differenziano tra loro solo per un diverso modo d'incurvamento degli umboni: essi sono prima piegati all'esterno e poi verso l'interno in *Rhaetomegalodon*, incurvati prima verso l'avanti e poi con apici tendenti a ruotare verso l'esterno in *Paramegalodus*." Zapfe (1969) discussed the genus extensively and established the type species but did not give a proper diagnosis of the genus (Allasinaz & Zardini, 1977, p. 117).

Stratigraphic range.—Upper Triassic (Norian–Rhaetian) (Allasinaz & Zardini, 1977). The genus was proposed by Végh-Neubrandt (1969) from the Rhaetian. Subsequently, it was also reported from the Norian (Allasinaz & Zardini, 1977).

Paleogeographic distribution.—western Tethys and Circumpacific (Fig. 46).

Tethys domain: Late Triassic: Norian of Italy (Allasinaz & Zardini, 1977; Végh-Neubrandt, 1982); Rhaetian of Hungary (Végh-Neubrandt, 1969, 1982), Bakony, Poland, and India (Végh-Neubrandt, 1982), Austria (Zapfe, 1969; Végh-Neubrandt, 1982), Turkey (Végh-Neubrandt & others, 1976; Végh-Neubrandt, 1982).

Circumpacific domain: Late Triassic: Rhaetian of Japan (Tamura, 1981).

Paleoautoecology.—B, E-Se, S, Un, Sed; R. See mode of life for *Conchodon* (p. 125).

Mineralogy.—Aragonitic (Carter, Barrera, & Tevesz, 1998). No details are known about *Rhaetomegalodon* shell microstructure. See discussion under *Conchodon* (p. 125).

Family DICEROCARDIIDAE Kutassy, 1934

Genus DICEROCARDIUM

Stoppani, 1865 in 1860–1865, p. 248

Type species.—*Dicerocardium jani* Stoppani, 1865 in 1860–1865, p. 249.

Stratigraphic range.—Upper Triassic (upper Carnian–Rhaetian). Cox and others (1969) assigned it a Norian–Rhaetian range, but later the genus was reported from upper Carnian beds of several localities (Allasinaz & Zardini, 1977; Tamura, 1981; Végh-Neubrandt, 1982).

Paleogeographic distribution.—Tethys and Circumpacific (Fig. 47).

Tethys domain: Late Triassic: ?Indonesia (Krumbeck, 1924); Carnian–Norian of Italy (Allasinaz & Zardini, 1977; Végh-Neubrandt, 1982); Norian of Hungary, Austria, India, and Slovenia (Végh-Neubrandt, 1982), Turkey (Végh-Neubrandt & others, 1976; Végh-Neubrandt, 1982); Rhaetian of the Alps (Zapfe, 1963, 1981), Himalayas (Stoliczka, 1866, 1871 in 1870–1871; Cox & others, 1969), ?India (Végh-Neubrandt, 1982).

Circumpacific domain: Late Triassic: Carnian–Norian of Japan (Tamura, 1981); Norian of Japan (Tamura, 1990).

Paleoautoecology.—B, E-Se, S-Ph, Un, Sed; R. *Dicerocardium* is morphologically similar to the living *Corculum*, which establishes photosymbiotic relationships with algae, and it was proposed that *Dicerocardium* may also have done this (Seilacher, 1990). The inferred life position of *Dicerocardium* was very similar to *Wallowaconcha* Yancey & Stanley, 1999, lying on the substrate with the so-called wings horizontally and in contact with it, maybe somewhat buried.

Mineralogy.—Aragonitic (Carter, Barrera, & Tevesz, 1998). No details are known about *Dicerocardium* shell microstructure. See discussion under *Conchodon* (p. 125).

Genus CORNUCARDIA Koken, 1913, p. 34

Type species.—*Craspedodon hornigii* Bittner, 1901c, p. 8.

Stratigraphic range.—Upper Triassic (Carnian) (Broglia-Loriga, Ietto, & Posenato, 1993). *Cornucardia* was restricted to the Carnian (Cox & others, 1969).

Paleogeographic distribution.—Tethys (Fig. 47).

Tethys domain: Late Triassic: Iran (Hautmann, 2001b); Carnian of Timor (Indonesia) (Krumbeck, 1924; Végh-Neubrandt, 1982), Italy (Leonardi, 1943; Rau & Tongiorgi, 1966; Corazzari & Lucchi-Garavello, 1980; Végh-Neubrandt, 1982; Broglia-Loriga, Ietto, & Posenato, 1993), southern Alps (Bittner, 1901b), northern Alps (Austria) (Zapfe, 1972; Végh-Neubrandt, 1982), Germany (Tichy, 1980a), Hungary (Tichy, 1980a; Végh-Neubrandt, 1982), Slovenia (Jurkovsek, 1978), Turkey (Végh-Neubrandt & others, 1976; Végh-Neubrandt, 1982), Yugoslavia (Végh-Neubrandt, 1982).

Paleoautoecology.—B, E-Se, S, Un, Sed; R. *Cornucardia* had a heavy shell, strongly inflated and coiled umbos, and it most likely lived reclining on the substrate, like most members of the superfamily Megalodontoidea. Since the shell was usually large and heavy, it is possible that it could be partially buried.

Mineralogy.—Aragonitic (Carter, Barrera, & Tevesz, 1998). No details are known about *Cornucardia* shell microstructure. See discussion under *Conchodon* (p. 125).

Genus PHYSOCARDIA Wöhrmann, 1894, p. 671

Type species.—*Physocardia ogilviae* Wöhrmann, 1894, p. 672.

Stratigraphic range.—Middle Triassic (Anisian)–Upper Triassic (Carnian) (Fantini Sestini, 1984). Cox and others (1969) reported it from the Carnian of the Alps. Subsequently, it was also recorded from the Middle Triassic (middle Anisian) (Fantini Sestini, 1984). This author referred to an Iranian specimen, morphologically very similar to specimens studied in that paper, which could be the oldest of the genus.

Paleogeographic distribution.—western Tethys (Fig. 47).

Tethys domain: Middle Triassic: Anisian of Turkey and Iran (Fantini Sestini, 1984); ?Ladinian of Turkey (Végh-Neubrandt, 1982); Late Triassic: Carnian of the Alps (Frech, 1904; Fürsich & Wendt, 1977; Végh-Neubrandt, 1982), Dolomites (Italy) (Végh-Neubrandt, 1982); Turkey (Végh-Neubrandt & others, 1976; Végh-Neubrandt, 1982).

Paleoautoecology.—B, E-Se, S, Un, Sed; R. Similar to *Cornucardia*.

Mineralogy.—Aragonitic (Carter, Barrera, & Tevesz, 1998). No details are known about *Physocardia* shell microstructure. See discussion under *Conchodon* (p. 125).

Genus CARINOCARDIA Termier & Verriez, 1974, p. 161

Type species.—*Carinocardia atalantiensis* Termier & Verriez, 1974, p. 161.

Stratigraphic range.—Upper Triassic (lower Carnian) (Termier & Verriez, 1974). *Carinocardia* was proposed by Termier and Verriez (1974) from the Upper Triassic (lower Carnian) of Atalanti (Greece).

Paleogeographic distribution.—western Tethys (Fig. 47).

Tethys domain: Late Triassic: Carnian of Greece (Termier & Verriez, 1974).

Paleoautoecology.—B, E-Se, S, Un, Sed; R. Similar to *Cornucardia*.

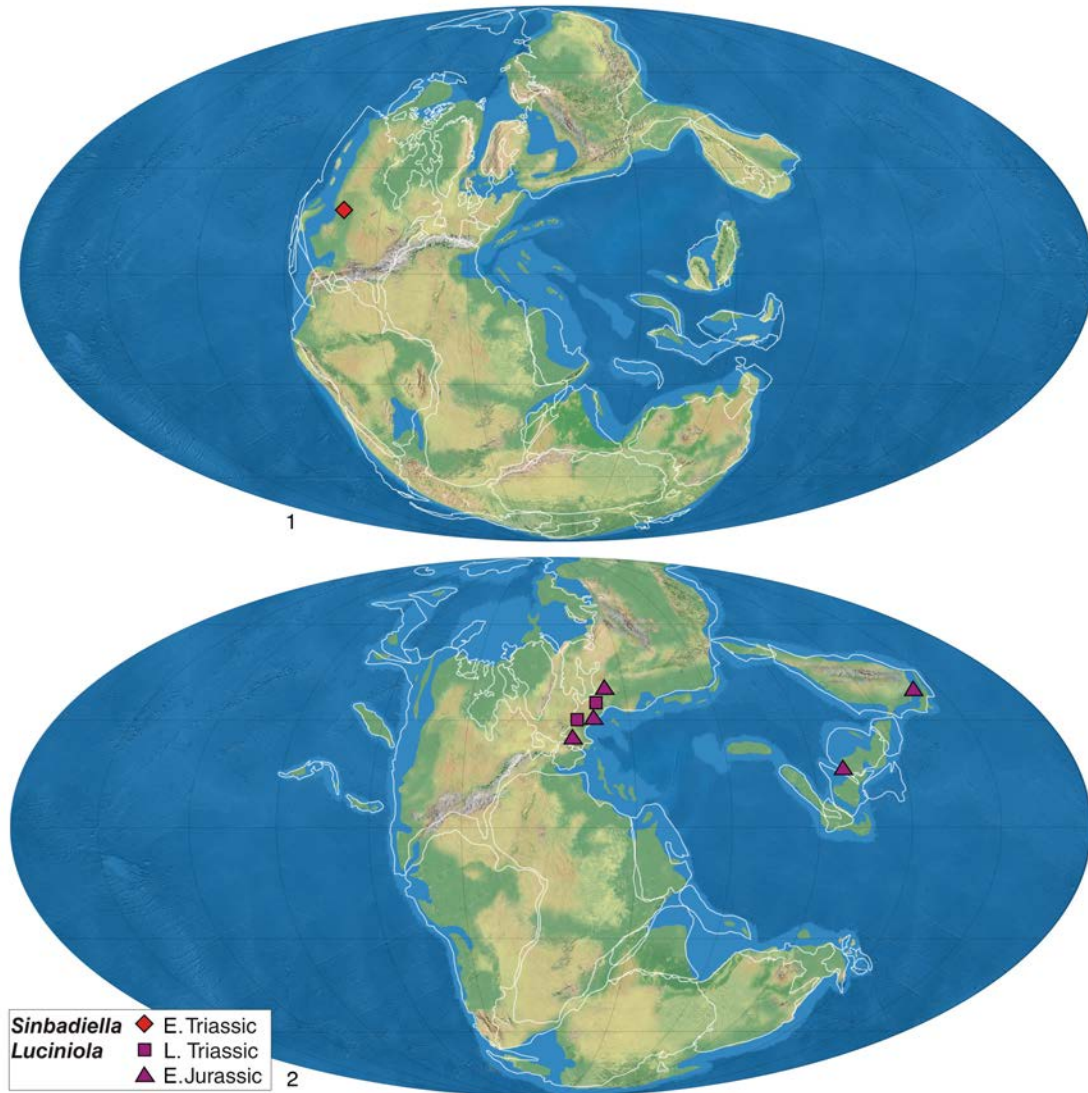


Figure 48. Paleogeographical distribution of Lucinidae (*Sinbadiella*, *Luciniola*). 1, Early Triassic; 2, Late Triassic–Early Jurassic.

Mineralogy.—Aragonitic (Carter, Barrera, & Tevesz, 1998). No details are known about *Carinocardia* shell microstructure. See discussion under *Conchodon* (p. 125).

Genus LAUBEIA Bittner, 1895, p. 26

Type species.—*Cardita strigilata* Klipstein, 1845 in 1843–1845, p. 35.

Remarks.—Allasinaz (1966) included *Laubeia* in the family Megalodontidae. Later, Cox and others (1969) argued that its features did not even fit in the class Bivalvia. Hallam (1981) indicated that *Laubeia* was a bivalve but belonged to an uncertain order. Finally, Végé-Neubrandt (1982) decided to include this monospecific genus in the family Dicerocardiidae.

Stratigraphic range.—Upper Triassic (Carnian) (Cox & others, 1969). *Laubeia* was a monospecific genus and had a Carnian

range (Bittner, 1895; Allasinaz, 1966; Cox & others, 1969; Végé-Neubrandt, 1982).

Paleogeographic distribution.—western Tethys (Fig. 47).

Tethys domain: Late Triassic: Carnian of southern Tirol (Austria) (Bittner, 1895), southern Alps (Italy) (Allasinaz, 1966; Végé-Neubrandt, 1982).

Paleoautoecology.—B, E-Se, S, Un, Sed; R. Similar to *Cornucardia*.

Mineralogy.—Aragonitic (Carter, Barrera, & Tevesz, 1998). No details are known about *Laubeia* shell microstructure. See discussion under *Conchodon* (p. 125).

Family WALLOWACONCHIDAE Yancey & Stanley, 1999

Genus WALLOWACONCHA Yancey & Stanley, 1999, p. 7

Type species.—*Wallowaconcha raylenea* Yancey & Stanley, 1999, p. 10.

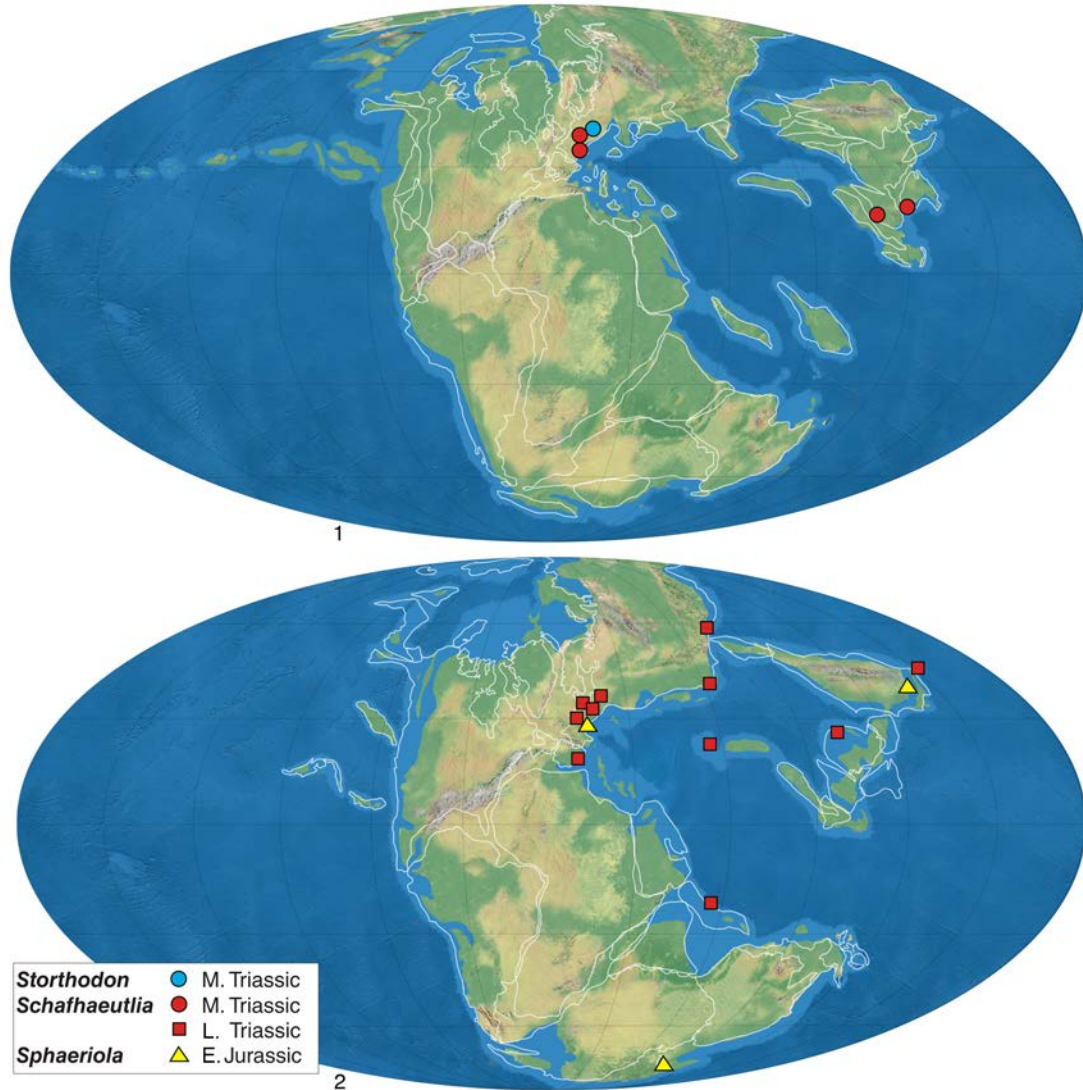


Figure 49. Paleogeographical distribution of Thyasiridae (*Storthodon*) and Fimbriidae (*Schafhaeutlia*, *Sphaeriola*). 1, Middle Triassic; 2, Late Triassic–Early Jurassic.

Stratigraphic range.—Upper Triassic (Norian) (Yancey & others, 2005). Although *Wallowaconcha* was proposed by Yancey and Stanley (1999), it had previously been reported from the Upper Triassic by the same authors (1987, 1996). It had a Norian range (Yancey & others, 2005).

Paleogeographic distribution.—Tethys and Circumpacific (Fig. 47).

Tethys domain: Late Triassic: Norian of United Arab Emirates (Woods & Yancey, 2004; Yancey & others, 2005), Himalaya (north-western India) (Yancey & others, 2005).

Circumpacific domain: Late Triassic: Norian of Oregon (United States) (Yancey & Stanley, 1987, 1999), Yukon (Canada) (Yancey & Stanley, 1999; Yarnell, Stanley, & Hart, 1999), and Sonora (Mexico) (Yancey & Stanley, 1999).

Paleoautoecology.—B, E-Se, S-Ch-Ph, Un, Sed; R. *Wallowaconcha* lived reclining on the substrate with the commissural plane vertical, with the wings being horizontal on the substrate (see Yancey & Stanley, 1999, fig. 7). It had a gregarious mode of life. Its aberrant morphology indicates that it could establish symbiotic relationships with microorganisms. There are

certain features, such as the heavy shell, large size, and poor capacity to open the valves, that indicate the possibility of chemo- or photosymbiotic relations (see Yancey & Stanley, 1999, p. 19–20). In addition, wallowaconchids lived in tropical environments, another criterion that helps to identify the photosymbiosis in fossil organisms according to Seilacher (1990).

Mineralogy.—Aragonitic (Carter, Barrera, & Tevesz, 1998). The mineralogy and microstructure of *Wallowaconcha* are unknown, but probably part of the shell had a prismatic microstructure (Yancey & Stanley, 1999). Carter, Barrera, and Tevesz (1998) considered that members of the superfamily Megalodontoidea had a completely aragonitic shell.

Superfamily LUCINOIDEA Fleming, 1828

Family LUCINIDAE Fleming, 1828

Genus SINBADIELLA Hautmann & Nützel, 2005, p. 1132

Type species.—*Sinbadiella pygmaea* Hautmann & Nützel, 2005, p. 1133.

Stratigraphic range.—Lower Triassic (Olenekian) (Hautmann & Nützel, 2005). Hautmann and Nützel (2005) proposed *Sinbadiella* from the Olenekian of the Moenkopi Formation. This is the only record of a bivalve of the order Heterodonta from the Lower Triassic.

Paleogeographic distribution.—Circumpacific (Fig. 48).

Circumpacific domain: Early Triassic: Olenekian of Utah (United States) (Hautmann & Nützel, 2005).

Paleoautoecology.—B, Is, S-?Ch, SM; Sb. Hautmann and Nützel (2005) assumed that *Sinbadiella*, like living lucinids, established chemosymbiotic relations, since the Early Triassic was a time with reduced primary productivity and anoxia-dominated environments after the end of the P/T extinction, although this may be implausible. Most likely, it was a shallow burrower, since the deep burrowers did not appear until later when the recovery of the extinction was complete (Twitchett, 2006).

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1973). The shell mineralogy and microstructure of *Sinbadiella* is unknown. J. D. Taylor, Kennedy, and Hall (1973) described three aragonitic shell layers in members of the superfamily Lucinoidea: a prismatic outer layer and middle and inner layers with cross-lamellar microstructure.

Genus LUCINIOLA Skeat & Madsen, 1898, p. 86

Type species.—*Venus pumila* Münster, 1841, in Goldfuss, 1833–1841, p. 243.

Stratigraphic range.—Upper Triassic (Rhaetian)–Lower Jurassic (Pliensbachian). Cox and others (1969) recorded it from the European Lower Jurassic. *Luciniola* was long considered to have appeared in the Hettangian just after Triassic–Jurassic extinction event (Hallam, 1987, 1990). However, the species *Luciniola stoppaniana* (Dittmar, 1864) was also mentioned from the Rhaetian (McRoberts, Newton, & Allasinaz, 1995). This species was originally referred to *Lucina* Bruguière, 1797, a Cretaceous to Recent (Cox & others, 1969) genus. *Luciniola stoppaniana* was abundant in the Alpine Rhaetian and in Hungary (Borghi, 1937; Chiesa, 1949; Vörös, 1981; McRoberts, Newton, & Allasinaz, 1995).

Paleogeographic distribution.—Tethys and Circumpacific (Fig. 48). *Luciniola* was regarded as a genus endemic in the western Tethys (Cox & others, 1969), but it was subsequently reported from Japan and China.

Tethys domain: Late Triassic: Rhaetian of the Italian Alps (Borghi, 1937; Chiesa, 1949; McRoberts, Newton, & Allasinaz, 1995), Hungary (Vörös, 1981); Early Jurassic: Hettangian of China (Z. Huang, 1986); Hettangian or Sinemurian of China (Stiller, 2006, and references therein); Hettangian–Sinemurian of Europe (Hallam, 1976, 1977, 1987); Sinemurian of China (J. Yin, H. Yao, & Sha, 2004).

Circumpacific domain: Early Jurassic: Sinemurian of Japan (Hayami, 1975).

Paleoautoecology.—B, Is, S-?Ch, SM; Sb. Many living Lucinidae establish chemosymbiotic relationships with sulfate-reducing bacteria (Beesley, Ross, & Wells, 1998). Similar relationships may have been already established by Mesozoic times, and this can explain some of their morphological features (Seilacher, 1990). There are some shell features associated with symbiosis that can be recognized in fossil shells, such as the position of the anterior adductor muscle scars (J. D. Taylor & Glover, 2000, 2006). Lucinidae are infaunal

siphonate burrowers. According to Stiller (2006), *Luciniola* was a shallow burrower.

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1973). The shell mineralogy and microstructure of *Luciniola* is unknown. See discussion in *Sinbadiella* (p. 132).

Family THYASIRIDAE Dall, 1901

Genus STORTHODON Giebel, 1856, p. 102

Type species.—*Storthodon liscaviensis* Giebel, 1856, p. 79.

Stratigraphic range.—Middle Triassic (Ladinian) (Hallam, 1981). *Storthodon* was proposed by Giebel (1856) from the Muschelkalk of Germany. Chavan (in Cox & others, 1969) included it in the family Thyasiridae, but J. D. Taylor and others (2007) and J. D. Taylor, Williams, and Glover (2007) argued that this family had a Early Cretaceous origin and that *Storthodon* did not belong there. They did not give any indication of possible relationships, so we provisionally follow Chavan (in Cox & others, 1969). Giebel (1856) noticed that there was some resemblance between his new genus and *Lucina*, but some aspects, such as the hinge, are not comparable. Hallam (1981) recorded it from Ladinian times.

Paleogeographic distribution.—western Tethys (Fig. 49).

Tethys domain: Middle Triassic: Muschelkalk of Germany (Giebel, 1856).

Paleoautoecology.—Unknown. Living Thyasiridae species normally inhabit deep waters, and, as in Lucinidae, they may have sulphate-reducing bacteria in their gills. But it is very unlikely that *Storthodon* belongs to this family.

Mineralogy.—Unknown. The shell mineralogy and microstructure of *Storthodon* are unknown. Because its taxonomic relations are not clear, we cannot use the dominant mineralogy in the family.

Family FIMBRIIDAE Nicol, 1950

Genus SCHAFHAEUTLIA Cossmann, 1897, p. 51

[*nom. nov. pro Gonodon* Schafhäutl, 1863, p. 382, *non* Held, 1837, p. 918]

Type species.—*Gonodon schafhaeutli* Salomon, 1895, p. 169 [= *Gonodon ovatum* Schafhäutl, 1863, p. 382, *non Cyprina ovata* Stoppani, 1860 in 1858–1860, *nec Isocardia ovata* Münster, 1837, in Goldfuss, 1833–1841] (see Hautmann, 2001b, p. 123–124).

Remarks.—*Krumbeckia* Diener, 1915, was regarded as a synonym of *Schafhaeutlia* by Hautmann (2001a) (see discussion for *Krumbeckia* in Genera not Included, p. 163) and *Isocardioides* Fan, 1963, probably is also a junior synonym of *Schafhaeutlia*, according to Gu and others (1976) and Z. Fang and others (2009).

Stratigraphic range.—Middle Triassic (Anisian)–Upper Triassic (Rhaetian) (Hautmann, 2001b; Komatsu, Chen, & others, 2004). Cox and others (1969) assigned it an Upper Triassic range and a European and South American distribution. Subsequently, the range was expanded by new Middle Triassic records. The range of this genus is most probably artificially extended, as many species were attributed to *Schafhaeutlia* simply on the basis of external form and ornamentation, regardless of internal characters (Monari, 2003), as happened with records of the genus from the eastern coast of the Paleopacific (see paleogeographic distribution).

Paleogeographic distribution.—Tethys, Boreal, and Circumpacific (Fig. 49). For a more complete distribution in the western Tethys, see

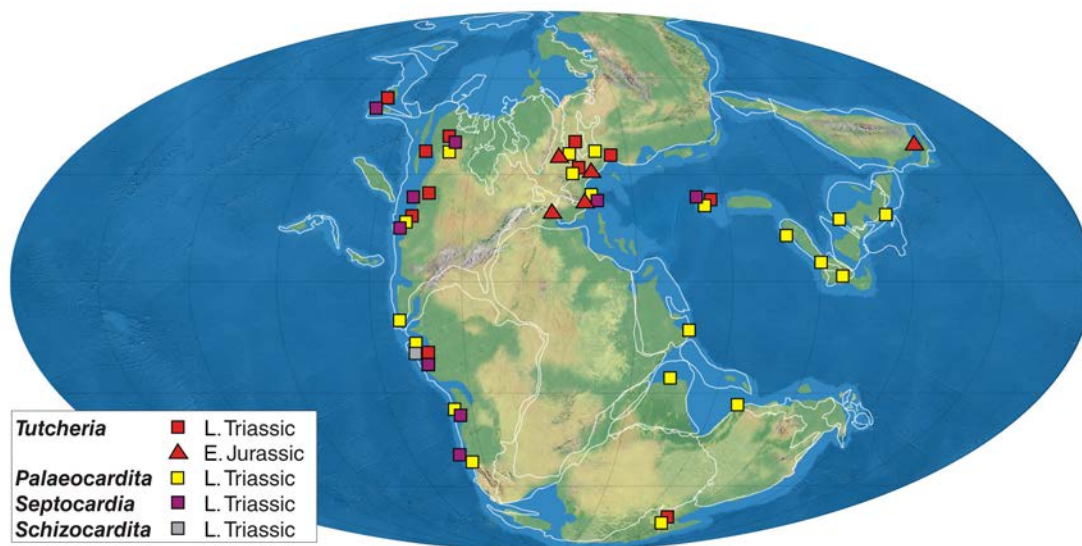


Figure 50. Paleogeographical distribution of Carditidae (*Tutcheria*, *Palaeocardita*, *Septocardia*, *Schizocardita*). Late Triassic–Early Jurassic.

Monari (2003, p. 882–883). The genus was reported from Rhaetian beds of Nevada (Laws, 1982; Hallam & Wignall, 2000), but none of these papers contain descriptions or figures of the specimens. McRoberts (1997a) recorded *Schafhaeutlia* sp. from the Rhaetian of Sonora (Mexico), but he assigned his two valves to the genus on the basis of external morphology alone, as internal characters were not observed. The same applies to records from the Upper Triassic of Chile (Hayami, Maeda, & Ruiz-Fuller, 1977; Chong & Hillebrandt, 1985) and Peru (Cox, 1949). Therefore, we consider the presence of this genus in the eastern Paleopacific as doubtful.

Tethys domain: Middle Triassic: Anisian of southern China (Sha, Chen, & Qi, 1990; Komatsu, Chen, & others, 2004), southern Alps (Monari, 2003), northern Vietnam (Komatsu, Huyen, & Huu, 2010); Ladinian of Italy (Rossi Ronchetti, 1959), China (Sha, Chen, & Qi, 1990), northern Vietnam (Komatsu, Huyen, & Huu, 2010); Late Triassic: Carnian of the Alps (Italy) (Leonardi, 1943; Allasinaz, 1964, 1966; Gelati & Allasinaz, 1964; Fürsich & Wendt, 1977), Yugoslavia (Jurkovsek & Jelen, 1990), Slovenia (Jelen, 1988), Spain (Pérez-Valera & others, 2007); Norian of western China (H. Yao & others, 2007), Afghanistan (Polubotko, Payevskaya, & Repin, 2001); Norian–Rhaetian of Iran (Hautmann, 2001b); Rhaetian of ?Tibet (J. Yin & McRoberts, 2006), ?Hungary (Vörös, 1981).

Circumpacific domain: Late Triassic: Carnian of Japan (Hayami, 1975).

Boreal domain: Late Triassic: Carnian of Primorie (Kiparisova, 1972).

Paleoautoecology.—B, Is, S, SM; Sb. Living species of *Fimbria*, the only extant genus of Fimbriidae, are slow infaunal burrowers (Beesley, Ross, & Wells, 1998; see discussion in Monari, 2003) and they are found among corals in shallow waters. *Schafhaeutlia globosa* had a globose shell, similar to some species of *Fimbria*, and it was most likely a slow burrower. However, Hautmann (2001b) proposed an epibenthic mode of life for *Schafhaeutlia sphaerioides* (Boettger, 1880), living freely resting on the substrate.

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1973). There are no data about *Schafhaeutlia* shell mineralogy or microstructure. J. D. Taylor, Kennedy, and Hall (1973) described three aragonitic shell layers in members of superfamily Lucinoidea: a prismatic outer shell layer and middle and inner shell layers of cross-lamellar microstructure. Monari (2003) studied the shell microstructure of *Cerkesia contiae* Monari, 2003, an Upper Jurassic member of family Fimbriidae from Turkey, and found the same structure.

Genus SPHAERIOLA Stoliczka, 1871 in 1870–1871, p. 247

Type species.—*Cardium madridi* Archiac, 1843, p. 373.

Stratigraphic range.—Lower Jurassic (Sinemurian)–Middle Jurassic (Callovian) (Monari, 2003). Cox and others (1969) assigned it a Jurassic (Domerian [=Pliensbachian]–Bathonian) range. However, Monari (2003) reviewed the history of *Sphaeriola* and proposed a Sinemurian to Callovian range.

Paleogeographic distribution.—Tethys, Circumpacific, and Austral (Fig. 49). *Sphaeriola* was doubtfully mentioned from the Hettangian–Sinemurian boundary of the Neuquén Basin (Damborenea & Manceñido, 2005b).

Tethys domain: Early Jurassic: Sinemurian of the southern Alps (Italy) (Parona, 1890; Monari, 2003).

Circumpacific domain: Early Jurassic: Sinemurian of Japan (Hayami, 1975).

Austral domain: Early Jurassic: Hettangian–Sinemurian of New Zealand (Marwick, 1953).

Paleoautoecology.—B, Is, S-Ch, SM; Sb. Living *Fimbria* species are shallow burrowers, but the foot is not as developed as in other Lucinoidea, and they are slow burrowers (Beesley, Ross, & Wells, 1998). Like other Lucinidae, they also have sulphate-reducing bacteria in their gills, at least in *F. fimbriata* (Linnaeus, 1758), studied by J. D. Taylor and Glover (2000). We assume that *Sphaeriola* had a similar mode of life.

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1973). There are no data about *Sphaeriola* shell mineralogy or microstructure. See discussion in *Schafbaeutlia* (p. 133).

Superfamily CARDITOIDEA Férussac, 1822 in 1821–1822

Family CARDITIDAE Férussac, 1822 in 1821–1822

Genus TUTCHERIA Cox, 1946, p. 35

Type species.—*Cardium submulticostatum* d'Orbigny, 1850, p. 235.

Remarks.—Cox (1946) included *Tutcheria* in the family Astartidae. However, Chavan in Cox and others (1969) and Hayami (1969b) transferred it to the Carditidae.

Stratigraphic range.—Upper Triassic (Carnian)–Middle Jurassic (Aalenian) (Cox, 1946). According to Cox (1946), *Tutcheria* had an Upper Triassic (Carnian)–Middle Jurassic (Aalenian) range. The oldest species was *T. parvula* (Trechmann, 1918), and the most recent is *T. aalensis* Cox, 1946, of which only one specimen is known. This range was repeated in Cox and others (1969). Subsequently, it was reported from the Lower Jurassic (Pliensbachian) (Hallam, 1977; Hölder, 1995; Szente, 1997; Harries & Little, 1999).

Paleogeographic distribution.—Tethys, Circumpacific, and Austral (Fig. 50).

Tethys domain: Late Triassic: Norian of the western Carpathians (Kollarova & Kochanová, 1973); Norian–Rhaetian of Iran (Hautmann, 2001b); Rhaetian of the Alps (Hautmann, 2001b), England (Ivimey-Cook & others, 1999); Early Jurassic: Germany (Hölder, 1995); Hettangian of England (Cox, 1946), Italy (Gaetani, 1970); Sinemurian of Portugal (Liu, 1995).

Circumpacific domain: Late Triassic: Norian of southwestern Alaska (United States) (Newton, 1986; McRoberts & Blodgett, 2000), Peru (Körner, 1937; Cox, 1946, 1949), Oregon (United States) (Newton in Newton & others, 1987), Vancouver (Canada) (Tozer, 1962), Nevada (United States) (Laws, 1982); Rhaetian of British Columbia (Canada) (Wignall & others, 2007); Early Jurassic: Sinemurian of Japan (Hayami, 1969b).

Austral domain: Late Triassic: Carnian of New Zealand (Trechmann, 1918; Cox, 1946; Marwick, 1953).

Paleoautoecology.—B, Is, S, SM; Sb. Their rounded outer shapes, the presence of a lunule, and absence of a pallial sinus indicate that *Tutcheria* was a nonsiphonate burrower (Newton in Newton & others, 1987; Hautmann, 2001b). According to the type of facies where it is recorded, it lived in shallow-water sandy substrates (Newton in Newton & others, 1987).

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1973). There are no data about *Tutcheria* shell mineralogy or microstructure. Members of the superfamily Carditoidea have a completely aragonitic shell, usually with an outer shell layer of cross-lamellar structure and an inner shell layer of complex cross-lamellar structure (J. D. Taylor, Kennedy, & Hall, 1973).

Genus PALAEOCARDITA Conrad, 1867, p. 11

Type species.—*Cardium austriacum* Hauer, 1853, p. 736.

Stratigraphic range.—Upper Triassic (Carnian–Rhaetian). Although Cox and others (1969) assigned it a Middle–Upper Triassic range, we only located Upper Triassic records. *Cardita crenata* Münster, 1838, which was reported from Ladinian beds (e.g., Arthaber, 1908), was referred to *Palaocardita* by Chavan in Cox and others

(1969). However, this species is now assigned to *Septocardia* Hall & Whitfield, 1877, for well-justified reasons (see Schneider & Carter, 2001, p. 613).

Paleogeographic distribution.—Tethys, Circumpacific, and Austral (Fig. 50). *Palaocardita* was also reported from Upper Triassic of Primorie (Kiparisova, 1972), but the figured material is too poor and its record is considered doubtful.

Tethys domain: Late Triassic: China (Cowper-Reed, 1927; Wen & others, 1976; Gou, 1993), Timor (Indonesia) (Krumbeck, 1924); Carnian of Italy (Corazzari & Lucchi Garavello, 1980), the Alps (Italy) (Fürsich & Wendt, 1977); Norian of western China (H. Yao & others, 2007); Norian–Rhaetian of Iran (Hautmann, 2001b), Yunnan province (China) (J. Yin & McRoberts, 2006), Australia (Grant-Mackie, 1994), Oman (Arabia) (R. Hudson & Jefferies, 1961); Rhaetian of the eastern Alps (Austria) (Tomašových, 2006b), Tibet (China) (Hautmann & others, 2005; J. Yin & McRoberts, 2006), Iran (Repin, 2001), England (Ivimey-Cook & others, 1999), ?Vietnam (Vu Khuc & Huyen, 1998), Sumatra (Boettger, 1880), Hungary (Vörös, 1981), the Alps (Italy) (Diener, 1923; Desio, 1929; S. Conti, 1954), Burma (Healey, 1908).

Circumpacific domain: Late Triassic: Norian of Oregon (United States) (Newton in Newton & others, 1987), Peru (Cox, 1949), Sonora (Mexico) (G. D. Stanley & others, 1994; Goodwin, 1997; McRoberts, 1997a; G. D. Stanley, 1997), Chile (Hayami, Maeda, & Ruiz-Fuller, 1977; Chong & Hillebrandt, 1985); Rhaetian of British Columbia (Wignall & others, 2007).

Austral domain: Late Triassic: Carnian–Norian of New Zealand (Trechmann, 1918; Marwick, 1953); Rhaetian of Argentina (Riccardi & others, 1997, 2004; Damborenea & Manceñido, 2012).

Paleoautoecology.—B, Is, S, Endo-Un, Sed-SM; By-Sb. S. M. Stanley (1970) considered two major modes of life in the family Carditidae: shallow burrower and endobysate infaunal. To differentiate between both types, he proposed to use the degree of elongation (ratio between length and height of the shell). Both interpretations were found in the literature. *Palaocardita silberlingii* Newton in Newton & others, 1987, and *P. stoecklini* Hautmann, 2001b, interpreted by Newton in Newton and others (1987) and by Hautmann (2001b), respectively, as infaunal bivalves living very near the surface, and endobysate on rocks or other hard fragments within the sediment, similar to the living *Cardita floridana* Conrad, as discussed by S. M. Stanley (1970). However, *P. iranica* Hautmann, 2001b, was interpreted by its author as a slow, shallow burrower in fine-grained sediments and low-energy environments.

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1973). Members of the superfamily Carditoidea have a completely aragonitic shell, usually with an outer shell layer of cross-lamellar structure and an inner shell layer of complex cross-lamellar structure (J. D. Taylor, Kennedy, & Hall, 1973). The same was interpreted by Hayami, Maeda, and Ruiz-Fuller (1977) for their specimens of *P. peruviana* Cox, 1949.

Genus SEPTOCARDIA Hall & Whitfield, 1877, p. 294

Type species.—*Septocardia typica* Hall & Whitfield, 1877, p. 295.

Remarks.—Following Schneider and Carter (2001), who suggested that this genus is closely related to *Palaocardita*, we include *Septocardia* in Carditidae. It includes the species S.

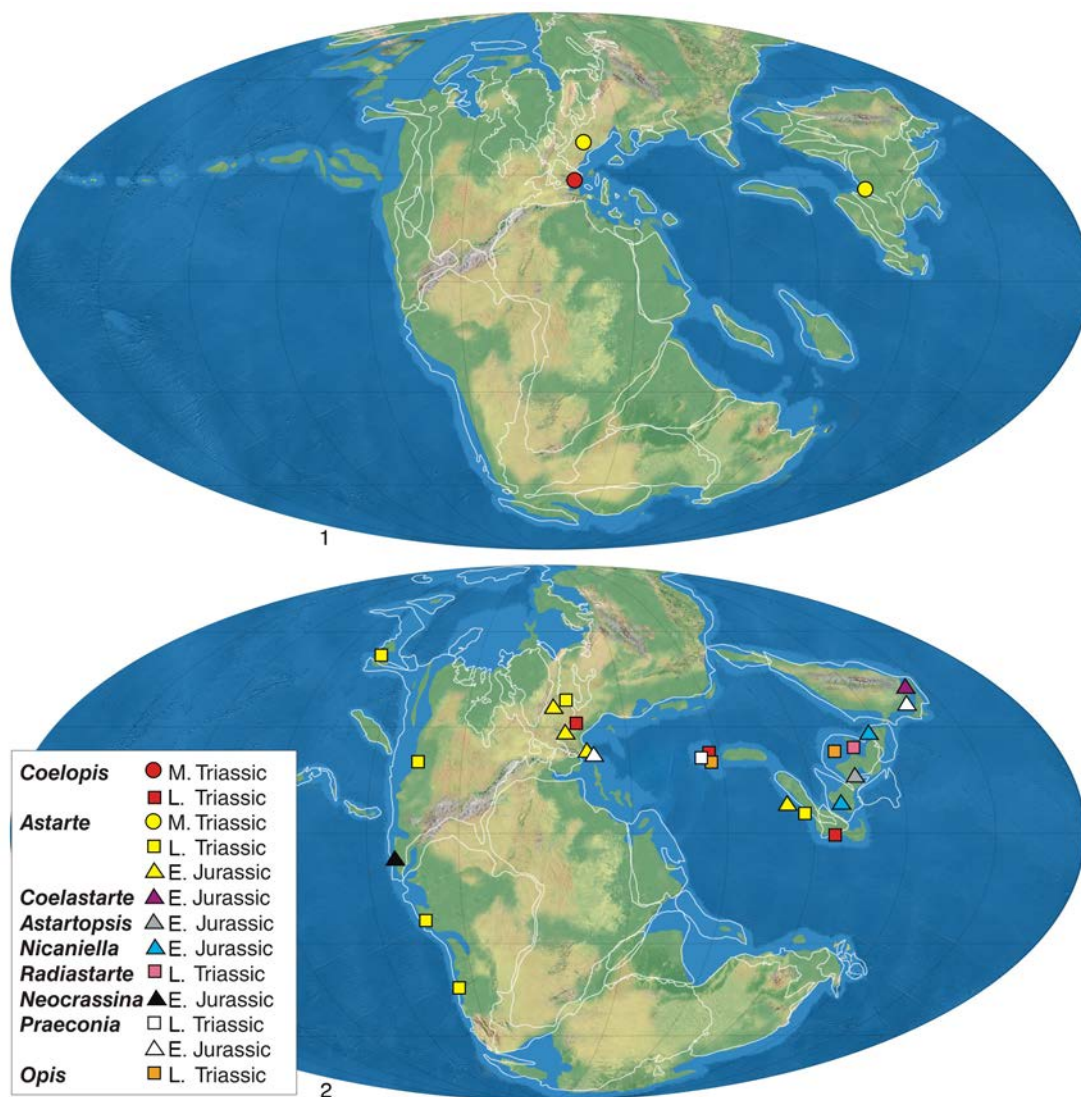


Figure 51. Paleogeographical distribution of Astartidae (*Coelopsis*, *Astarte*, *Coelastarte*, *Astartopsis*, *Nicaniella*, *Radiastarte*, *Neocrassina*, *Praeconia*, *Opis*). 1, Middle Triassic; 2, Late Triassic–Early Jurassic.

crenata (Münster, 1838) and *S. pichleri* (Bittner, 1895), which were referred by other authors to *Palaeocardita* (see Schneider & Carter, 2001, p. 613).

Stratigraphic range.—Upper Triassic (Carnian–Rhaetian). Although Arthaber (1908) mentioned the species *Cardita crenata* from the Ladinian of the Alps, Diener (1923) considered this, and all other records of this species, to be Carnian in age. This species was widely distributed during the Late Triassic, but it was not recorded from Ladinian times, as shown by Cox and others (1969, p. 554). Cox and others (1969) reported the genus from the Norian of North and South America (not including *S. crenata* and *S. pichleri*), expanding both the stratigraphic range and the paleogeographic distributions of this genus.

Paleogeographic distribution.—Tethys, Circumpacific, and Austral (Fig. 50). Goodwin (1997) and McRoberts (1997a) reported *Sep-*

tocardia sp. from the Norian of Sonora (Mexico), but they did not figure the specimens.

Tethys domain: Late Triassic: Carnian of Italy (Bittner, 1895; Schneider & Carter, 2001); Norian of Iran (Repin, 2001).

Circumpacific domain: Late Triassic: Norian of Peru (Cox, 1949), southwestern Alaska (McRoberts & Blodgett, 2000), Oregon (United States) (Newton in Newton & others, 1987), Chile (Hayami, Maeda, & Ruiz-Fuller, 1977; Chong & Hillebrandt, 1985); Rhaetian of British Columbia (Canada) (Wignall & others, 2007), Nevada (United States) (Silberling, 1961; Laws, 1982; Hallam & Wignall, 2000; Guex & others, 2003; Lucas & Tanner, 2004).

Austral domain: Late Triassic: Norian–Rhaetian of Argentina (Riccardi & others, 1997, 2004; Damborenea & Manceñido, 2012).

Paleoautoecology.—B, Is, S, Endo-Un, Sed-SM; By-Sb. S. M. Stanley (1972) proposed that *S. crenata* was an endobysate infaunal bivalve, living buried very near the surface. However, as in *Palaeocardita* (already discussed), the interspecific variation within the genus is significant, so other species, such as *S. typica* Hall & Whitfield, 1877, could have been shallow burrowers.

Mineralogy.—Aragonitic (Schneider & Carter, 2001). See Schneider and Carter (2001) for a complete discussion of the microstructure of the species *S. crenata* and *S. pichleri*.

Genus SCHIZOCARDITA Körner, 1937, p. 194

Type species.—*Schizocardita cristata* Körner, 1937, p. 194.

Stratigraphic range.—Upper Triassic (Norian) (Hallam, 1981). Körner (1937) proposed *Schizocardita* as a subgenus of *Cardita* from the Upper Triassic of Peru. By comparison with European faunas of the Cassian Formation or Raibl Alpine Triassic, Hallam assigned it a Ladinian or Carnian age, since the first formation was then dated as Middle Triassic, but it is now considered to be Carnian in age. Cox (1949) studied the fauna of the same area and assigned it a Norian age. Subsequently, Hallam (1981) assigned the genus a Norian range in South America. Cox and others (1969) considered *Schizocardita* as a genus and assigned it a Triassic range.

Paleogeographic distribution.—Circumpacific (Fig. 50). The genus is endemic to the northern Andes (Kobayashi & Tamura, 1983b; Damborenea, 2002b).

Circumpacific domain: Late Triassic: Norian of Peru (Körner, 1937; Hallam, 1981).

Paleoautoecology.—B, Is-Se, S, SM; Sb. Members of the family Carditidae exhibit a variety of modes of life: shallow infaunal, semi-infaunal, byssate, and even nestler bivalves. Körner (1937) indicated that it is difficult to know how *Schizocardita* lived, because no similar morphology is known. According to its trigoniform external form, it was probably infaunal or semi-infaunal.

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1973). There are no data about *Schizocardita* shell mineralogy or microstructure. Members of the superfamily Carditoidea have a completely aragonitic shell, usually with an outer shell layer of cross-lamellar structure and an inner shell layer of complex cross-lamellar structure (J. D. Taylor, Kennedy, & Hall, 1973).

Superfamily CRASSATELLOIDEA

Férussac, 1822 in 1821–1822

Family ASTARTIDAE d'Orbigny, 1844 in 1844–1848

Genus COELOPIS Fischer, 1887 in 1880–1887, p. 1019

Type species.—*Cardita lunulata* J. Sowerby, 1819, p. 55.

Stratigraphic range.—Middle Triassic (Ladinian)–Lower Cretaceous (?) (Cox & others, 1969). Cox and others (1969) included two subgenera within *Coelopsis*: *C. (Coelopsis)* from the Middle Triassic to Lower Cretaceous, and *C. (Cryptocoelopsis)* Bittner, 1895 from the Middle Triassic (Ladinian). Kutassy (1931) assigned a Carnian age to the records that Cox and others (1969) referred to the Ladinian, and he disregarded the reference of Wurm (1913) from the Ladinian of Menorca in the Balearic Islands. Although Cox and others (1969) recorded *Coelopsis* up to the Lower Cretaceous, we could

only confirm its presence up to the Upper Jurassic (Hayami, 1975; Delvene, 2000).

Paleogeographic distribution.—Tethys (Fig. 51).

Tethys domain: Middle Triassic: Ladinian of Spain (Wurm, 1913); Late Triassic: Carnian of the Alps (Bittner, 1895; Corazzari & Luchi Garavello, 1980); Norian of Seram (Indonesia) (Hautmann, 2001b); Norian–Rhaetian of Iran (Hautmann, 2001b).

Paleoautoecology.—B, E, S, Epi, Sed; By. Some authors (Delvene, 2000, 2003; Fürsich & others, 2001; Gahr, 2002) interpreted *Coelopsis* as a nonsiphonate infaunal bivalve, shallow burrower, like most astartids (S. M. Stanley, 1970). However, Hautmann (2001b) compared the morphology of *Coelopsis (Coelopsis) aurea* Hautmann, 2001b, and *Coelopsis (Coelopsis) krumbeki* Hautmann, 2001b, with *Opisoma* Stoliczka, 1871 in 1870–1871, which was interpreted as an epibenthic reclined bivalve that lived with the shell partially buried (see Aberhan & Hillebrandt, 1999). Hautmann (2001b) interpreted these species in the same way, but, given their small size, he supposed they instead lived epibyssate rather than reclined, as does *Opisoma*. The last interpretation seems more accurate, according to the morphology of most species attributed to *Coelopsis*.

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1973). There are no studies on *Coelopsis* shell mineralogy or microstructure. The shell of members of family Astartidae is entirely aragonitic, with an outer cross-lamellar layer and an inner layer formed by myostracal-type prisms and traces of complex cross-lamellar or homogeneous structure (J. D. Taylor, Kennedy, & Hall, 1973).

Genus ASTARTE J. Sowerby, 1816, p. 85

Type species.—*Venus scotica* Maton & Rackett, 1807, p. 81.

Stratigraphic range.—Middle Triassic (Anisian)–Holocene (Cox & others, 1969; Baumgarte, 1973). Cox and others (1969) assigned it a Jurassic–Holocene range, as did authors who suggested a Hettangian origin for *Astarte* (Hallam, 1987, 1990; Schneider, 1995; Sepkoski, 2002). But other authors considered a Late Triassic origin (Marincovich, Barinov, & Oleinik, 2002). However, *Astarte triasina* Roemer, 1851, from the Middle Triassic (Muschelkalk) (Busse, 1972; Baumgarte, 1973; Busse & Horn, 1978) is the oldest record of this genus. An astartid species was reported from the Upper Triassic of South America (*Astarte inca* Jaworski, 1922), but Riccardi and others (1997, 2004) refer it only doubtfully to *Astarte*.

Paleogeographic distribution.—Tethys, Circumpacific, and ?Austral (Fig. 51).

Tethys domain: Middle Triassic: Muschelkalk of Germany (Busse, 1972; Baumgarte, 1973; Busse & Horn, 1978); Anisian of China (Komatsu, Chen, & others, 2004); Late Triassic: Rhaetian of Tibet (China) (J. Yin & McRoberts, 2006), England (Ivimey-Cook & others, 1999); Early Jurassic: Hettangian of China (Gu & others, 1976; Z. Huang, 1986), Tibet (China) (J. Yin & McRoberts, 2006), England (Liu, 1995), Italy (Gaetani, 1970); Sinemurian of England and France (Liu, 1995).

Circumpacific domain: Late Triassic: Peru (Jaworski, 1922); Norian of ?southwestern Alaska (McRoberts & Blodgett, 2000), Oregon (United States) (Newton & others, 1987).

Austral domain: Late Triassic: Rhaetian of ?Argentina (Riccardi & others, 1997, 2004).

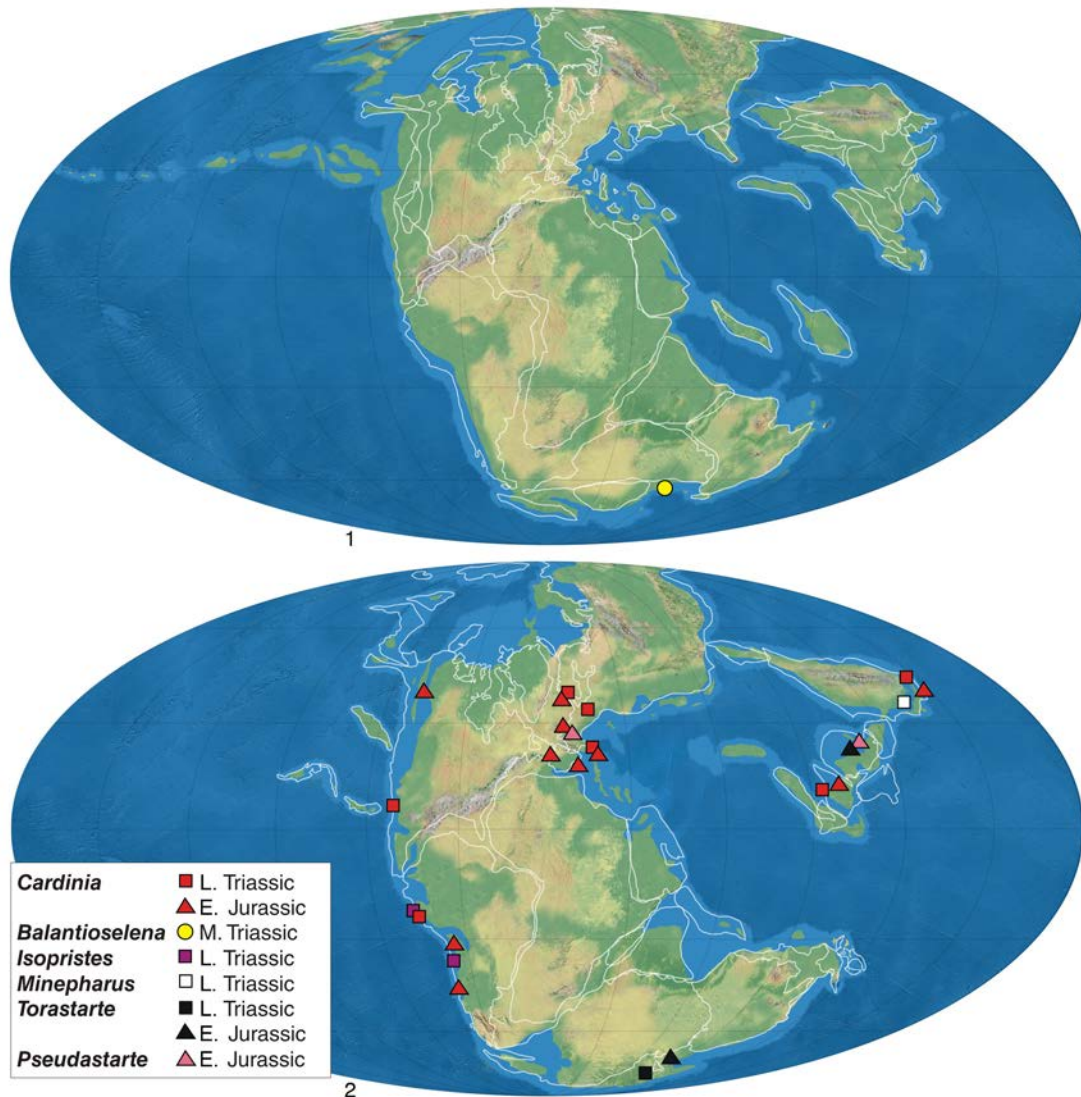


Figure 52. Paleogeographical distribution of Cardiniidae (*Cardinia*, *Balantioselena*, *Isopristes*, *Minepharus*, *Torastarte*, *Pseudastarte*). 1, Middle Triassic; 2, Late Triassic–Early Jurassic.

Paleoautoecology.—B, Is, S, SM; Sb. S. M. Stanley (1970) examined several living *Astarte* species and indicated they are all slow, shallow, nonsiphonate burrowers. We assume a similar mode of life for the Mesozoic species.

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1973). J. D. Taylor, Kennedy, and Hall (1973) studied the shell microstructure of several living species, corroborating that all are completely aragonitic, with an outer cross-lamellar layer and an inner layer formed by homogeneous or complex cross-lamellar structure, according to species, and myostracal-type prisms.

Genus COELASTARTE Böhm, 1893, p. 174

Type species.—*Astarte excavata* J. Sowerby, 1819, p. 57.

Remarks.—Prior to the paper by Hayami (1958d), *Coelastarte* was regarded as a subgenus of *Astarte* J. Sowerby, 1816. Hayami raised it to generic level, because it was easily distinguishable from *Astarte* and other related genera. Cox and others (1969) relegated *Coelastarte*

to a subgenus of *Neocrassina* Fischer, 1886 in 1880–1887. However, Gardner and Campbell (2002) decided to maintain the two taxa as separate and raised *Coelastarte* to generic level. This decision is supported by differences in the hinge of both genera, among other aspects, and this opinion is followed here.

Stratigraphic range.—Lower Jurassic (Hettangian)–Upper Cretaceous (Turonian) (Hayami, 1958d; Cox & others, 1969). Cox and others (1969) assigned it a Middle Jurassic (Aalenian)–Upper Cretaceous (Turonian) range. However, *Coelastarte* originated in the Hettangian of Japan (Hayami, 1958d, 1975; Sato & Westermann, 1991). Although the youngest record we found is from the Upper Jurassic (Tithonian) (Hayami, 1975; Fürsich, 1981), we follow Cox and others (1969), in considering Turonian to be the top of the range, as we could not access the original source of this quotation.

Paleogeographic distribution.—Circumpacific (Fig. 51). Although during our interval it was only recorded from Japan, it had a broader

distribution during the rest of the Jurassic (Cox & others, 1969; Gardner & Campbell, 2002).

Circumpacific domain: Early Jurassic: Hettangian of Japan (Hayami, 1958d, 1975; Sato & Westermann, 1991; Sugawara & Kondo, 2004; Kondo & others, 2006).

Paleoautoecology.—B, Is, S, SM; Sb. Similar to *Praeconia*.

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1973). There are no studies on *Coelastarte* shell mineralogy or microstructure. See discussion in *Astarte* (p. 137).

Genus ASTARTOPSIS de Loriol, 1891, p. 218

Type species.—*Astartopsis elongata* de Loriol, 1891, p. 219.

Stratigraphic range.—Lower Jurassic (Sinemurian), Upper Jurassic (Oxfordian). According to Cox and others (1969), *Astartopsis* is known from Jurassic deposits (L. Lusitanian). Septfontaine (1995) noticed that the syntypes of *A. elongata* are from the Rauracian (=Oxfordian) from Switzerland. In addition to these Upper Jurassic records, the genus was only reported from the Lower Jurassic (Sinemurian) of southern China by J. Chen (1988), who described three species: *A. menkei* (Dunker) in Xintianmen, Tianmen'ao, and Upper Jinji formations; *A. subovalis* Chen in Xintianmen Formation, and *A. sp.* in Upper Jinji Formation.

Paleogeographic distribution.—Eastern Tethys (Fig. 51).

Tethys domain: Early Jurassic: Sinemurian of southern China (J. Chen, 1988).

Paleoautoecology.—B, Is, S, SM; Sb. According to its external shell morphology, *Astartopsis* was probably a shallow burrower.

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1973). There are no studies on *Astartopsis* shell mineralogy or microstructure. See discussion in *Astarte* (p. 137).

Genus NICANIELLA Chavan, 1945, p. 43

Type species.—*Astarte communis* Zittel & Goubert, 1861, p. 201.

Stratigraphic range.—Lower Jurassic (Hettangian)–Paleocene (Hayami, 1964; Cox & others, 1969). Cox and others (1969) assigned to *Nicaniella* a Middle Jurassic–Paleocene range and doubtfully also recorded it from the Pliocene, but the genus had already been reported from the Hettangian of Vietnam (Hayami, 1964). Damborenea and Manceñido (2012) doubtfully referred to *Nicaniella* specimens identified as *N.?* cf. *inca* (Jaworski, 1922) from Rhaetian beds in Argentina.

Paleogeographic distribution.—Eastern Tethys (Fig. 51). *Nicaniella* was originally distributed in the Eastern Tethys, but, starting with Pliensbachian times, its distribution significantly broadened (Hallam, 1976, 1977; Fürsich & others, 1991, 2001, 2005; Liu, 1995; Holzapel, 1998; Harries & Little, 1999; Gahr, 2002; Delvene, 2003; Fürsich & Thomsen, 2005).

Tethys domain: Early Jurassic: Hettangian–Sinemurian of China (Stiller, 2006, and references therein), Vietnam (Hayami, 1964; Sato & Westermann, 1991).

Paleoautoecology.—B, Is, S, SM; Sb. *Nicaniella* is regarded as a slow, shallow burrower, nonsiphonate bivalve according to its external morphology: “strongly inflated shell, marked comarginal lines and thick shell” (Delvene, 2000, p. 132).

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1973). There are no studies on *Nicaniella* shell mineralogy or microstructure. See discussion in *Astarte* (p. 137).

Genus RADIASTARTE

Chen & Liu in Gu & others, 1976, p. 99

Type species.—*Radiastarte yizhangensis* Chen & Liu in Gu & others, 1976, p. 99.

Stratigraphic range.—Upper Triassic (Carnian) (Gu & others, 1976). Chen and Liu (in Gu & others, 1976) proposed *Radiastarte* from the Carnian of Hunnan (China).

Paleogeographic distribution.—Eastern Tethys (Fig. 51). The genus was endemic to China (Kobayashi & Tamura, 1983a).

Tethys domain: Late Triassic: Carnian of Hunnan province (China) (Gu & others, 1976; Kobayashi & Tamura, 1983a).

Paleoautoecology.—B, Is, S, SM; Sb. Similar to *Nicaniella*.

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1973). There are no studies on *Radiastarte* shell mineralogy or microstructure. See discussion in *Astarte* (p. 137).

Genus NEOCRASSINA

Fischer, 1887 in 1880–1887, p. 1016

[*nom. nov. pro Crassinella* Bayle, 1878, expl. pl. 105, *non* Guppy, 1874, p. 442]

Type species.—*Astarte obliqua* Deshayes, 1830 in 1830–1832, expl. pl. 22.

Stratigraphic range.—Lower Jurassic (Hettangian)–Lower Cretaceous (Berriasian) (Hayami, 1975; Scholz, Aberhan, & González-León, 2008). Cox and others (1969) included two subgenera within *Neocrassina*: *N. (Neocrassina)* and *N. (Coelastarte)* Böhm, 1893. We only consider the first, since *Coelastarte* is here regarded as a separate genus (see discussion for *Coelastarte*, p. 138). The range assigned to *N. (Neocrassina)* by Cox and others (1969) is Lower Jurassic (upper Liassic)–Lower Cretaceous. Subsequently, Damborenea in Damborenea and González-León (1997) reported some specimens from Lowest Jurassic (?Hettangian, ?Sinemurian), which were doubtfully assigned to this genus, as internal characters were not observed. Later, Scholz, Aberhan, and González-León (2008) confirmed the presence of the genus from the same age and area (*N. gueuxi* d'Orbigny, 1850).

Paleogeographic distribution.—Circumpacific (Fig. 51). Although during our study interval *Neocrassina* was only reported from the Circumpacific domain, subsequently it extended to the Tethys (Hallam, 1972, 1976, 1977; Pugaczewska, 1986; Liu, 1995; Holzapel, 1998; Gahr, 2002), the Austral domain (Gardner & Campbell, 1997, 2002) and Boreal domain (Fürsich, 1982).

Circumpacific domain: Early Jurassic: Hettangian–Sinemurian of Sonora (Mexico) (Damborenea in Damborenea & González-León, 1997; Scholz, Aberhan, & González-León, 2008).

Paleoautoecology.—B, Is, S, SM; Sb. By comparison with modern species of the family Astartidae, *Neocrassina* was probably a shallow burrower bivalve. According to the thickness of its shell and its external form, it was probably a slow burrower.

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1973). There are no studies on *Neocrassina* shell mineralogy or microstructure. See discussion in *Astarte* (p. 137).

Genus PRAECONIA Stoliczka, 1871 in 1870–1871, p. 278

Type species.—*Astarte terminalis* Roemer, 1842, p. 15.

Stratigraphic range.—Upper Triassic (Norian)–Upper Jurassic (Tithonian) (Liu, 1995; Hautmann, 2001b). Cox and others (1969) assigned it a Jurassic (Lias.–Lusitan.) range. Subsequent findings extended the observed stratigraphic range from Upper Triassic (Hautmann, 2001b) to Upper Jurassic (Hallam, 1976, 1977; Liu, 1995).

Paleogeographic distribution.—Tethys and Circumpacific (Fig. 51). It was recorded from the Triassic–Jurassic transition of southern Tibet by Hautmann and others (2005), but they did not discuss systematically or nor figure the specimens.

Tethys domain: Late Triassic: Norian–Rhaetian of Iran (Hautmann, 2001b); Early Jurassic: Hettangian–Sinemurian of Italy (Gaetani, 1970).

Circumpacific domain: Early Jurassic: Sinemurian of Japan (Hayami, 1975).

Paleoautoecology.—B, Is, S, SM; Sb. The living species of this family are shallow burrowers, not very active, that live in cold water (Beesley, Ross, & Wells, 1998). Probably, *Praeconia* was a filtering shallow burrower, living very near the surface of the sediment, as interpreted by Hautmann (2001b) and Gahr (2002).

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1973). There are no studies on *Praeconia* shell mineralogy or microstructure. See discussion in *Astarte* (p. 137).

Genus OPIS Defrance, 1825a, p. 219

Type species.—*Trigonia cardisoides* Lamarck, 1819, p. 65.

Stratigraphic range.—Upper Triassic (Norian)–Upper Cretaceous (Maastrichtian) (Hautmann, 2001b; Hayami, 1975). Cox and others (1969) considered three subgenera within *Opis*: *O. (Opis)*, *O. (Pachyopis)* Bigot, 1895, and *O. (Trigonopis)* Fischer, 1887 in 1880–1887, assigning a Jurassic to Upper Cretaceous range. Of these three subgenera, the only one reported from our study interval is *O. (Trigonopis)*.

Gardner and Campbell (2002) raised *Trigonopis* to generic level, distinguishing it from *Opis* by its hinge dentition features. This is difficult to apply when the hinge is not observed, for example, in specimens assigned to *O. (Trigonopis)* from the Upper Triassic by Hautmann (2001b).

Paleogeographic distribution.—Eastern Tethys (Fig. 51). Although during the Late Triassic, *Opis* was only reported from the eastern Tethys, in the Jurassic, its distribution was broader (Hayami, 1975; Liu, 1995; Gardner & Campbell, 2002).

Tethys domain: Late Triassic: Norian of Iran and China (Hautmann, 2001b); Rhaetian of Iran (Hautmann, 2001b).

Paleoautoecology.—B, E, S, Un, Sed; R. Considering shell morphology, Hautmann (2001b) assigned *Opis* a mode of life similar to *Coelopis* Fischer, 1887 in 1880–1887, since it is unlikely that these bivalves were burrowers. But the specimens assigned to *O. (Trigonopis)* by Hautmann show no evidence of byssus, therefore he proposed they lived in low-energy environments.

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1973). There are no studies on *Opis* shell mineralogy or microstructure. See discussion in *Astarte* (p. 137).

Family CARDINIIDAE Zittel, 1881**Genus CARDINIA Agassiz, 1841 in 1840–1845, p. 220**

[nom. conserv. ICZN, 1954, Opinion 292, see discussion in C. Palmer, 1975]

Type species.—*Unio listeri* J. Sowerby, 1817, p. 123 (ICZN, 1954, Opinion 292).

Stratigraphic range.—Upper Triassic (Carnian)–Lower Jurassic (Toarcian) (Cox & others, 1969). Cox and others (1969) assigned a Carnian–Toarcian range, noting that the Bajocian records of *Cardinia* were not taken into account, because they were based on poorly preserved material.

Paleogeographic distribution.—Cosmopolitan (Fig. 52). Although we did not find any record from the Boreal domain, Cox and others (1969) assigned it a cosmopolitan distribution, and Kobayashi and Tamura (1983b) suggested *Cardinia* originated in Japan and eastern Siberia during the Late Triassic.

Tethys domain: Late Triassic: Rhaetian of Switzerland (Diener, 1923; Kutassy, 1931), Italy (Mariani, 1919), Vietnam (Vu Khuc & Huyen, 1998), England (Ivimey-Cook & others 1999); Early Jurassic: Hettangian of Italy (S. Conti, 1954; Gaetani, 1970); Hettangian–Sinemurian of Vietnam (Hayami, 1964; Sato & Westermann, 1991), England (Palmer, 1975) and Spain (Liu, 1995); Sinemurian of Portugal and France (Liu, 1995), England (Palmer 1975).

Circumpacific domain: Late Triassic: Peru (Rangel, 1978); Carnian of California (United States) (J. P. Smith, 1927), Japan (Nakazawa, 1956; Hayami, 1975); Early Jurassic: Hettangian of Yukon (Canada) (Poulton, 1991); Sinemurian of Japan (Hayami, 1975), ?Chile (Covacevich, Pérez, & Escobar, 1991).

Austral domain: Early Jurassic: Sinemurian of Argentina (Riccardi & others, 1991; Damborenea & Manceñido, 2005b).

Paleoautoecology.—B, Is, S, SM; Sb. The external morphology of *Cardinia* suggests it was a superficial and nonsiphonate burrower, since the pallial line lacks a sinus. The shell thickness and its somewhat globose morphology indicate it was a slow burrower, as were other members of this family.

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1973). The shell microstructure of *Cardinia* is not known. Members of the superfamily Crassatelloidea have an entirely aragonitic shell (J. D. Taylor, Kennedy, & Hall, 1973).

Genus BALANTIOSELENA**Speden in Gair, Gregg, & Speden, 1962, p. 96**

Type species.—*Balantioselena gairi* Speden in Gair, Gregg, & Speden, 1962, p. 99.

Remarks.—Speden (in Gair, Gregg, & Speden, 1962) proposed *Balantioselena* and included it in the family Astartidae. Subsequently, however, it was referred to the family Cardiniidae, with which is more closely related (Cox & others, 1969; Morris, 1978).

Stratigraphic range.—Middle Triassic (Ladinian) (Speden in Gair, Gregg, & Speden, 1962). Speden (in Gair, Gregg, & Speden, 1962) reported *Balantioselena* from the Ladinian. Subsequently, it was recorded from the same age in several papers without being discussed systematically (J. D. Campbell & Force, 1973; Retallack & Ryburn, 1982; H. J. Campbell, 1987).

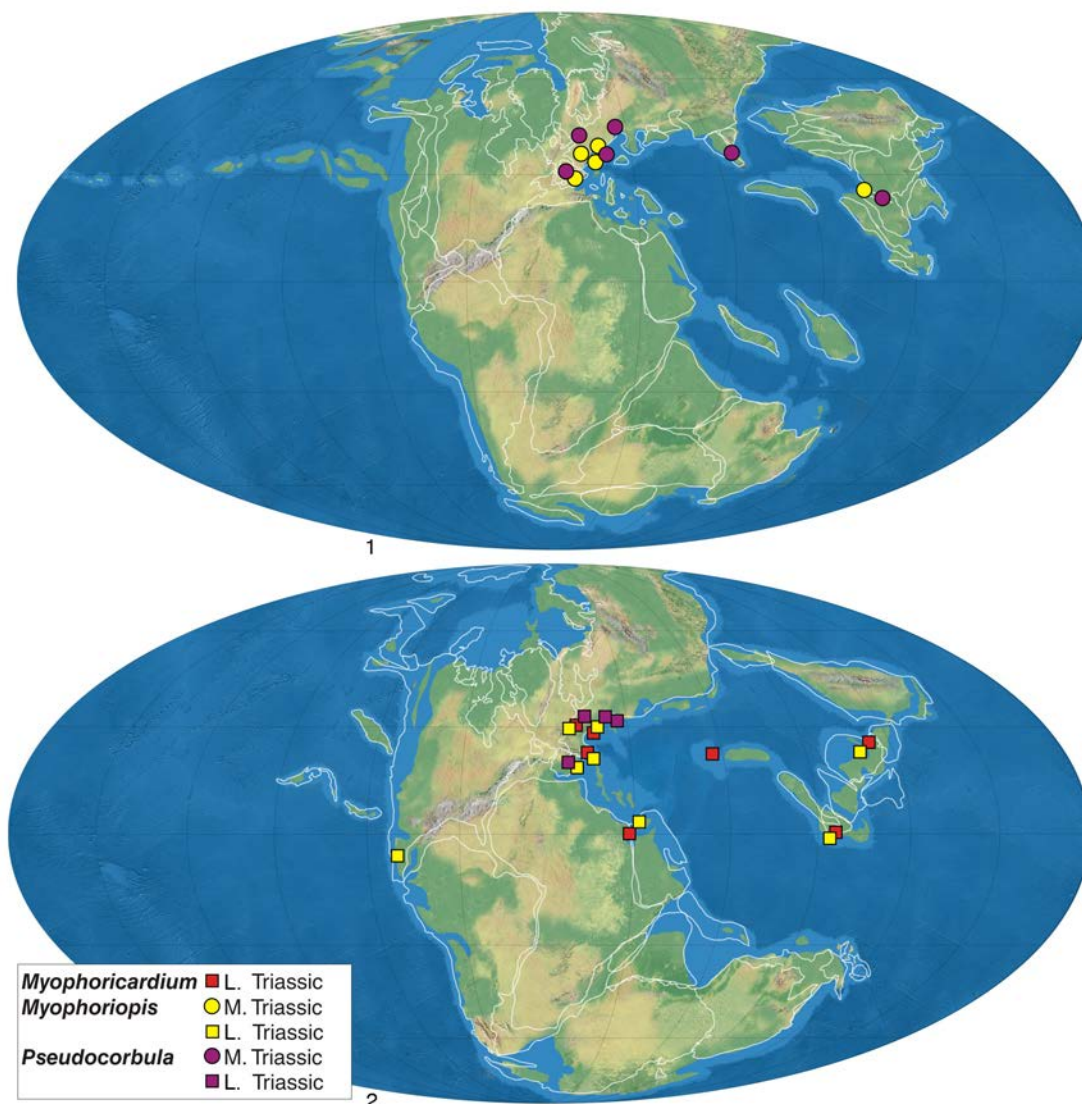


Figure 53. Paleogeographical distribution of Myophoricardiidae (*Myophoricardium*, *Myophoriopsis*, *Pseudocorbula*). 1, Middle Triassic; 2, Late Triassic–Early Jurassic.

Paleogeographic distribution.—Austral (Fig. 52).

Austral domain: Middle Triassic: Ladinian of New Zealand (Speden in Gair, Gregg, & Speden, 1962).

Paleoautoecology.—B, Is, S, SM; Sb. Within this family there are genera with compact shapes and others with elongated forms (S. M. Stanley, 1972). The first are often shallow burrowers, while the others would be rather endobyssate. The shell morphology of *Balantioselena* (see description and figures in Speden in Gair, Gregg, & Speden, 1962), its subcircular outline, thick and inflated shell, prosogyrous beaks, and deep lunule indicate it was a nonsiphonate, slow, shallow-burrower bivalve.

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1973). The shell microstructure of *Balantioselena* is not known. Members of the superfamily Crassatelloidea have an entirely aragonitic shell (J. D. Taylor, Kennedy, & Hall, 1973).

Genus ISOPRISTES Nicol & Allen, 1953, p. 344

Type species.—*Isopristes crassus* Nicol & Allen, 1953, p. 345.

Stratigraphic range.—Upper Triassic (Norian). The genus was originally described from the Norian of Peru (Cox & others, 1969) and was subsequently reported from the Norian of Chile (Hayami, Maeda, & Ruiz-Fuller, 1977).

Paleogeographic distribution.—Circumpacific (Fig. 52). *Isopristes* was endemic to the northern Andes (Damborenea, 2002b).

Circumpacific domain: Late Triassic: Norian of Peru (Cox & others, 1969), Chile (Hayami, Maeda, & Ruiz-Fuller, 1977).

Paleoautoecology.—B, Is, S, SM; Sb. Similar to *Cardinia*.

Mineralogy.—Aragonitic (Hayami, Maeda, & Ruiz-Fuller, 1977). Hayami, Maeda, and Ruiz-Fuller (1977) observed an entirely aragonitic shell with a cross-lamellar outer shell layer and a complex cross-lamellar or homogeneous inner shell layer in *Isopristes* sp.

Genus MINEPHARUS Tokuyama, 1958, p. 296

Type species.—*Palaeopharus (Minepharus) triadicus* Tokuyama, 1958, p. 297.

Remarks.—*Minepharus* was originally proposed as a subgenus of *Palaeopharus* (family Actinodontophoridae) (Hayami, 1975), but Newell (in Cox & others, 1969) included it, with certain doubts, in the family Cardiniidae. Later, Hayami (1975, p. 170) justified this change of family and discussed Tokuyama's reasons to include it as a subgenus of *Palaeopharus*.

Stratigraphic range.—Upper Triassic (Carnian) (Hayami, 1975). *Minepharus* was reported from Carnian beds of Japan (Hayami, 1975). Waller (in Waller & Stanley, 2005) found a single valve of what could be a new species of *Minepharus*, but neither included it in the genus nor described the specimen while waiting for better material.

Paleogeographic distribution.—Circumpacific (Fig. 52).

Circumpacific domain: Late Triassic: Carnian of Japan (Hayami, 1975).

Paleoautoecology.—B, Se, S, Endo, Sed; By. *Minepharus* had an elongated shell, modioliform, like other members of the superfamily Crassatelloidea (S. M. Stanley, 1972). It was likely an endobysate bivalve, living as did the Paleozoic *Cypricardinia* Hall, 1859 in 1859–1861 (S. M. Stanley, 1972).

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1973). The shell microstructure of *Minepharus* is not known. Members of the superfamily Crassatelloidea have an entirely aragonitic shell (J. D. Taylor, Kennedy, & Hall, 1973).

Genus TORASTARTE Marwick, 1953, p. 70

Type species.—*Torastarte bensoni* Marwick, 1953, p. 70.

Remarks.—*Torastarte* was originally included in the family Astartidae (Marwick, 1953). Subsequently, specimens with the hinge preserved showed that it was closely related to *Cardinia* Agassiz, 1841 in 1840–1845, and it was assigned to the Cardiniidae (Fleming, 1957), where it was maintained by Cox and others (1969). Hallam (1981) recorded "*Toroastarte*" (typographic error) from the Upper Triassic of New Zealand.

Stratigraphic range.—Upper Triassic (Rhaetian)–Lower Jurassic (Toarcian) (Marwick, 1953; Kear, 1961). Marwick (1953) proposed *Torastarte* from sediments dated as Otapirian (=Rhaetian) from New Zealand. Subsequently, the genus was also reported from the Ururoan (=Hettangian–Toarcian according to N. Hudson [2003]; Pliensbachian–Toarcian according to H. J. Campbell, Raine, & Wilson in Cooper [2004]).

Paleogeographic distribution.—Tethys and Austral (Fig. 52). At first, it was considered endemic to New Zealand, but new records from the eastern Tethys expanded its distribution.

Tethys domain: Early Jurassic: Sinemurian of China (J. Chen, 1988; Stiller, 2006).

Austral domain: Late Triassic: Rhaetian of New Zealand (Marwick, 1953; Fleming, 1957); Early Jurassic: Hettangian–Sinemurian of New Zealand (Kear, 1961).

Paleoautoecology.—B, Is, S, MS; Sb. Similar to *Cardinia*.

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1973). The shell microstructure of *Torastarte* is not known. Members of

the superfamily Crassatelloidea have an entirely aragonitic shell (J. D. Taylor, Kennedy, & Hall, 1973).

Genus PSEUDASTARTE Cossmann, 1921, p. 17

Type species.—*Astarte (Pseudastarte) emarginata* Cossmann, 1921, p. 17.

Stratigraphic range.—Lower Jurassic (Hettangian–Sinemurian) (Stiller, 2006). Cox and others (1969) assigned it a Hettangian range in France, based on the only species then referred to *Pseudastarte*. Subsequently, J. Chen (1988) referred the species *Cardinia exigua* Terquem, 1855, from the Sinemurian of China to *Pseudastarte*. Stiller (2006) recorded it as *Pseudastarte* aff. *exigua* (Terquem, 1855), since he believed that the Chinese specimens were different from the European ones, but new material is needed to see the hinge in the Chinese specimens.

Paleogeographic distribution.—Tethys (Fig. 52).

Tethys domain: Early Jurassic: Hettangian of France (Cossmann, 1921); Hettangian or Sinemurian of China (Stiller, 2006); Sinemurian of China (J. Chen, 1988).

Paleoautoecology.—B, Is, S, SM; Sb. Similar to *Cardinia*.

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1973). *Pseudastarte* shell microstructure is not known. Members of the superfamily Crassatelloidea have an entirely aragonitic shell (J. D. Taylor, Kennedy, & Hall, 1973).

Family MYOPHORICARDIIDAE Chavan in Vokes, 1967**Genus MYOPHORICARDIUM Wöhrmann, 1889, p. 226**

Type species.—*Myophoricardium lineatum* Wöhrmann, 1889, p. 227.

Stratigraphic range.—Upper Triassic (Carnian–Rhaetian) (Hautmann, 2001b). Cox and others (1969) assigned it a Carnian range. Subsequently, new records expanded the observed stratigraphic range up to the Rhaetian (Hautmann, 2001b). It was also reported from the Anisian of China (Komatsu, Chen, & others, 2004), but without description or figures.

Paleogeographic distribution.—Tethys (Fig. 53). The genus was also recorded from the Upper Triassic of Nevada (United States) (Laws, 1982; Hallam & Wignall, 2000), but as the specimens were neither figured nor described, we consider this to be a doubtful record.

Tethys domain: Late Triassic: Carnian of the Alps (Austria) (Wöhrmann, 1889), Italy (Allasinaz, 1966), Slovenia (Jurkovsek, 1978; Jelen, 1988), Yunnan province (China) (Cowper-Reed, 1927), China (Wen & others, 1976), Jordan (Cox, 1924); Norian of Sumatra (Indonesia) (Krumbeck, 1914), China (Gu & others, 1976); Norian–Rhaetian of Iran (Hautmann, 2001b).

Paleoautoecology.—B, Is, S, FM; Sb. Hautmann (2001b) interpreted *M. lineatum* Wöhrmann, 1889, and *M. subquadratum* Hautmann, 2001b, as fast, shallow burrowers with short siphons.

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1973). *Myophoricardium* shell microstructure is not known. Members of the superfamily Crassatelloidea have an entirely aragonitic shell (J. D. Taylor, Kennedy, & Hall, 1973).

Genus MYOPHORIOPIS Wöhrmann, 1889, p. 221

Type species.—*Myophoria lineata* Münster, 1841, p. 88.

Stratigraphic range.—Middle Triassic (Anisian)—Upper Triassic (Rhaetian). Cox and others (1969) assigned a Ladinian–Norian range. However, several reports established its range from the Anisian to Rhaetian (see paleogeographic distribution).

Paleogeographic distribution.—Tethys and Circumpacific (Fig. 53).

Tethys domain: Middle Triassic: Anisian of China (Sha, Chen, & Qi, 1990; J. Chen, 2003), the Alps (Switzerland) (Zorn, 1971), Italy (Posenato, 2008a); Ladinian of Austria (Bittner, 1895), Spain (Wurm, 1913; Busnardo, 1970; Márquez-Aliaga, 1983; Calvet & others, 1994); Late Triassic: Carnian of Italy (Bittner, 1895; Broili, 1904; Allasinaz, 1964, 1966; Fürsich & Wendt, 1977), southern Alps (Austria) (Wöhrmann, 1889), China (Gu & others, 1976; Sha, Chen, & Qi, 1990; Sha & Grant-Mackie, 1996), Jordan (Cox, 1924), Slovenia (Boué, 1835, as *Corbula*); Norian of Sumatra (Indonesia) (Krumbeck, 1914); Rhaetian of Spain (Goy & Márquez-Aliaga, 1998), Hungary (Vörös, 1981), Italy (Chiesa, 1949; Allasinaz, 1962; Gelati & Allasinaz, 1964; Sirna, 1968), eastern Alps (Austria) (Tomašových, 2006a).

Circumpacific domain: Late Triassic: Norian of Sonora (Mexico) (Damborenea in Damborenea & González-León, 1997).

Paleoautoecology.—B, Is, S, FM; Sb. The mode of life of *Myophoriopsis* was probably similar to *Myophoricardium*.

Mineralogy.—Aragonitic (Schneider & Carter, 2001). Schneider and Carter (2001) studied the shell microstructure of *Myophoriopsis carinata* Bittner, 1895, from the Italian Carnian and observed that it was composed of a prismatic outer layer, a cross-lamellar middle layer, and a complex cross-lamellar inner layer.

Genus PSEUDOCORBULA E. Philippi, 1898, p. 168

Type species.—*Nucula gregaria* Münster, 1837, in Goldfuss, 1833–1841, p. 152.

Stratigraphic range.—Middle Triassic (Anisian)—Upper Triassic (Rhaetian). Cox and others (1969) assigned it a Lower–Upper Triassic range. According to Klets (2006), *Pseudocorbula* originated in the Induan of the Boreal domain. Dagys and Kurushin (1985) mentioned the species *Pseudocorbula gregaroides* Philippi, 1898, from the Olenekian and Anisian of Siberia, but they did not describe the specimens. According to Diener (1923), this species was reported from the Muschelkalk (currently equivalent to the Middle Triassic of Germany).

We did not locate any Lower Triassic published record. Hautmann and Nützel (2005) indicated that the Triassic record in Cox and others (1969) was questionable since there was no material showing internal characters, and they recognized an Anisian origin for the genus. *Pseudocorbula* is widely recorded from the Middle Triassic, but many species were erroneously attributed to this genus (Márquez-Aliaga, 1985), due to its great interspecific variability. *Pseudocorbula* is only occasionally reported from the Upper Triassic and not in younger sediments, so this is a typically Triassic genus.

Paleogeographic distribution.—Tethys (Fig. 53).

Tethys domain: Middle Triassic: Hungary (Szente, 1997), China (Ling, 1988; Sha, Chen, & Qi, 1990), Poland (Assmann, 1916; Senkowiczowa, 1985), Germany (Philippi, 1898; Walther, 1927), Spain (Wurm, 1911); Anisian of Poland (Kaim, 1997), Bulgaria (Encheva, 1969); Ladinian of Spain (Márquez-Aliaga, 1983, 1985; Márquez-Aliaga, Hirsch, & López-Garrido, 1986;

Llompart & others, 1987; López-Gómez & others, 1987, 1994; Márquez-Aliaga & others, 1987, 2004; Márquez-Aliaga & López-Gómez, 1989; Márquez-Aliaga & García-Gil, 1991; Márquez-Aliaga & Montoya, 1991; Márquez-Aliaga & others 2002; Márquez-Aliaga & Ros, 2002, 2003), Germany (Ürlich, 1992), Afghanistan (Farsan, 1975); Late Triassic: Carnian of Spain (Martín-Algarra & others, 1993; Martín-Algarra, Solé de Porta, & Márquez-Aliaga, 1995; Freneix, 1999), Italy (Allasinaz, 1964); Norian of Germany (Warth, 1994; Arp & others, 2005); Rhaetian of Austria (Tomašových, 2006a), Spain (Goy & Márquez-Aliaga, 1998; Márquez-Aliaga, Plasencia, & Ros, 2005), Hungary (Vörös, 1981), Italy (S. Conti, 1954).

Paleoautoecology.—B, Is, S, FM; Sb. The mode of life of *Pseudocorbula* was probably similar to that assigned to *Myophoricardium*.

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1973). *Pseudocorbula* shell microstructure is not known. Members of the superfamily Crassatelloidea have an entirely aragonitic shell (J. D. Taylor, Kennedy, & Hall, 1973).

Superfamily CARDIOIDEA Lamarck, 1809

Family CARDIIDAE Lamarck, 1809

Genus PROTOCARDIA von Beyrich, 1845, p. 17

Type species.—*Cardium hillanum* J. Sowerby, 1813, p. 41.

Stratigraphic range.—Upper Triassic (Norian)—Upper Cretaceous (Maastrichtian) (Cox & others, 1969; Hautmann, 2001b). Cox and others (1969) assigned it an Upper Triassic–Upper Cretaceous range. This is also recognized here, since the post-Maastrichtian records are dubious (e.g., Marincovich, 1993). Schneider (1995) considered that it ranged from the Rhaetian, but Hautmann (2001b) reported it from Norian beds.

Paleogeographic distribution.—Tethys and Circumpacific (Fig. 54).

Tethys domain: Late Triassic: Norian–Rhaetian of China (Gu & others, 1976; Guo, 1988), Iran (Hautmann, 2001b); Rhaetian of eastern Alps (Austria) (Tomašových, 2006b), Burma (Healey, 1908), Spain (Márquez-Aliaga & Ros, 2002; Márquez-Aliaga & others, 2004; Márquez-Aliaga, Plasencia, & Ros, 2005), Tibet (China) (J. Yin & Grant-Mackie, 2005), England (Castell & Cox, 1975; Ivimey-Cook & others, 1999), Italy (Allasinaz, 1962; Gelati & Allasinaz, 1964; Sirna, 1968), Oman (Arabia) (R. Hudson & Jefferies, 1961); Early Jurassic: Hettangian of England (Liu, 1995; Ivimey-Cook & others, 1999), China (Z. Huang, 1986); Hettangian–Sinemurian of China (Stiller, 2006, and references therein); Sinemurian of China (J. Chen, 1988), France and Portugal (Liu, 1995).

Circumpacific domain: Early Jurassic: Sinemurian of Japan (Hayami, 1975).

Paleoautoecology.—B, Is, S, SM; Sb. Living Cardiidae are shallow burrowers; they have short siphons and a large foot with which they can burrow rapidly (Beesley, Ross, & Wells, 1998). *Protocardia* most likely had the same mode of life, but its globose shell indicates a slow burrower (Fürsich, 1982).

Mineralogy.—Aragonitic (Schneider & Carter, 2001). Schneider and Carter (2001) studied the shell microstructure of two species of *Protocardia* from the Upper Jurassic and Cretaceous. Although the two species differ in some details, they interpreted the shell as being completely aragonitic with a prismatic outer layer, a cross-lamellar middle layer, and a complex cross-lamellar inner layer.

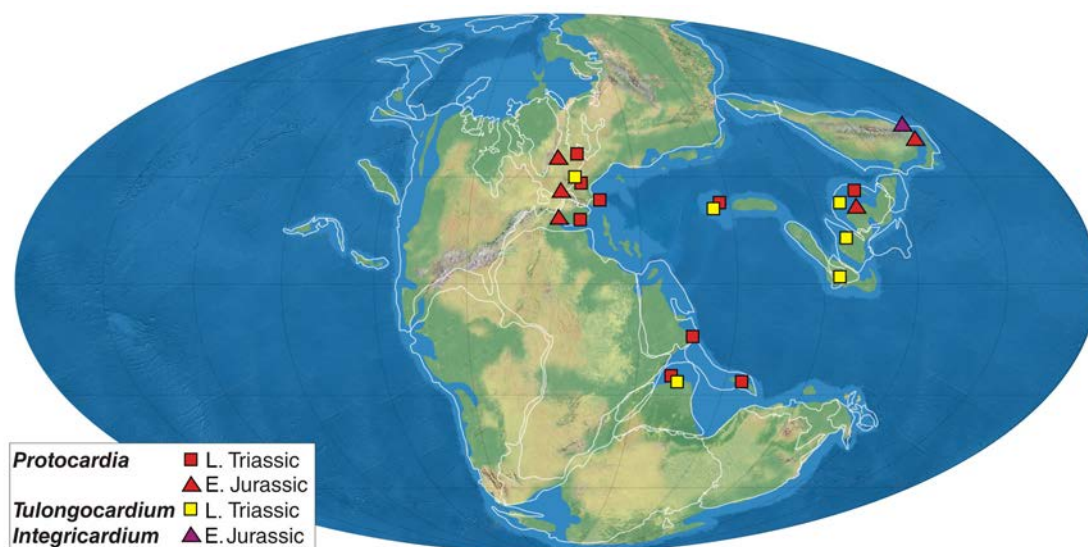


Figure 54. Paleogeographical distribution of Cardiidae (*Protocardia*, *Tulongocardium*, *Integricardium*). Late Triassic–Early Jurassic.

Genus TULONGOCARDIUM

Chen, Chen, & Zhang in Wen & others, 1976, p. 31

Type species.—*Cardium* (*Tulongocardium*) *pluriradiatum* Chen, Chen, & Zhang in Wen & others, 1976, p. 32.

Remarks.—Although *Tulongocardium* was originally proposed as a subgenus of *Cardium* (Wen & others, 1976) and some authors (e.g., Z. Fang & others 2009) still maintain this taxonomic position, following Schneider (1995), we consider it as a different genus, with *Vietnamicardium* Vu Khuc, 1977a, p. 678, as the junior synonym (see discussion for *Vietnamicardium* in Genera not Included, p. 172). However, Hautmann (2001b) considered *Vietnamicardium* as a valid genus. See Schneider (1995, p. 322) for a thorough discussion.

Stratigraphic range.—Upper Triassic (Norian–Rhaetian) (Wen & others, 1976). The genus *Tulongocardium* was originally reported from the Norian of China, and its range was later extended to the Rhaetian when several species were reassigned to it (see Wen & others, 1976, p. 31–32).

Paleogeographic distribution.—Tethys (Fig. 54). Kobayashi and Tamura (1983a) also reported it from the Himalayas, southern Tibet, and Malaysia, but systematic treatment was not provided.

Tethys domain: Late Triassic: Sumatra (Krumbeck, 1914), China (Gou, 1993); Norian of China (Wen & others, 1976), Vietnam (Vu Khuc, 1977a; Vu Khuc & Huyen, 1998), Iran (Hautmann, 2001b), China (Sha, Chen, & Qi, 1990); Rhaetian of Germany (Kutassy, 1931), the Alps (Diener, 1923), Burma (Healey, 1908), Vietnam (Vu Khuc & Huyen, 1998).

Paleoautoecology.—B, Is, S, SM; Sb. Similar to *Protocardia*.

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1973). There are no data about *Tulongocardium* shell microstructure. The shells of the living species of the superfamily Cardioidea are totally aragonitic with a cross-lamellar outer layer and complex cross-lamellar inner layer (J. D. Taylor, Kennedy, & Hall, 1973).

Genus INTEGRICARDIUM

Rollier, 1912 in 1911–1918, p. 127

Type species.—*Cardium dupinianum* d'Orbigny, 1844 in 1844–1848, p. 26.

Remarks.—The genus *Yokoyamaina* Hayami, 1958b, p. 23, was proposed by Hayami (1958b), with *Cyrena elliptica* Yokoyama, 1904, as type species and doubtfully assigned to the family Arcticiidae. Subsequently, Cox and others (1969) included it in the family Corbiculidae, also with doubts. Hayami (1975) reexamined the type species and concluded that *Yokoyamaina* was a cardiid and considered it to be a subgenus of *Integricardium*, an arrangement followed here (see discussion for *Yokoyamaina* in Genera not Included, p. 172).

Stratigraphic range.—Lower Jurassic (Hettangian)–Paleocene (Danian) (Hayami, 1975; Marincovich, 1993). Cox and others (1969) assigned it a Middle Jurassic–Upper Cretaceous range. With the inclusion of *Yokoyamaina* as subgenus of *Integricardium* (Hayami, 1975), the genus ranges back to the Hettangian. The record of *Integricardium* from the Danian (Marincovich, 1993) extend its range to the Paleocene.

Paleogeographic distribution.—Circumpacific (Fig. 54).

Circumpacific domain: Early Jurassic: Hettangian of Japan (Hayami, 1958d, 1975; Sugawara & Kondo, 2004; Kondo & others, 2006).

Paleoautoecology.—B, Is, S, MS; Sb. Similar to *Protocardia*.

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1973). There are no data about *Integricardium* shell microstructure. See previous discussion in *Tulongocardium*.

Superfamily TELLINOIDEA Blainville, 1814

Family SOWERBYIDAE Cox, 1929

Genus RHAETIDIA Bittner, 1895, p. 222

Type species.—*Rhaetidia zittelii* Bittner, 1895, p. 223.

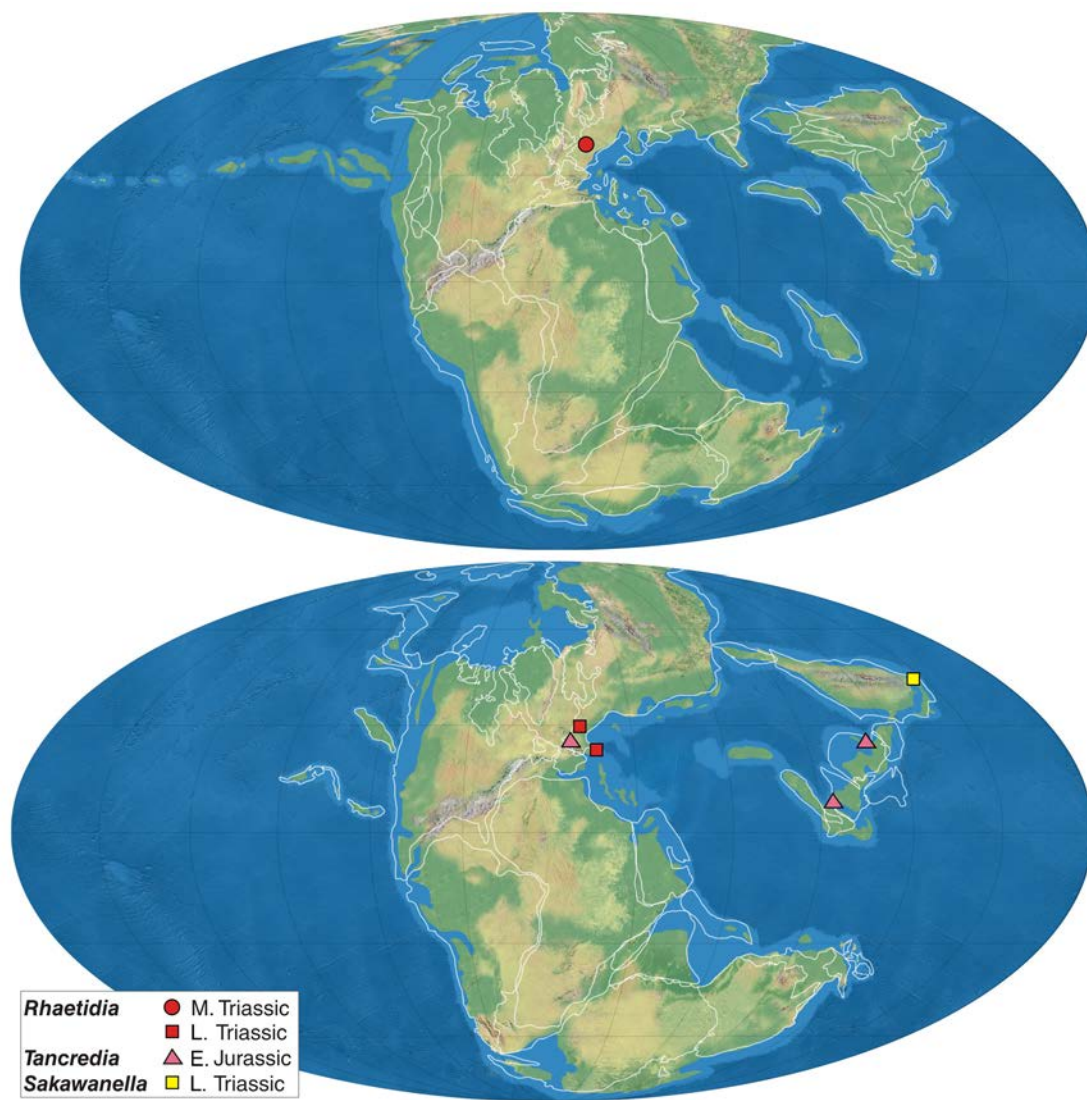


Figure 55. Paleogeographical distribution of Sowerbyidae (*Rhaetidia*) and Tancrediidae (*Tancredia*, *Sakawanella*). 1, Middle Triassic; 2, Late Triassic–Early Jurassic.

Remarks.—Cox and others (1969) doubtfully included *Rhaetidia* in the family Sowerbyidae due to its external morphology being similar to *Sowerbya* d'Orbigny, 1850, but *Rhaetidia* differs from *Sowerbya* by the lack of cardinal teeth and pallial sinus (Jablonski & Bottjer, 1990). Furthermore, these authors noticed a time span of 50 myr between the genera, yet another reason to doubt the relation of this genus to Sowerbyidae. We treat it in this family, pending further studies.

Stratigraphic range.—Middle Triassic (Ladinian)–Upper Triassic (Norian) (Bittner, 1895; S. Conti, 1954). Cox and others (1969) assigned it a Triassic range. According to the included species, its range was Ladinian–Norian. The type species, *R. zitteli* Bittner, 1895, was reported from the Carnian (Bittner, 1895). Other species attributed to this genus are: *R. praenuntia* (Stoppani, 1859 in 1858–1860) and *R. salomoni* Bittner, 1895, both from the Ladinian (Bittner, 1895; Rossi Ronchetti, 1959). Moreover, *Rhaetidia* was also mentioned from the Upper Triassic of Timor (Krumbeck, 1924), with *R. timorensis*

Krumbeck, 1924, and from the Norian of China, with *R. aff. zitteli* Bittner, 1895 (Cowper-Reed, 1927). These last two records were rejected by Jablonski and Bottjer (1990). In the first, they argued that Krumbeck's specimens did not belong to the genus and probably not even to the superfamily Tellinoidea. In the second, they referred to the poor preservation of the specimens studied by Cowper-Reed (1927). Jablonski and Bottjer (1990) recorded *Rhaetidia* from the upper Anisian, but this could not be corroborated in the published literature. The oldest systematic record is Ladinian.

Paleogeographic distribution.—western Tethys (Fig. 55).

Tethys domain: Middle Triassic: Ladinian of the Alps (Bittner, 1895; Rossi Ronchetti, 1959); Late Triassic: Carnian of the Alps (Bittner, 1895); Norian of Italy (S. Conti, 1954).

Paleoautoecology.—B, Is, ?S, SM; Sb. The external form of the shell indicates it probably lived infaunally; perhaps it was a shallow, nonsiphonate (or with short siphons) burrower,

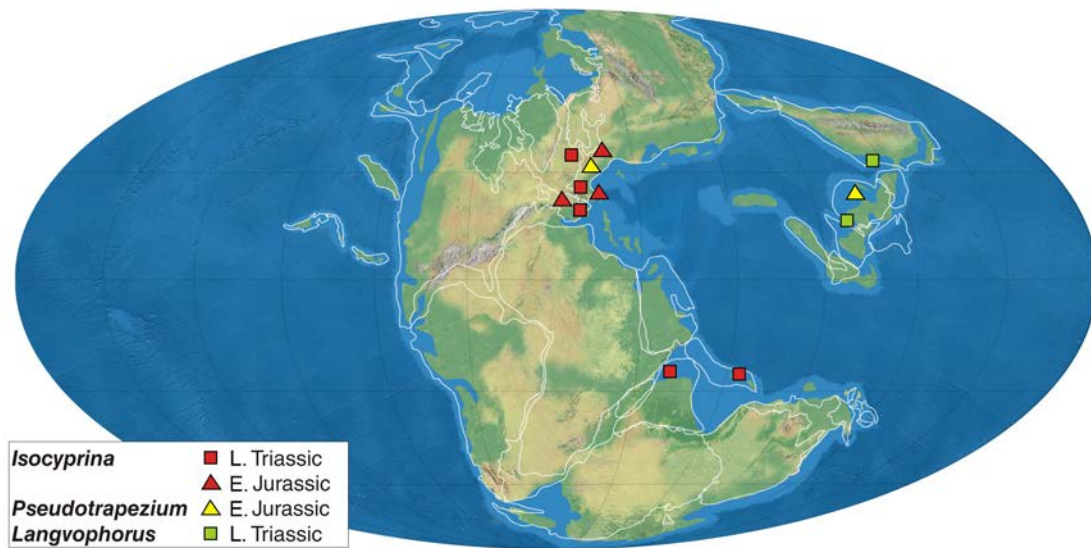


Figure 56. Paleogeographical distribution of Arcticidae (*Isocyprina*, *Pseudotrachezium*) and Trapeziidae (*Langvophorus*). Late Triassic–Early Jurassic.

contrary to living Tellinoidea, which often have long siphons and burrow deeply.

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1973). There are no data about *Rhaetidia* shell microstructure. In living tellinoid species studied by J. D. Taylor, Kennedy, and Hall (1973), the shell was entirely aragonitic. Some species have a prismatic outer shell layer, a cross-lamellar middle layer, and a complex cross-lamellar or homogeneous inner layer; in other species, only the last two layers are present.

Family TANCREDIIDAE Meek, 1864
Genus TANCREDIA Lycett, 1850, p. 407

Type species.—*Tancredia donaciformis* Lycett, 1850, p. 424.

Stratigraphic range.—Lower Jurassic (Sinemurian)–Paleocene (Danian) (Marincovich, 1993; Stiller, 2006). Cox and others (1969) assigned an Upper Triassic–Upper Cretaceous range to *Tancredia*, but, curiously, all the subgenera included in it had their origin in the Jurassic. Except for some dubious records provided by Hallam (1981) from the Norian of North America and by Polubotko and Repin (1990) and Kurushin (1990) from the Upper Triassic of north-eastern Asia, *Tancredia* was not reported from the Triassic. None of the three mentioned papers figured or described the specimens, nor did they indicate the original data source. The oldest sure record is Sinemurian, and the youngest is Danian.

Paleogeographic distribution.—Tethys (Fig. 55). Although we can only confirm its record from the Sinemurian of the Tethys domain, *Tancredia* was also recorded from the Sinemurian of South America (Damborenea, 1996a) and Greenland (Liu, 1995).

Tethys domain: Early Jurassic: Sinemurian of China (J. Chen, 1988; Stiller, 2006), Vietnam (Counillon, 1908), France (Martin, 1860).

Paleoautoecology.—B, Id, S, FM; Db. The superfamily Tellinoidea includes suspensivorous and detritivorous bivalves; it is accepted that

the oldest were suspensivorous and that the detritivorous did not appear until the Early Cretaceous (Jablonski & Bottjer, 1990). S. M. Stanley (1977) considered the members of the family Tancrediidae to be fast burrowers. *Tancredia* had a pallial sinus, indicating long siphons, and therefore it was probably a deep burrower (Fürsich, 1982; Stiller, 2006).

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1973). There are no data about *Tancredia* shell microstructure. See discussion in *Rhaetidia* (p. 144).

Genus SAKAWANELLA Ichikawa, 1950, p. 245

Type species.—*Sakawanella triadica* Ichikawa, 1950, p. 246.

Stratigraphic range.—Upper Triassic (Carnian) (Hayami, 1975). Cox and others (1969) and Ichikawa (1950) assigned it the same range: Upper Triassic. Later, Hayami (1975) noticed that *Sakawanella* had only been recorded from the Carnian.

Paleogeographic distribution.—Circumpacific (Fig. 55). *Sakawanella* was an endemic genus of Japan (Kobayashi & Tamura, 1983b).

Circumpacific domain: Late Triassic: Carnian of Japan (Ichikawa, 1950; Hayami, 1975).

Paleoautoecology.—B, Id, S, FM; Db. Similar to *Tancredia*.

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1973). There are no data about *Sakawanella* shell microstructure. See discussion in *Rhaetidia* (p. 144).

Superfamily ARCTICOIDEA Newton, 1891

Family ARCTICIDAE Newton, 1891

Genus ISOCYPRINA Röder, 1882, p. 90

Type species.—*Cardium cyreniforme* Buvignier, 1852, p. 15.

Remarks.—Ivimey-Cook and others (1999) noticed that, in most specimens attributed to *Isocyprina*, the hinge is not known and that they were assigned to the genus on the basis of the external shell shape. We follow these authors in their included species list, and

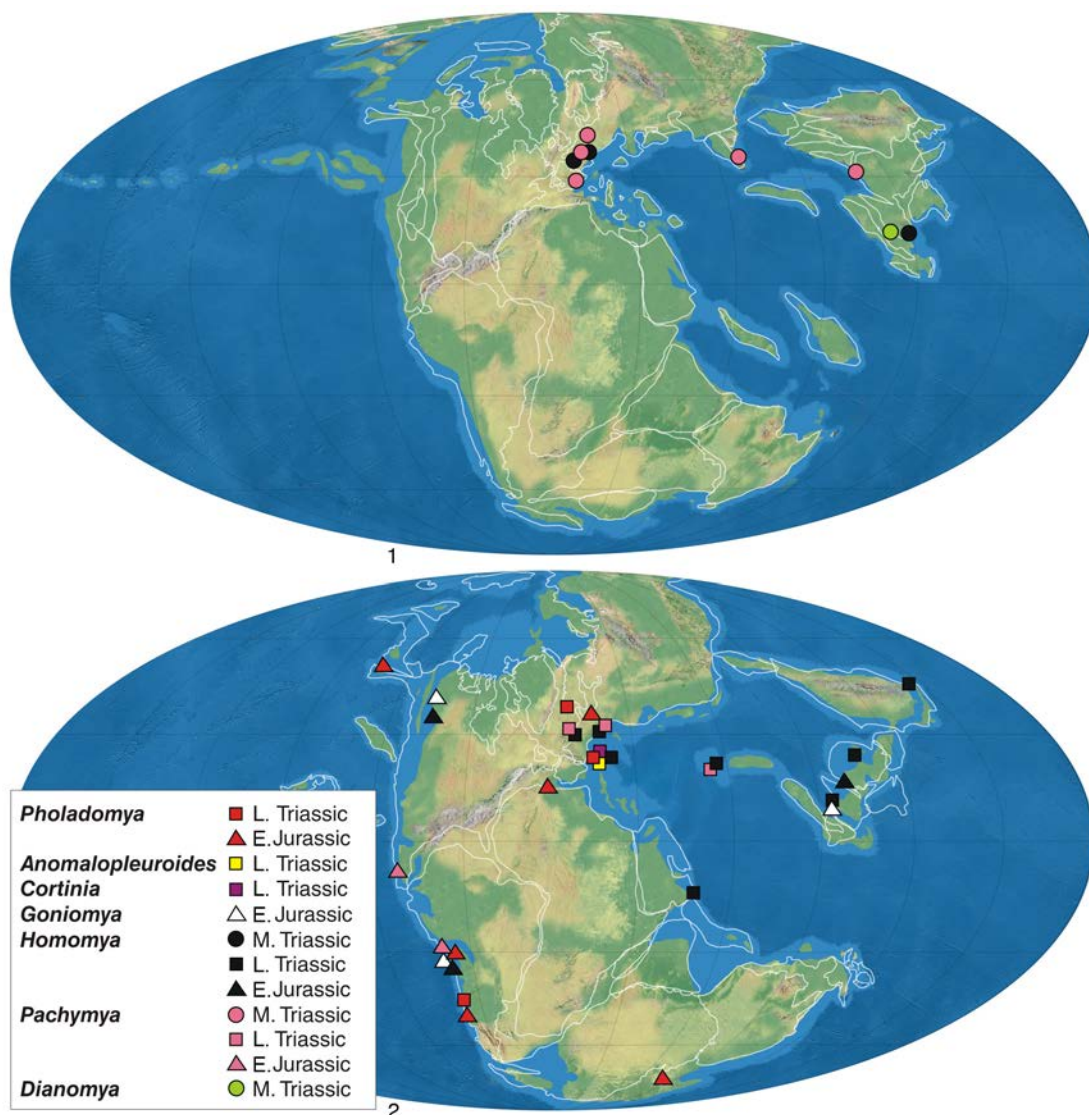


Figure 57. Paleogeographical distribution of Pholadomyidae (*Pholadomya*, *Anomalopleuroidea*, *Cortinia*, *Goniomya*, *Homomya*, *Pachymya*, *Dianomya*). 1, Middle Triassic; 2, Late Triassic–Early Jurassic.

regard *Eotrapezium* Douvillé, 1913, as a subgenus of *Isocyprina*, as Cox and others (1969) did.

Stratigraphic range.—Upper Triassic (Rhaetian)–Lower Cretaceous (Aptian) (Healey, 1908; Hayami, 1975). Cox and others (1969) assigned it an Upper Triassic–Upper Jurassic range, as did Gardner (2005), who proposed the new family Isocyprinidae. However, Hayami (1975) mentioned *I. aliquantula* (Amano, 1957) from the Aptian of Japan. The oldest record of the genus is Rhaetian (see paleogeographic distribution).

Paleogeographic distribution.—Tethys (Fig. 56). Vu Khuc and Huyen (1998) reported the species *I. ewaldi* (Bornemann, 1854) from the Rhaetian of Vietnam. It is the only record from that area, and the specimens were not figured. Damborenea (1996a) recorded *I. ancatruzi* (A. F. Leanza, 1942) from the Sinemurian of South America, but the only figured specimens (A. F. Leanza, 1942) are Pliensbachian in age. This same species is reported from the Pliensbachian of Sonora (Mexico) (Scholz, Aberhan, & González-León,

2008). However, Hallam (1981) listed *Isocyprina* from the Upper Triassic of South America and Europe. Note that Hallam mainly followed Cox and others (1969) and, particularly from South America, Körner (1937), Cox (1949), and Hayami, Maeda, and Ruiz-Fuller (1977). However, none of these three papers discussed *Isocyprina* or any species that was later assigned to it.

Tethys domain: Late Triassic: Rhaetian of the eastern Alps (Austria) (Tomašových, 2006a, 2006b), Burma (Healey, 1908), England (Wright & Benton, 1987; Ivimey-Cook & others, 1999), Tibet (“Lasha block”) (J. Yin & Grant-Mackie, 2005), Spain (Gómez, Goy, & Márquez-Aliaga, 2005; Márquez & others, 2010); Early Jurassic: Hettangian of Sweden (Troedsson, 1951), northwestern Europe (Hallam, 1987), Italy (S. Conti, 1954), Portugal (J. C. Fischer & Palain, 1971), Spain (Márquez & others, 2010); Hettangian–Sinemurian of Portugal (Liu, 1995).

Paleoautoecology.—B, Is, S, FM; Sb. Most likely, *Isocyprina* was a moderately fast burrower. Since there is no pallial sinus, it was probably a shallow burrower.

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1973). There are no data about the shell microstructure of *Isocyprina*. In living arcticoid species studied by J. D. Taylor, Kennedy, and Hall (1973), the shell is entirely aragonitic. Some species have a prismatic outer shell layer, a cross-lamellar middle layer, and a complex cross-lamellar or homogeneous inner layer; in other species, only the last two layers are observed.

Genus PSEUDOTRAPEZIUM
Fischer, 1887 in 1880–1887, p. 1075

Type species.—*Cypricardia bathonica* d'Orbigny, 1850, p. 308.

Stratigraphic range.—Lower Jurassic (Hettangian)–Upper Jurassic (Oxfordian) (Z. Huang, 1986; Hallam, 1987). Cox and others (1969) assigned it a Jurassic (Lias.–Portland.) range. Later, Z. Huang (1986) reported two species from the Hettangian of China that he attributed to *Pseudotrapezium*. These species are *Cypricardia triangularis* Terquem, 1855, and *Cypricardia praelonga* Terquem & Piette, 1865, both recorded from Hettangian beds of Luxemburg and France. It is difficult to know which is the youngest record of this genus, because the information at hand is rather limited. We indicate Oxfordian, following Hallam (1976, 1977, 1987).

Paleogeographic distribution.—Tethys (Fig. 56). *Pseudotrapezium* was recorded from the Hettangian of Morocco and the Sinemurian of France (Liu, 1995), but we did not locate information about these data.

Tethys domain: Early Jurassic: Hettangian of China and Europe (Z. Huang, 1986).

Paleoautoecology.—B, Is, S, FM; Sb. Similar to *Isocyprina*.

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1973). There are no data about *Pseudotrapezium* shell microstructure. See discussion in *Isocyprina* (p. 146).

Family TRAPEZIIDAE Lamy, 1920
Genus LANGVOPHORUS Vu Khuc, 1977a, p. 677

Type species.—*Tancredia (Hettangia) garandi* Mansuy, 1912, p. 65.

Remarks.—Vu Khuc (1977a) introduced this new genus in the family Trapeziidae; if this is correct, *Langvophorus* extends the range of the family back to the Triassic, but it was formerly regarded as a family with Cretaceous origins (Cox & others, 1969).

Stratigraphic range.—Upper Triassic (Norian–Rhaetian) (Vu Khuc, 1977a). Vu Khuc (1977a) proposed the genus *Langvophorus*, based on the species *T. garandi* Mansuy, 1912, and including *T. chovoensis* Mansuy, 1912, both reported from the Rhaetian of Tonkin (today part of southern China and Vietnam). He assigned it a Norian–Rhaetian range.

Paleogeographic distribution.—Eastern Tethys (Fig. 56). *Langvophorus* is endemic to southeastern Asia (Vu Khuc & Huyen, 1998).

Tethys domain: Late Triassic: Norian–Rhaetian of China (Cowper-Reed, 1927; Vu Khuc, 1977a); Rhaetian of Vietnam (Vu Khuc, 1977a; Vu Khuc & Huyen, 1998), Tonkin (Vietnam and southern China) (Mansuy, 1912).

Paleoautoecology.—Unknown. It is difficult to interpret how *Langvophorus* lived, because there is not much information on its morphology nor on the sediments in which it was recorded. It had an elongated shell with a continuous pallial line; if it had siphons,

these were very short. The living species of the family Trapeziidae are usually byssate, and some are nestlers (Beesley, Ross, & Wells, 1998).

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1973). There are no data about *Langvophorus* shell microstructure. See discussion in *Isocyprina* (p. 146).

Superfamily PHOLADOMYOIDEA King, 1844
Family PHOLADOMYIDAE King, 1844
Genus PHOLADOMYA G. B. Sowerby I, 1823
in 1821–1825, p. unnumbered

Type species.—*Pholadomya candida* G. B. Sowerby I, 1823 in 1821–1825, p. unnumbered.

Stratigraphic range.—Upper Triassic (Rhaetian)–Holocene (Ivimey-Cook & others, 1999; Harper, Dreyer, & Steiner, 2005). Cox and others (1969) assigned it an Upper Triassic–Holocene range. The oldest record is from the European Rhaetian (Ivimey-Cook & others, 1999). Nowadays, this genus is represented only by its type species and has a very restricted distribution (Harper, Dreyer, & Steiner, 2005).

Paleogeographic distribution.—Tethys, Circumpacific, and Austral (Fig. 57).

Tethys domain: Late Triassic: Rhaetian of England (Ivimey-Cook & others, 1999), Lombardy (Italy) (Chiesa, 1949); Early Jurassic: Hettangian of Europe (Ivimey-Cook & others, 1999), Luxemburg (Terquem, 1855); Hettangian–Sinemurian of Europe and Morocco (Liu, 1995).

Circumpacific domain: Early Jurassic: late Hettangian of Chile (Aberhan, 2004); Sinemurian of Yukon (Canada) (Poulton, 1991), Chile (Aberhan, 1993, 2004).

Austral domain: Late Triassic: Rhaetian of Argentina (Damborenea & Manceñido, 2012). Early Jurassic: Hettangian–Sinemurian of New Zealand (H. J. Campbell & Grant-Mackie, 1995); Sinemurian of Argentina (Damborenea, 1996a; Damborenea & Manceñido, 2005b; Damborenea & Lanés, 2007).

Paleoautoecology.—B, Id, S, SM; Db. The only living species, *P. candida* G. B. Sowerby I, 1823 in 1821–1825, is a deep burrower with long siphons, especially slow or almost sedentary (Checa & Jiménez-Jiménez, 2003a). It has never been observed alive, and the only information available was provided by two specimens found in the 19th century (Harper, Dreyer, & Steiner, 2005). They have elongated shells with a posterior gape and a deep pallial sinus, which supports the interpretation of a deep burrower. Mehl and Rehfeld (1992) found some specimens of the Bajocian *P. fidicula* G. B. Sowerby, 1823 in 1821–1825, in which the proximal part of the siphon was preserved by pyritization. In addition, Fürsich (1980) found specimens of several species attributed to *Pholadomya* in life position, included vertically in the sediment with the posterior part up. Most likely, they had an almost sedentary mode of life, and once they were buried at their living depth, it was unlikely they could reburrow if removed from the sediment (Checa & Jiménez-Jiménez, 2003a). While the living species normally inhabits deep water, Mesozoic species lived in shallow water (Cox in Cox & others, 1969). A similar mode of life is assumed for the family Pholadomyidae.

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1973). There are no studies on the shell microstructure of *Pholadomya*; however, J. D. Taylor, Kennedy, and Hall (1973) studied a fragment

of the shell of *P. candida*, and it is aragonitic. In other living species of the superfamily Pholadomyoidea, they observed that the shells were always aragonitic and frequently consisted of three layers: an outer prismatic one and nacreous middle and inner layers.

Genus ANOMALOPLEUROIDEA Cox, 1964, p. 45

nom. nov. pro Anomalopleura Leonardi, 1943, p. 62, *non* Kleine, 1916, p. 70.

Type species.—*Anomalopleura elisae* Leonardi, 1943, p. 62.

Stratigraphic range.—Upper Triassic (Carnian) (Leonardi, 1943). Cox and others (1969) reported it from the Upper Triassic of Austria and mentioned *Anomalopleura* was proposed in 1948. However, Leonardi proposed this new genus in 1943 from the Carnian of Costalares in Cortina d'Ampezzo (Italy).

Paleogeographic distribution.—western Tethys (Fig. 57).

Tethys domain: Late Triassic: Carnian of Italy (Leonardi, 1943).

Paleoautoecology.—B, ?Id, S, SM; ?Db The internal characters of *Anomalopleuroidea* are not known, so it is difficult to assign, with certainty, a mode of life. It had an elongated shell and a large posterior gape, which might indicate it was a deep burrower. Moreover, the strong inflation of the shell suggests a poor burrower.

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1973). There are no data about *Anomalopleuroidea* shell microstructure. See discussion in *Pholadomya* (p. 148).

Genus CORTINIA Leonardi, 1943, p. 63

Type species.—*Cortinia catharinae* Leonardi, 1943, p. 63.

Stratigraphic range.—Upper Triassic (Carnian) (Leonardi, 1943). Cox and others (1969) reported it from the Upper Triassic of Austria and mentioned it was proposed in 1948. However, Leonardi proposed this new genus in 1943 from the Carnian of Costalares in Cortina d'Ampezzo (Italy).

Paleogeographic distribution.—western Tethys (Fig. 57). Gou (1993) proposed a new species from the Upper Triassic of China, which he doubtfully attributed to *Cortinia*, *C. ? elongata* Gou, 1993.

Tethys domain: Late Triassic: Carnian of Italy (Leonardi, 1943).

Paleoautoecology.—B, ?Is, S, SM; ?Sb. *Cortinia* internal characters are unknown, so it is difficult to know if it was a shallow or deep burrower. The shell is small and has no gape, thus it was probably a shallow burrower.

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1973). There are no data about the shell microstructure of *Cortinia*. See discussion in *Pholadomya* (p. 148).

Genus GONIOMYA Agassiz, 1841 in 1840–1845, p. 1

Type species.—*Mya angulifera* J. Sowerby, 1819, p. 46.

Stratigraphic range.—Lower Jurassic (Hettangian)–Upper Cretaceous (Maastrichtian) (Hayami, 1964; Abdel-Gawad, 1986). Cox and others (1969) assigned it a Jurassic–Upper Cretaceous range and also recorded it from the Eocene. The earliest records are from Upper Cretaceous (Maastrichtian) (e.g., Abdel-Gawad, 1986), but we did not find any record from the Eocene. *Goniomya* is especially reported from the Middle Jurassic and Cretaceous, but it originated in the lower Jurassic (Hayami, 1964). According to Septfontaine (1995), the syntypes of the species *G. renevieri* Jeannel, 1913, deposited in the Cantonal Museum of Geology of Lausanne, are from the Het-

tangian of Switzerland. In the Lower Jurassic, it was also recorded from the Pliensbachian and Toarcian (Riegraf, 1977; Monari, 1994; Liu, 1995; Harries & Little, 1999; Fürsich and others, 2001; Gahr, 2002; Scholz, Aberhan, & González-León, 2008).

Paleogeographic distribution.—Circumpacific (Fig. 57). In the time interval analyzed here, the genus was recorded from Vietnam and also from the Sinemurian of the Canadian Arctic islands (Aberhan, Hrudka, & Poulton, 1998), with *G. rhombifera* (Goldfuss), but the specimens were not figured or discussed systematically. It was also recorded from the same stage from South America (Damborenea, 1996a; Damborenea & Manceñido, 2005b; Damborenea & Lanés, 2007) and from England (Liu, 1995).

Circumpacific domain: Early Jurassic: middle–late Hettangian of Chile (Aberhan, 2004); Hettangian–Sinemurian of Vietnam (Hayami, 1964; Vu Khuc & Huyen in Sato & Westermann, 1991); Sinemurian of Yukon (Canada) (Poulton, 1991).

Paleoautoecology.—B, Id, S, SM; Db. *Goniomya*, like most members of the family Pholadomyidae, was probably a deep burrower. It had a very elongated shell, inequilateral, moderately inflated, with anterior and posterior gapes and a pallial sinus, characteristics that indicate this mode of life unequivocally. Fürsich (1980, 1982) found specimens belonging to *Goniomya* in life position, with the shell upright in the sediment with the posterior part upward.

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1973). There are no data about the shell microstructure of *Goniomya*. See discussion in *Pholadomya* (p. 148).

Genus HOMOMYA Agassiz, 1843 in 1840–1845, p. 154

Type species.—*Mactra gibbosa* J. Sowerby, 1813, p. 91.

Stratigraphic range.—Middle Triassic (Anisian)–Lower Cretaceous (Valanginian) (Mader, 1982; Lazo, 2007b). Cox and others (1969, p. 832) pointed out that Muschelkalk species attributed to *Homomya* fit better into *Pachymya* (*Arcomya*). However, they assigned it a Middle Triassic (Muschelkalk)–Upper Jurassic (Portland.) range. It is difficult to refer specimens to these and other similar genera (such as *Pleuromya* Agassiz, 1842 in 1840–1845), because frequently the key internal characters are not observed (Neri & Posenato, 1985). Although these authors were aware of the indications given by Cox and others (1969) regarding the Muschelkalk species, they decided to refer their specimens to “*Homomya*,” following the original conception of the genus rather than Cox's review, because it is not clear which species were transferred to *Pachymya* (*Arcomya*). There are no proper discussions of this question. Most Muschelkalk species traditionally attributed to *Homomya* were relocated in other genera, but there are two species, *Homomya albertii* (Goldfuss, 1841 in 1833–1841) and *Homomya impressa* (Alberti, 1864), which are still considered in the literature as belonging to this genus (see e.g., Gall, 1971; Busnardo, 1975; Mader, 1982).

According to Mader (1982), the oldest record of *Homomya* is from the Anisian. Regarding the youngest one, Lazo (2007b) considered that *Pholadomya sanctaerucis* Pictet & Campiche, 1864 in 1864–1867, and *Pholadomya valangiensis* Pictet & Campiche, 1864 in 1864–1867, from the Valanginian of various localities, are synonyms and belong to *Homomya*, thus the range was extended here.

Paleogeographic distribution.—Tethys and Circumpacific (Fig. 57).

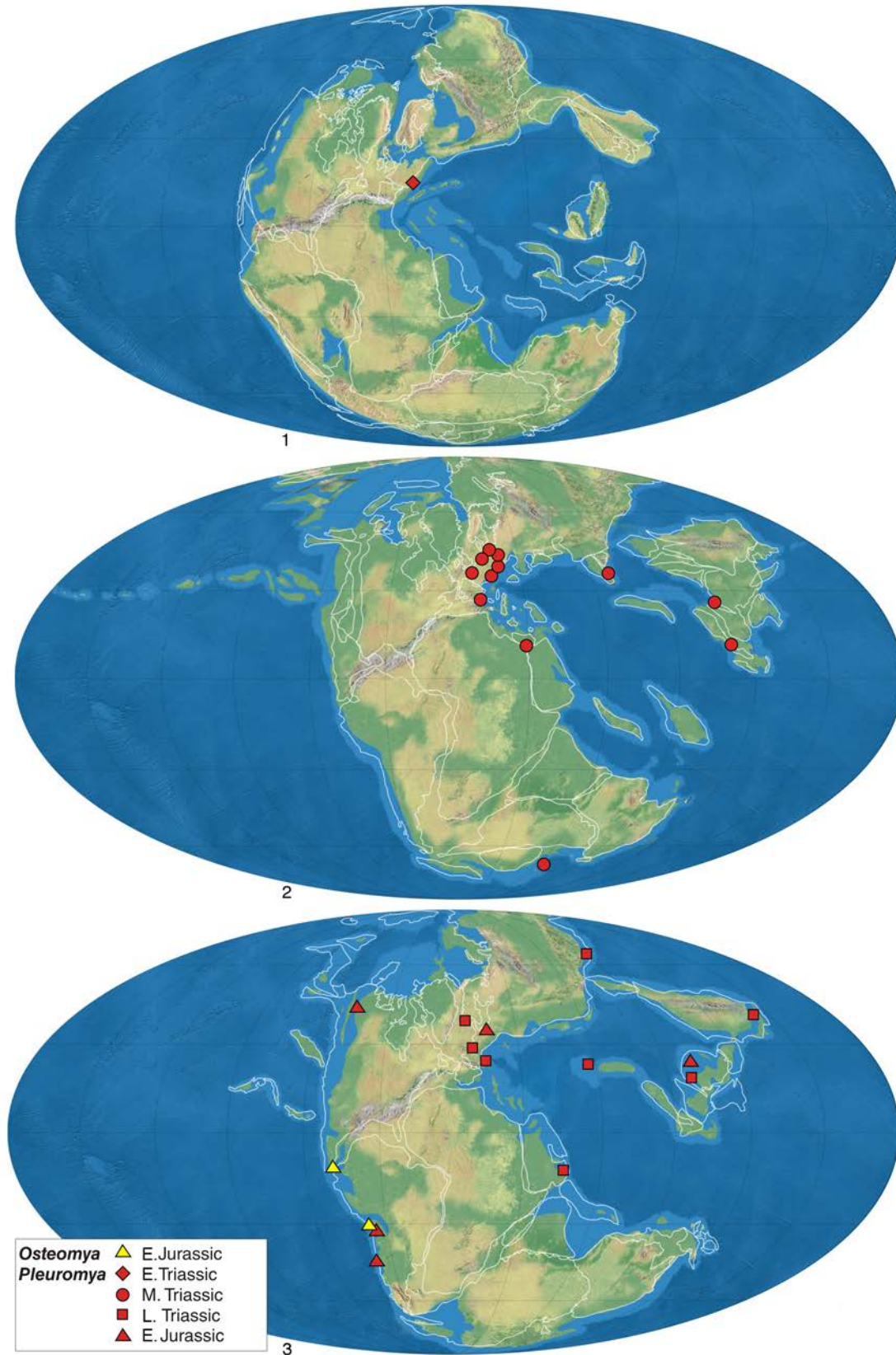


Figure 58. Paleogeographical distribution of Chaenomyidae (*Osteomya*) Pleuromyidae (*Pleuromya*). 1, Early Triassic; 2, Middle Triassic; 3, Late Triassic–Early Jurassic.

Tethys domain: Middle Triassic: Anisian of Germany (Mader, 1982), France (Gall, 1971), southeastern China (Z. Fang & others, 2009); Late Triassic: Yunnan province (China) (Gou, 1993; Hautmann, 2001b); Carnian of Lombardy (Italy) (Allasinaz, 1962, 1966); Norian of Oman (R. Hudson & Jefferies, 1961; Hautmann, 2001b), Indochina (Hautmann, 2001b); Norian–Rhaetian of Iran (Hautmann, 2001b); Rhaetian of the eastern Alps (Austria) (Tomašových, 2006a, 2006b; Siblík & others, 2010), Hungary (Vörös, 1981), Italy (Sirna, 1968); Early Jurassic: Hettangian of southern China (Z. Huang, 1986).

Circumpacific domain: Late Triassic: Carnian of Japan (Nakazawa, 1956; Hayami, 1975); Early Jurassic: ?Hettangian of Yukon (Canada) (Poulton, 1991); late Sinemurian of Chile (Aberhan, 2004).

Paleoautoecology.—B, Id, S, SM; Db. *Homomya* is externally very similar to *Pholadomya* and has a deep pallial sinus, so it most probably was a deep burrower (Runnegar, 1974). Fürsich (1980) reported *Homomya* sp. from the Bathonian of Poland in life position, buried with the posterior part up.

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1973). There are no data about *Homomya* shell microstructure. See discussion in *Pholadomya* (p. 148).

Genus PACHYMYA J. de C. Sowerby, 1826, p. 1

Type species.—*Pachymya gigas* J. de C. Sowerby, 1826, p. 2.

Stratigraphic range.—Middle Triassic (Anisian)–Upper Cretaceous (Turonian) (Cox & others, 1969; Sha, Chen, & Qi, 1990). Cox and others (1969) assigned it a Middle Triassic–Upper Cretaceous (Turonian) range. They included two subgenera, *P. (Pachymya)* and *P. (Arcomya)* Roemer, 1839, from the Cenomanian and Turonian respectively. The first record for *Pachymya* is from the Anisian of China (Sha, Chen, & Qi, 1990). There are no records after the Turonian, so we follow Cox and others (1969) for the top of the stratigraphic range.

Paleogeographic distribution.—Tethys and Circumpacific (Fig. 57). Cox and others (1969) considered it to be cosmopolitan, but during our study interval, it was only distributed in the Tethys and Circumpacific domains.

Tethys domain: Middle Triassic: Anisian of China (Sha, Chen, & Qi, 1990; Komatsu, Chen, & others, 2004); Ladinian of Spain (Márquez-Aliaga, 1985), Afghanistan (Farsan, 1975), Germany (Kutassy, 1931), southern Alps (Galdieri, 1908; Diener, 1923), Austria (Salomon, 1895); Late Triassic: ?Iran (Hautmann, 2001b); Carnian of the southern Alps (Galdieri, 1908); Norian of Hungary (Kutassy, 1931).

Circumpacific domain: Early Jurassic: late Sinemurian of Chile (Aberhan, 1993, 2004); Sinemurian of ?Sonora (Mexico) (Damborenea in Damborenea & González-León, 1997; Scholz, Aberhan, & González-León, 2008).

Paleoautoecology.—B, Id, S, SM; Db. *Pachymya* was most likely a deep burrower, indicated by its elongated shell and posterior gape (see Cox & others, 1969, p. 836, fig. 2b), although the pallial sinus is shallow or absent (Cox & others, 1969, p. 834).

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1973). There are no data about the shell microstructure of *Pachymya*. See discussion in *Pholadomya* (p. 148).

Genus DIANOMYA Guo, 1985, p. 229, 272

Type species.—*Dianomya lirulata* Guo, 1985, p. 229.

Remarks.—*Dianomya* was originally included in the family Pholadomyidae by Guo (1985), although Z. Fang and others (2009) suggested it may be better placed in Laternulidae.

Stratigraphic range.—Middle Triassic (Anisian) (Guo, 1985). Guo (1985) proposed *Dianomya* from the Anisian beds (Baifeng Formation) of China.

Paleogeographic distribution.—Eastern Tethys (Fig. 57).

Tethys domain: Middle Triassic: Anisian of southwestern China (Yunnan province) (Guo, 1985).

Paleoautoecology.—B, Id, S, SM; Db. *Dianomya*, like most Pholadomyidae, was probably a deep burrower. It had a very elongated shell, inequilateral, moderately inflated, with anterior and posterior gapes, characteristics that indicate this mode of life. In the diagnosis of the genus, the presence of a pallial sinus was not mentioned, and it is not seen in the figures offered by Guo (1985). *Dianomya* is the first Mesozoic pholadomyoid with oblique posterior costae; this type of ornamentation (Hautmann, Aghababalu, & Krystyn, 2011) could aid during burrowing.

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1973). There are no data about the shell microstructure of *Dianomya*. See discussion in *Pholadomya* (p. 148).

Family CHAENOMYIDAE Waterhouse, 1966

Genus OSTEOMYA Moesch, 1874 in 1874–1875, p. 19

Type species.—*Mya dilata* Phillips, 1829, p. 155.

Remarks.—Cox and others (1969) included this genus in the family Pholadomyidae. Following Runnegar (1974), we consider *Osteomya* to be in the family Chaenomyidae.

Stratigraphic range.—Lower Jurassic (Sinemurian)–Middle Jurassic (Callovian) (Cox & others, 1969; Scholz, Aberhan, & González-León, 2008). Cox and others (1969) assigned it a Toarcian–Callovian range. Later, Aberhan (2004) and Scholz, Aberhan, and González-León (2008), respectively, reported *O. dilata* (Phillips, 1829) from the Sinemurian of Chile and Mexico. Guo (1985) proposed a new subgenus, *Osteomya (Yunnanomya)*, from the Anisian of China. This is not taken into account, because Z. Fang and others (2009) regarded it as a junior synonym of *Homomya* Agassiz, 1843 in 1840–1845.

Paleogeographic distribution.—Circumpacific (Fig. 58). During the study interval, the genus was only mentioned from the Circumpacific domain, but, later in the Jurassic, *Osteomya* was also distributed in the Tethys domain (Jaitly, 1986; Fürsich & others, 2001; Gahr, 2002). Liu (1995) and Damborenea (1996a) reported it from the Hettangian and Sinemurian of Greenland and South America, respectively, but there are no published records to corroborate these data.

Circumpacific domain: Early Jurassic: late Sinemurian of Chile (Aberhan, 2004); Sinemurian of Sonora (Mexico) (Scholz, Aberhan, & González-León, 2008).

Paleoautoecology.—B, Id, S, SM; Db. The characteristics of the *Osteomya* shell suggest that, like other members of this superfamily, it was a deep burrower. It had an elongated shell, strongly inequilateral and a very broad posterior gape (Cox & others, 1969, p. 833). In the specimens figured by Runnegar (1974, pl. 3, 17–20), a shallow

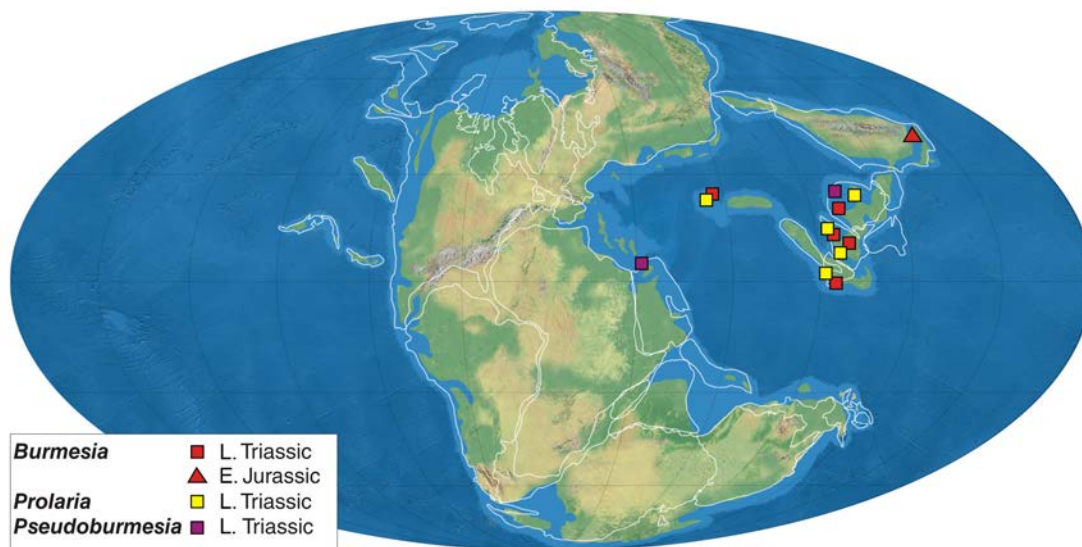


Figure 59. Paleogeographical distribution of Burmesiidae (*Burmesia*, *Prolaria*, *Pseudoburmesia*). Late Triassic–Early Jurassic.

pallial sinus is observed, which indicates that it probably was an intermediate burrower when compared to *Pholadomya*.

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1973). There are no data about the shell microstructure of *Osteomya*. See discussion in *Pholadomya* (p. 148).

Family PLEUROMYIDAE Dall, 1900 in 1896–1900

Genus PLEUROMYA Agassiz, 1845 in 1840–1845, p. 231

Type species.—*Mya gibbosa* J. de C. Sowerby, 1823, p. 19.

Stratigraphic range.—Lower Triassic (Olenekian)–Lower Cretaceous (Valanginian) (Sha & Fürsich, 1994; Posenato, 2008a). Cox and others (1969) assigned it a Triassic–Lower Cretaceous range. We did not find reliable records after the Lower Cretaceous; the youngest record of *Pleuromya* is Valanginian (Sha & Fürsich, 1994), although the specimens found by these authors are preserved as internal molds. There is some uncertainty concerning the oldest record of this genus. The members of the Lower Triassic “*Myacites*” group were transferred to various genera, including *Pleuromya* (see Neri & Posenato, 1985, for a discussion of this issue), but many of the specimens were assigned to this genus based on internal molds that did not show enough detail of characters to make a good generic assignment. Moreover, it is frequently difficult to distinguish between *Pleuromya* and *Homomya* (Neri & Posenato, 1985). According to these authors, the attribution of *P. elongata* (Schlotheim, 1820) to *Pleuromya* is correct if one considers the original concept of the genus. This same species is also recorded from the Triassic by Leonardi (1935) and Broglio-Loriga and others (1990), but the specimens in all cases are poorly preserved. Fraiser and Bottjer (2007a) and Posenato (2008a) reported *Pleuromya* from the “Gastropod Oolite” member of the Werfen Formation in Italy, but they did not figure or discuss the material systematically. Therefore, we considered the oldest Triassic record with certain reservations. From the Middle Triassic onward, *Pleuromya* was well represented (see paleogeographic distribution).

Paleogeographic distribution.—Tethys, Circumpacific, and Austral (Fig. 58). The genus was also mentioned in the Boreal domain, but not figured or described, from the Middle Triassic (Dagys & Kurushin, 1985) and Late Triassic (Kurushin, 1990; Polubotko & Repin, 1990).

Tethys domain: Early Triassic: Olenekian of ?Italy (Neri & Posenato, 1985; Broglio-Loriga & others, 1990; Fraiser & Bottjer, 2007a; Posenato, 2008a); Middle Triassic: Anisian of China (Gu & others, 1976; Sha, Chen, & Qi, 1990), Italy (Posenato, 2008b), Bulgaria (Encheva, 1969), northern Vietnam (Komatsu, Huyen, & Huu, 2010); Buntsandstein of France (Gall, 1971); Muschelkalk of France (Márquez-Aliaga & others, 2002), Spain (Márquez-Aliaga, 1983, 1985; Márquez-Aliaga, Hirsch, & López-Garrido, 1986; Budurov & others, 1991; López-Gómez & others, 1994; Márquez-Aliaga & Martínez, 1996; Márquez-Aliaga & others, 2002), Hungary (Szente, 1997), Poland (Senkowiczowa, 1985), Germany (Fuchs & Mader, 1980; Hagdorn, 1982); Ladinian of Italy (Posenato, 2002), China (Sha, Chen, & Qi, 1990), Afghanistan (Farsan, 1975), Israel (Lerman, 1960), northern Vietnam (Komatsu, Huyen, & Huu, 2010); Late Triassic: China (Gu & others, 1976; J. Chen, 1988); Carnian of China (Gu & others, 1976; Sha, Chen, & Qi, 1990), Italy (Desio, Rossi Ronchetti, & Vigano, 1960); Norian of Iran (Hautmann, 2001b), Oman (R. Hudson & Jefferies, 1961); Rhaetian of the Alps (Austria) (Tomašových, 2006a), Yunnan (China) (Guo, 1985), ?England (Ivimey-Cook & others, 1999), Italy (S. Conti, 1954; Sirna, 1968); Early Jurassic: Sinemurian of Sweden (Troedsson, 1951); ?Hettangian, Sinemurian of China (J. Chen, 1988; Stiller, 2006).

Circumpacific domain: Late Triassic: Carnian of Japan (Nakazawa, 1956; Hayami, 1975); Early Jurassic: early and late Hettangian of Chile (Aberhan, 2004); ?Hettangian, Sinemurian of Yukon (Canada) (Poulton 1991); Sinemurian of Chile (Aberhan, 1993).

Austral domain: Middle Triassic: Ladinian of New Zealand (Marwick, 1953); Early Jurassic: Sinemurian of Argentina (Damborenea & Manceñido, 2005b).

Boreal domain: Late Triassic: Carnian of Primorie (Kiparisova, 1972).

Paleoautoecology.—B, IP, S, SM; Db. *Pleuromya* is characterized by an elongated shell, with siphonal and pedal gapes and a deep pallial sinus. These features indicate it had long siphons and burrowed deep in the sediment, like most members of the superfamily Pholadomyoidea. Its shell is moderately to strongly inflated; it would have been a slow burrower. Fürsich (1982) found *Pleuromya* in life position, oriented vertically with the posterior part toward the sediment surface. He compared the mode of life of *Pleuromya* with the living species of *Mya* Linnaeus, 1758, which live deeply buried in the adult stage and are unable to return to their life position if unearthed.

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1973). There are no data about the shell microstructure of *Pleuromya*. See discussion in *Pholadomya* (p. 148).

Family BURMESIIDAE Healey, 1908

Genus BURMESIA Healey, 1908, p. 58

Type species.—*Burmesia latouchii* Healey, 1908, p. 58.

Stratigraphic range.—Upper Triassic (Carnian)–Lower Jurassic (Hettangian) (Hayami, 1975; J. Chen, 1985). Cox and others (1969) assigned it an Upper Triassic–Lower Jurassic range. *Burmesia* was reported from the Norian, Rhaetian, and Hettangian (see paleogeographic distribution). However, Huyen and Vu Khuc (in Sato & Westermann, 1991) mentioned it from the Pliensbachian. The specimens were neither figured nor discussed systematically, and we did not locate any publication to confirm these records.

Paleogeographic distribution.—Eastern Tethys and Circumpacific (Fig. 59).

Tethys domain: Late Triassic: Carnian of China (J. Chen, 1985); Norian of Indonesia (Diener, 1923), China (Gu & others, 1976; Wen & others, 1976; J. Chen, 1985; Gou, 1993; Y. Li, 1994), Iran (Hautmann, 2001b), Vietnam (Vu Khuc & Huyen, 1998; Hautmann, 2001b); Rhaetian of Burma (Healey, 1908), Iran (Hautmann, 2001b).

Circumpacific domain: Early Jurassic: Hettangian of Japan (Hayami, 1959, 1975; Hayami in Sato & Westermann, 1991).

Paleoautoecology.—B, Id, S, SM; Db. Although neither pallial line nor adductor muscles are observed, we assume *Burmesia* had a mode of life similar to other members of the superfamily Pholadomyoidea.

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1973). There are no data about *Burmesia* shell microstructure. See discussion in *Pholadomya* (p. 148).

Genus PROLARIA Healey, 1908, p. 60

Type species.—*Prolaria sollasi* Healey, 1908, p. 60.

Stratigraphic range.—Upper Triassic (Norian–Rhaetian) (Hautmann, 2001b). Cox and others (1969) assigned it a Rhaetian range, as the specimens described by Krumbeck (1914) from the Norian were not considered. Later, *Prolaria* was repeatedly recorded as being from the Norian (see paleogeographic distribution).

Paleogeographic distribution.—Eastern Tethys (Fig. 59).

Tethys domain: Late Triassic: Norian of China (Gu & others, 1976; Hautmann, 2001b), Sumatra (Indonesia) (Krumbeck, 1914),

Vietnam (Vu Khuc & Huyen, 1998; Hautmann, 2001b); Rhaetian of Burma (Healey, 1908), Iran (Hautmann, 2001b), Indochina (Diener, 1923).

Paleoautoecology.—B, Id, S, SM; Db. Similar to *Burmesia*.

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1973). There are no data about *Prolaria* shell microstructure. See discussion in *Pholadomya* (p. 148).

Genus PSEUDOBURMESIA Gou, 1993, p. 20, 26

Type species.—*Pseudoburmesia maantangensis* Gou, 1993, p. 21.

Remarks.—According to Sha, Chen, and Qi (1990), *Pseudoburmesia* and its type species were proposed by Gou in 1980, but they do not list the reference. Gou described the genus and its type species as being new in 1993. Sha, Chen, and Qi (1990) proposed a new species, *P. yushuensis* Sha, Chen, & Qi, 1990, and also included other species: *P. posteroradiata* (Cox, 1924) and *P. qinghaiensis* (Lu, 1981). Z. Fang and others (2009, p. 142) indicated: “It may be better to regard this genus as a synonym of *Anomalopleuroidea* Cox,” but no further explanation was given.

Stratigraphic range.—Upper Triassic (Carnian) (Sha, Chen, & Qi, 1990). According to Gou (1993), *Pseudoburmesia* had an Upper Triassic range. Lu (1981) reported *Burmesia? qinghaiensis* Lu, 1981, from the Norian, and Cox (1924) reported *Burmesia? posteroradiata* from the Carnian. Sha, Chen, and Qi (1990), taking into account all the species included in *Pseudoburmesia*, assigned it a Carnian range.

Paleogeographic distribution.—Tethys (Fig. 59).

Tethys domain: Late Triassic: Carnian of China (Sha, Chen, & Qi, 1990), Jordan (Cox, 1924; Sha, Chen, & Qi, 1990).

Paleoautoecology.—B, Id, S, SM; Db. Similar to *Burmesia*.

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1973). There are no data about *Pseudoburmesia* shell microstructure. See discussion in *Pholadomya* (p. 148).

Superfamily CERATOMYOIDEA Arkell, 1934 in 1929–1937

Family CERATOMYIDAE Arkell, 1934 in 1929–1937

Genus PTEROMYA Moore, 1861, p. 505

Type species.—*Pteromya crowcombeia* Moore, 1861, p. 506.

Stratigraphic range.—Upper Triassic (Rhaetian)–Lower Jurassic (Hettangian) (Cox, 1963). Cox and others (1969) assigned it a Rhaetian–Hettangian range, following his comprehensive review of *Pteromya* (Cox, 1963).

Paleogeographic distribution.—Western Tethys (Fig. 60). Damborenea (1996a) mentioned *Pteromya* from the southeastern Pacific margin, but it is not a systematic paper. As far as we know, it has only been recorded from Europe.

Tethys domain: Late Triassic: Rhaetian of England (Vokes, 1945; Cox, 1963; Ivimey-Cook & others, 1999), Spain (López-Gómez, Goy, & Márquez-Aliaga, 2005; Márquez-Aliaga & others, 2010); Early Jurassic: Hettangian of Spain (López-Gómez, Goy, & Márquez-Aliaga, 2005; Márquez-Aliaga & others, 2010), England (Cox, 1963; Ivimey-Cook & others, 1999), France (Freneix & Cubaynes, 1984).

Paleoautoecology.—B, Is, S, SM; Sb. According to Runnegar (1974), *Pteromya* was an intermediate burrower. The members of this family bury at different depths, for example, *Ceratomya* Sandberger, 1864, is a shallow burrower, and it is characterized by a robust shell, without siphonal gapes, with subequal adduc-

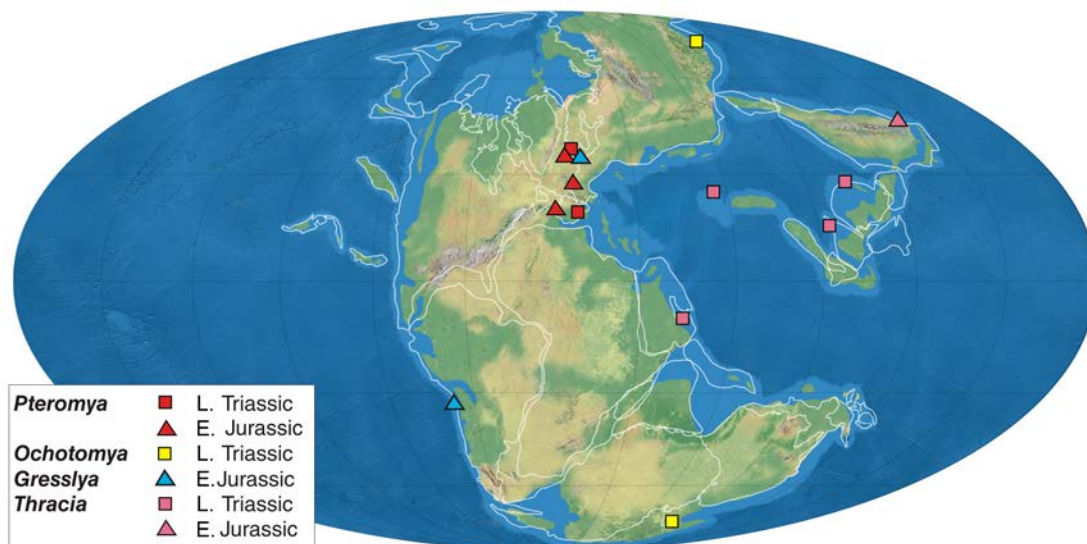


Figure 60. Paleogeographical distribution of Ceratomyidae (*Pteromya*, *Ochotomya*, *Gresslya*) and Thraciidae (*Thracia*). Late Triassic–Early Jurassic.

tor scars, deep pedal retractors insertions, and with a shallow pallial sinus (Runnegar, 1974). However, *Gresslya* Agassiz, 1843 in 1840–1845, had a deep pallial sinus and posterior gape; it is interpreted as a deep burrower. The shell of *Pteromya* was not as robust as that of *Ceratomya*, and it is more elongated and less inflated, but muscle scars or a pallial sinus are not observed. Since the siphons would have been short, we assign it a shallow burrower mode of life.

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1973). There are no data about *Pteromya* shell microstructure. See discussion in *Pholadomya* (p. 148).

Genus OCHOTOMYA Polubotko, 1966, p. 13

Type species.—*Ochotomya anyuensis* Polubotko, 1966, p. 16.

Stratigraphic range.—Upper Triassic (Norian–Rhaetian) (Polubotko, 1966). Polubotko (1966) proposed *Ochotomya* and included three species: *O. anyuensis* Polubotko, *O. anmandykanensis* (Tuchkov), and *O. terechovae* Polubotko. He reported *Ochotomya* from the Norian–Rhaetian beds of northeastern Russia and noticed that it was probably distributed through Russia, Japan, New Zealand, and North America, and perhaps Italy during the Lower and Middle Triassic. We did not find any record from Lower or Middle Triassic; all the records date from the Upper Triassic (Grant-Mackie, 1981; Okuneva, 1985; Kurushin, 1990; Polubotko & Repin, 1990; MacFarlan, 1998; Polubotko, 2010).

Paleogeographic distribution.—Austral and Boreal (Fig. 60).

Austral domain: Late Triassic: Norian–Rhaetian of New Zealand (Grant-Mackie, 1981; MacFarlan, 1998).

Boreal domain: Late Triassic: Norian–Rhaetian of northeastern Russia (Polubotko, 1966, 2010; Okuneva, 1985; Kurushin, 1990; Polubotko & Repin, 1990).

Paleoautoecology.—B, Is, S, SM; Sb. *Ochotomya* is very similar in external form to *Ceratomya* Sandberger, 1864 (see mode of life for *Pteromya*, p. 153). *Ochotomya* probably was a shallow burrower;

it had a robust and smooth globular shell and is usually preserved articulated (Grant-Mackie, 1981).

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1973). There are no data about *Ochotomya* shell microstructure. See discussion in *Pholadomya* (p. 148).

Genus GRESSLYA Agassiz, 1843 in 1840–1845, p. 202

Type species.—*Lutraria gregaria* von Zieten, 1833 in 1830–1833, p. 85.

Stratigraphic range.—Lower Jurassic (upper Hettangian)–Upper Jurassic (Kimmeridgian) (Tate & Blake, 1876; Arkell, 1933 in 1929–1937). Cox and others (1969) assigned it a Lower–Upper Jurassic range, and Sepkoski (2002) did the same, but he was more precise: upper Hettangian–upper Tithonian, referring to Hallam (1987) and Kelly (1984). *Gresslya* was reported from Hettangian–Sinemurian beds in several localities (Hallam, 1987; Liu, 1995; Damborenea, 1996a; Damborenea & Manceñido, 2005b), but none of these papers included a systematic treatment of the specimens; the only paper with figures is Tate and Blake (1876), who recorded *G. galathea* Agassiz from *angulata* to *oxynotum* zones (upper Hettangian–upper Sinemurian). Aberhan (2004) recorded and figured *Gresslya* sp. A from Sinemurian beds of Chile. Damborenea (in Damborenea & González-León, 1997) recorded *Gresslya rotundata* (Phillips) from Sinemurian–Toarcian beds of Europe and Canada, but no figures of the material were provided. Regarding the top of the *Gresslya* range, Kelly (1984) did not consider it in his study, but the youngest record is Kimmeridgian (Arkell, 1933 in 1929–1937). Some authors (e.g., Sha & others, 2009) mentioned it from the Lower Cretaceous, but we did not find any systematic study to corroborate this record.

Paleogeographic distribution.—Eastern Tethys and Circumpacific (Fig. 60). *Gresslya* was reported from Canada (Poulton, 1991), but he attributed the specimens to this genus only doubtfully.

Tethys domain: Early Jurassic: Hettangian–Sinemurian of England (Tate & Blake, 1876).

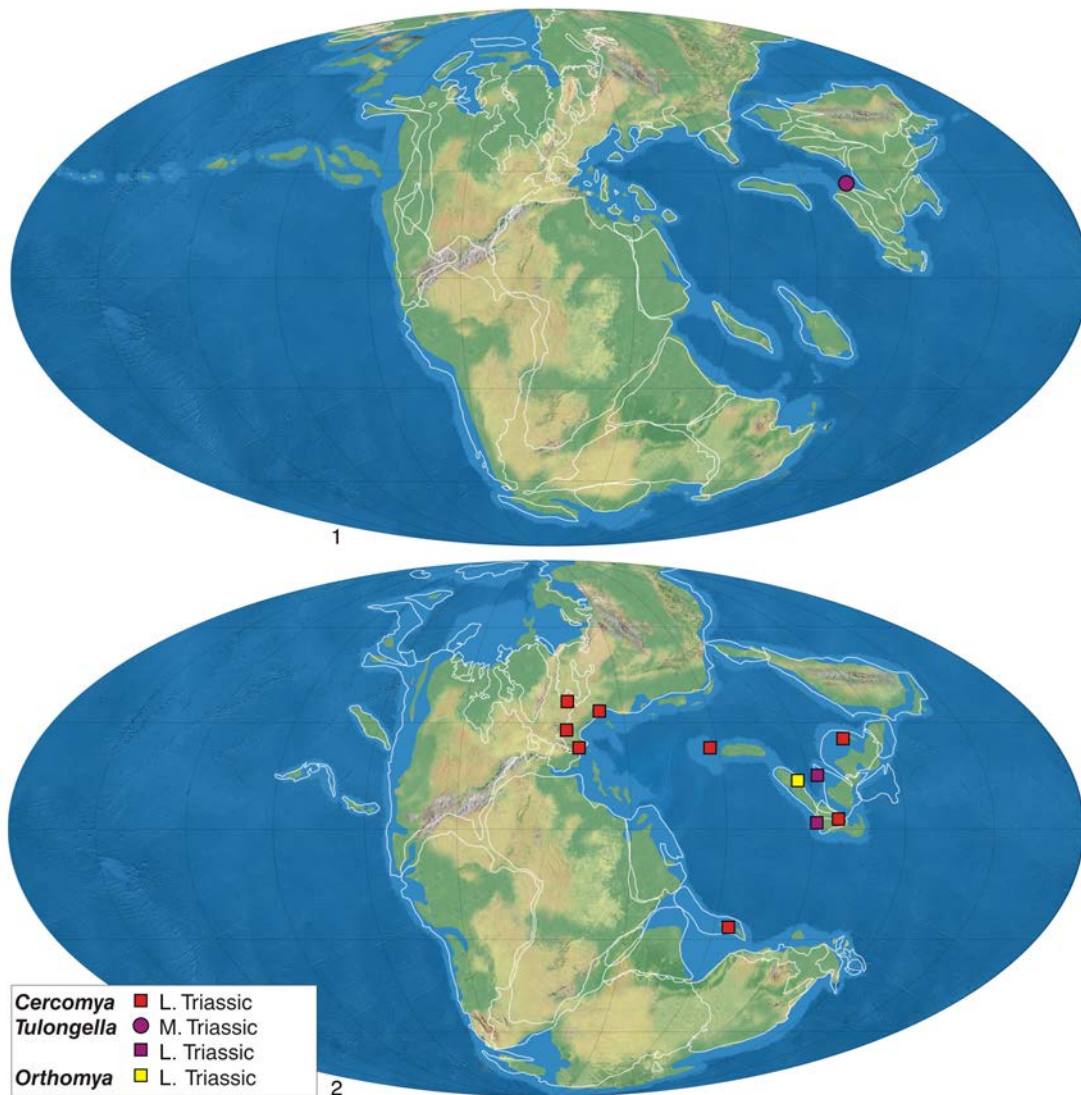


Figure 61. Paleogeographical distribution of Laternulidae (*Cercomya*, *Tulongella*, *Orthomya*). 1, Middle Triassic; 2, Late Triassic.

Circumpacific domain: Early Jurassic: Sinemurian of Chile (Aberhan, 2004).

Paleoautoecology.—B, Id, S, SM; Db. *Gresslya* had a deep pallial sinus and a posterior gape; it is interpreted as a deep burrower (Runnegar, 1974). A deep pallial sinus indicates it had long siphons, although its high inflation might influence its ability to penetrate into the sediment (Pugaczewska, 1986).

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1973). There are no data about *Gresslya* shell microstructure. See discussion in *Pholadomya* (p. 148).

Superfamily PANDOROIDEA Rafinesque, 1815

Family THRACIIDAE Stoliczka, 1870 in 1870–1871

Genus THRACIA Leach in J. de C. Sowerby, 1823, p. 20

Type species.—*Mya pubescens* Pulteney, 1799, p. 27.

Stratigraphic range.—Upper Triassic (Norian)–Recent. Although Cox and others (1969) assigned it a Jurassic–Holocene range, *Thracia*

was also recorded from the Upper Triassic. There are three species recorded from the Upper Triassic: *T. prisca* Healey, 1908, *T. proavita* R. Hudson & Jefferies, 1961, and *T. applanata* Krumbeck, 1913 (R. Hudson & Jefferies, 1961). Healey (1908) proposed *T. prisca* Healey, 1908, from the Rhaetian of Burma. Later, Gu and others (1976) quoted it from contemporary sediments of China. *Thracia* was also mentioned from the Upper Triassic of Iran (Hautmann, 2001b), the Norian of Oman (R. Hudson & Jefferies, 1961), Indochina (Kutassy, 1931), and Vietnam (Vu Khuc & Huyen, 1998).

Paleogeographic distribution.—Tethys and Circumpacific (Fig. 60).

Tethys domain: Late Triassic: Burma (Healey, 1908), China (Gu & others, 1976; Gou, 1993), Iran (Hautmann, 2001b), Oman (R. Hudson & Jefferies, 1961), Indochina (Kutassy, 1931).

Circumpacific domain: Early Jurassic: Hettangian of Japan (Hayami, 1958c, 1975; Kondo & others, 2006).

Paleoautoecology.—B, Id, S, SM; Db. Living species of *Thracia* are deep burrowers with long siphons, and they produce mucus chan-

nels around the siphons, to avoid exposure to the surface (Beesley, Ross, & Wells, 1998). In many of the fossil species, a deep pallial sinus and siphonal gapes are observed; so they probably lived in the same manner. Fürsich (1980) recorded *Thracia* specimens in life position, and they were included in the substrate vertically with the posterior part up.

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1973). The shell of living species of *Thracia* is completely aragonitic and is made of two layers, both of homogeneous microstructure (J. D. Taylor, Kennedy, & Hall, 1973). The shell of the Mesozoic specimens contained nacreous structure (Runnegar, 1974).

Family LATERNULIDAE Hedley, 1918

Genus CERCOMYA Agassiz, 1843 in 1840–1845, p. 143

Type species.—*Cercomya pinguis* Agassiz, 1843 in 1840–1845, p. 145.

Stratigraphic range.—Upper Triassic (Carnian)–Upper Cretaceous (Maastrichtian). Cox and others (1969) assigned it an Upper Triassic–Cretaceous range. The oldest mention of *Cercomya* dates from the Carnian (Sha, Chen, & Qi, 1990) and the youngest from the Maastrichtian (Abdel-Gawad, 1986).

Paleogeographic distribution.—Tethys (Fig. 61). Damborenea (1996a) mentioned it from the Hettangian–Sinemurian of the south-eastern Pacific margin, but the first figured specimens are Pliensbachian (Aberhan, 1994a; Scholz, Aberhan, & González-León, 2008).

Tethys domain: Late Triassic: Carnian of China (Sha, Chen, & Qi, 1990), ?Italy (Allasinaz, 1966); Norian–Rhaetian of Iran, the Alps, Burma, Vietnam, and Yunnan (China) (Hautmann, 2001b); Rhaetian of Tibet (so-called Lhasa block) (J. Yin & Grant-Mackie, 2005), England (Ivimey-Cook & others, 1999), ?Hungary (Vörös, 1981).

Paleoautoecology.—B, Id, S, SM; Db. The mode of life of *Cercomya* was probably similar to *Laternula* species, the only living genus of this family. *Laternula* is a deep burrower that has long siphons and anterior and posterior gapes. In juvenile stages, it burrows and buries, but as an adult, it cannot rebury because the foot is atrophied (Beesley, Ross, & Wells, 1998). A pallial line is not observed in *Cercomya*, so we cannot estimate the size of its siphons, but a posterior siphonal gape is present.

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1973). There are no data about the shell microstructure of *Cercomya*. J. D. Taylor, Kennedy, and Hall (1973) studied the shells of various current species of the superfamily Pandoroidea, and, in all except in those belonging to the family Thraciidae, there are three shell layers: a prismatic outer layer and nacreous middle and inner layers.

Genus TULONGELLA Chen & J. Chen in Wen & others, 1976, p. 68

Type species.—*Tulongella xizangensis* Chen & J. Chen in Wen & others, 1976, p. 69.

Remarks.—*Enosolen* Guo, 1988, is considered to be a junior synonym of *Tulongella* (Z. Fang & others, 2009).

Stratigraphic range.—Middle Triassic (Anisian)–Upper Triassic (Rhaetian) (Lu & Chen, 1986; Chen & Chen in Wen & others, 1976). Chen and J. Chen (in Wen & others, 1976) erected *Tulongella* and included in it the type species from the Norian of China, *Cuspi-*

daria sp. indet. in Healey (1908) from the Rhaetian of Burma, and *Cuspidaria? problematica* Chen from Upper Triassic of China. Later, Lu and Chen (1986) proposed a new species, *Tulongella qinghaiensis*, from the Anisian of Qinghai (Naocangjiangou Formation). *Enosolen ensatus* Guo, 1988 (type species of *Enosolen*) was also reported from the Anisian (Guo, 1988; Z. Fang & others, 2009).

Paleogeographic distribution.—Eastern Tethys (Fig. 61).

Tethys domain: Middle Triassic: Anisian of Qinghai (China) (Lu & Chen, 1986), western Yunnan (China) (Guo, 1988; Z. Fang & others, 2009); Late Triassic: Norian of China (Xizang, Tibet) (Wen & others, 1976); Rhaetian of Burma (Healey, 1908).

Paleoautoecology.—B, Id, S, SM; Db. See previous discussion of mode of life for *Cercomya*.

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1973). There are no data about the shell microstructure of *Tulongella*. J. D. Taylor, Kennedy, and Hall (1973) studied the shells of various current species of the superfamily Pandoroidea, and, in all except in those belonging to the family Thraciidae, there are three shell layers: a prismatic outer layer and nacreous middle and inner layers.

Genus ORTHOMYA Guo, 1985, p. 234, 273

Type species.—*Orthomya puerensis* Guo, 1985, p. 234.

Stratigraphic range.—Upper Triassic (Carnian) (Guo, 1985). Guo (1985) proposed *Orthomya* and reported it from Carnian of China. No more records of *Orthomya* were located.

Paleogeographic distribution.—Eastern Tethys (Fig. 61).

Tethys domain: Late Triassic: Carnian of southwestern China (Yunnan province) (Guo, 1985).

Paleoautoecology.—B, Id, S, SM; Db. See mode of life for *Cercomya*.

Mineralogy.—Aragonitic (J. D. Taylor, Kennedy, & Hall, 1973). There are no data about the shell microstructure of *Orthomya*. J. D. Taylor, Kennedy, and Hall (1973) studied the shells of various current species of the superfamily Pandoroidea, and, in all except in those belonging to the family Thraciidae, there are three shell layers: a prismatic outer layer and nacreous middle and inner layers.

GENERA NOT INCLUDED

ACHARAX Dall, 1908a, p. 2

No data are available for the study interval, although Recent *Acharax* is regarded as being of Paleozoic origin. Cox and others (1969) listed the stratigraphic range of this genus as Miocene to Recent, but they pointed out that probably some fossil species that are similar to *Solemya* Lamarck, 1818, with external ligament and without internal ribs, known since the Devonian, could be included in *Acharax*. Pojeta (1988) emended its diagnosis and assigned it a continuous range from lower Permian (Leonardian) to Recent and even accepted a doubtful extension of the range into the Middle Devonian (Eifelian), and Carboniferous (Middle Pennsylvanian). Carter (1990a) emended the diagnosis again and proposed a new subgenus, *Acharax (Nacrosolemya)*, from Carboniferous (Pennsylvanian) beds of Kentucky, and he argued for the need of a good revision of this genus, since there are Devonian and Carboniferous poorly known species attributed to *Solemya*, which probably would fit better in *Acharax*. It is interesting to point out that although there are many species attributed to *Acharax* from Paleozoic deposits, they seem to be far less common in Triassic or Jurassic beds,

because no records were found in deposits of those ages. Although their activity traces are known from Mesozoic beds (Seilacher, 1990), there is no direct relation with actual specimens. It is even possible that none of them were present during our study interval, and that the apparently discontinuous stratigraphic range is in fact due to morphologic convergence.

AGUILERIA White, 1887, p. 34

Aguileria was relatively frequent during the Late Jurassic (Fürsich & Werner, 1988; Liu, 1995) and more abundant during Cretaceous times (Muster, 1995). However, Muster (1995) assigned it an Upper Triassic–Upper Cretaceous range. The Carnian record originated from the reference of *Bakevella* (*Bakevelloides*) *hekiensis* (Kobayashi & Ichikawa, 1952) figured by Hayami (1975, pl. 2,4) as *Aguileria renauxiana* (Mathéron, 1842 in 1842–1843) by Muster (1995), but she did not study Hayami's specimens (deposited in the University of Tokyo Museum). We follow Hayami (1975), since we do not agree that a doubtful single specimen is enough to expand the genus range by more than 50 m.y.

AMERINUMOPECTEN Kasum-Zadeh, 2003, p. 44

This monospecific genus was described by Kasum-Zadeh (2003) from the Upper Triassic of Italy, with the type species *Entolium? amerinum* Sirna, 1968, p. 771. We regard this nomination as unjustified, since the author did not adequately compare it or justify it. Although the ornamentation of this species is unique when compared with other species of *Entolium*, other features (absence of byssal sinus, shape of the auricles, cardinal margin) are perfectly consistent with its attribution to *Entolium*, and the difference in ornamentation may be due to ecological factors (Allasinaz, 1972).

ANGUSTELLA Waagen, 1907, p. 98

Angustella was considered as a junior synonym of *Gervillia* (*Cultrioipsis*) Cossmann, 1904 (Cox & others, 1969, p. 308), but some authors considered it to be a distinct genus, without justification (Sha, Chen, & Qi, 1990; X. Wang & others, 2008), or as a subgenus of *Gervillia* (Wen & others, 1976). The name *Angustella* was later used for a gastropod and a hemipteran (see *Nomenclator Zoologicus* online: <http://uio.mbl.edu/NomenclatorZoologicus/>).

ANOMIA Linnaeus, 1758, p. 700

No occurrence from Induan–Sinemurian interval. Cox and others (1969) regarded it as Cretaceous–Holocene and also indicated its doubtful occurrence from the Permian. The origin of the family Anomiidae is now regarded as Jurassic (Todd & Palmer, 2002; Malchus, 2004). Hölder (1990) mentioned *Anomia alpina* Winkler from the Rhaetian. This species was relocated first into *Placunopsis* (Ivimey-Cook & others, 1999) and then into *Pseudoplacunopsis* (Checa & others, 2003) (see discussion for *Pseudoplacunopsis* in Included Genera, p. 70).

ANRADULONECTITES Shurygin & Lutikov, 1991, p. 64

No occurrence from Induan–Sinemurian interval. According to the *Zoological Record*: “*Anradulonectites* (Pectinacea): Gen nov, of Pectinidae, Type species *A. intricatus*, p. 64, Lower Jurassic (Shurygin, B. N. & Lutikov, O.A. 1991. Rossiiskaya Akademiya Nauk Sibirskoe

Otdelenie Trudy Instituta Geologii I Geofiziki, 769: 47–78).” Its oldest record is from Pliensbachian times (Zakharov & others, 2006).

ANSHUNOPECTEN (no author)

Anshunopecten was mentioned by Xu (in Z. Yao & others, 1980, table 8, p. 34), without description, figures, or other information accompanying the name. The genus was quoted from the upper Permian of China (H. Yin, 1985; M. Lin & Yin, 1991; L. Li, 1995) and taken into account in Sepkoski (2002) and PBDB (online), but *Anshunopecten* was not formally described, and it is thus invalid (*nomen nudum*) (Z. Fang, personal communication, 2008).

APHANAIA de Koninck, 1877, p. 164

Following Kauffman and Runnegar (1975), *Aphanaia* is regarded as a subgenus of *Atomodesma*. Other authors such as Waterhouse (1979a, 1983, 1987), Astafieva (1991), and Biakov (1992) considered it to be at genus level but none of them justified it. Waterhouse (1958, 1959) included it as a subgenus of *Atomodesma* (the same position was given in Cox & others [1969]), but, later, Waterhouse (1979a) considered it to be at generic level without discussion, even though he mentioned Kauffman and Runnegar (1975).

ARCOMYTIUS Agassiz in J. Sowerby, 1842 in 1842–1844, p. 318

No occurrence from Induan–Sinemurian interval, although it was quoted quite frequently from the Lower Jurassic (Winkler, 1886; Hayami, 1958a, 1975; Cox & others, 1969; Liu, 1999; Fürsich & others, 2001; Gahr, 2002), the oldest record appears to be Pliensbachian.

ARCTOTIS Bodylevsky, 1960, p. 44

No occurrences from the Induan–Sinemurian interval, although Cox and others (1969) assigned it a range from the Lower Jurassic, but all consulted references consider it to be from the Pliensbachian (Kelly, 1984; Jeletzky & Poulton, 1987; Liu, 1995; Sha, 1996; Aberhan, 1998a, 1998b, 2001; Damborenea, 2001; Zakharov & others, 2006). Sepkoski (2002) mentioned its oldest record as Sinemurian, data provided by Hallam (1977), who listed *Arctotis* from Sinemurian of the Arctic region, but we could not confirm it.

ASTARTELLA Hall, 1858, p. 715

Astartella was considered to be a typical Paleozoic genus (e.g., Boyd & Newell, 1968; Cox & others, 1969; Sepkoski, 2002) with a Viséan (Carboniferous) origin (Hoare, Heaney, & Mapes, 1989), and its last records were Permian (Ciriacks, 1963; Nakazawa & Newell, 1968; Hayami & Kase, 1977; Biakov, 2002; Clapham & Bottjer, 2007). Recently, Hautmann and others (2011) reported *Astartella* from the Lower Triassic (Induan) of southern China. The specimens reported by the authors were four valves without internal shell characters; they were attributed to *Astartella* by the external shape and ornamentation pattern. They resemble astartids but are not clearly referable in particular to *Astartella*. More available material is necessary to maintain the survivorship of *Astartella* in the Lower Triassic.

ASTARTOPIS Wöhrmann, 1889, p. 222

Chavan in Cox and others (1969) considered *Astartopis* to be a distinct genus, indicating that Cox regarded it as a subjective synonym

of *Myophoriopsis* Wöhrmann, 1889, and he referred it to the family Myophoriopidae. In the *Treatise*, there is no family with this name, and under *Myophoriopsis*, Cox does not refer to *Astartopsis*. However, *Astartopsis* (type: *Myophoria richthofeni* Stur, 1868) was considered to be a synonym of *Myophoriopsis* by many authors (e.g., Bittner, 1895; Diener, 1923; Kutassy, 1931; Leonardi, 1943; Allasinaz, 1966), and this is the position followed here, since no substantial differences were noted between the genera.

BARBATIA Gray, 1842, p. 81

No occurrences from the Induan–Sinemurian interval are considered, as records from the Triassic are doubtful. Cox and others (1969) assigned it a Jurassic–Holocene range and mentioned its occurrence from the Triassic with doubts. Sepkoski (2002) assigned it a Triassic (Norian)–Holocene range, referring to Hallam (1981), but, in this paper, the genus was not considered, although in other papers by the same author (Hallam, 1972, 1976, 1977), the oldest recognized record of the genus is Pliensbachian. It was widely distributed during the Middle and Late Jurassic (Kelly, 1984; Fürsich, Palmer, & Goodyear, 1994; Liu, 1995; Delvene, 2000, 2003).

BOSNIOPECTEN Kasum-Zadeh, 2003, p. 55

This genus was proposed by Kasum-Zadeh (2003) from the Carnian of Bosnia, with *Pecten volaris* Bittner, 1903, p. 634, as type species, and he included two other species: *Pecten inaequicostatus* Reis, 1926, and *Pecten subaequicostatus* Bittner, 1895. The author neither compared species nor justified the proposal, and the three species were assigned to *Chlamys* (*Chlamys*) by Allasinaz (1972), which is followed here. In addition, Kasum-Zadeh (2003) considered his new genus as being present only in the Carnian of Bosnia, but these species were also recorded from Ladinian and Rhaetian beds of Austria and Italy (Allasinaz, 1972).

BRACHIDONTES Swainson, 1840, p. 384

No occurrences from Induan–Sinemurian interval are considered, although Cox and others (1969) and Sepkoski (2002) assigned it a Jurassic–Holocene and Lower Jurassic (?)–Holocene range, respectively. However, the oldest record of *Brachidontes* is from the Pliensbachian of the Iberian Peninsula (Hallam, 1972).

BUPECTEN Guo, 1988, p. 118

Junior synonym of *Entolium* Meek, 1865 (Z. Fang & others, 2009). Guo (1988, p. 118) mentioned it has two oxborn-shaped auricles in the diagnosis of the genus, and differed from *Entolium* by “two acuminate and high, shooting [projecting] auricles” [translation of the diagnosis offered by Z. Fang & others, 2009, p. 48]. In the opinion of these last authors: “The so-called oxbornlike auricles seem to be artificially processed and polished up,” they also noted that, although in Guo’s (1988) material there are no right valves of the type species, he included a description of them in his text. We follow Z. Fang and others (2009).

BUREIOMYA Voronetz, 1938, p. 58

Bureiomya was considered as a junior synonym of *Pholadomya* (*Bucardiomya*) Rollier in Cossmann, 1912 (Cox & others, 1969, p. 829). According to Kobayashi and Tamura (1983b, p. 209), the

genus was proposed from the Triassic of northeastern Siberia. We accept the synonymy, and, therefore, we disregard other records of this genus (e.g., Bychkov & others, 1976; Kurushin, 1990; Polubotko & Repin, 1990).

CALVAENTOLIUM Romanov, 1985, p. 35

Romanov (1985) gave generic names to the four groups established by Staesche (1926) within *Entolium s. l.* (see discussion in Damboarena, 2002a, p. 42–44). Staesche’s *Entolium behlii* d’Orbigny group was included by Romanov (1985) in the new genus *Calvaentolium* (type species: *Pecten magneauritus* Kittl, 1904, from the Anisian of Yugoslavia), plus several Triassic species [*C. pseudodiscites* (Guembel), *C. tribevicianum*, *C. magneauritum* (Kittl), *C. tridentini* (Bittner), *C. inornatum* (Stoppani), *C. saccoi* (Parona), *C. cainalloi* (Stoppani), *C. contemptibile* (Stoppani)] and Jurassic species [*C. calvum* (Goldfuss, 1935 in 1833–1841), *C. behlii* (d’Orbigny)]. He assigned it a Triassic–Jurassic range in Europe and Asia. In the absence of a good review on the *Entolium* group, we follow a conservative view and consider this group to be within *Entolium*, following Staesche (1926).

Waller (2006) regarded it as a valid genus and included it in his new family Entoliolidae Waller, 2006, along with other genera, and he even considered *Crenamussium* Newton in Newton & others, 1987, to be a junior synonym of *Calvaentolium* (see discussion for the family Entoliidae in Included Genera, p. 103).

CARDIOMORPHA de Koninck, 1841 in 1841–1844, p. 101

There are no occurrences from the Induan–Sinemurian interval. Cox and others (1969, p. 818) assigned it a Carboniferous range, but they also indicated (p. 115) that some species were reported from the Triassic. Several Triassic species were attributed to *Cardiomorpha* and described prior to 1969 (Trechmann, 1918; Diener, 1923, p. 229; Krumbeck, 1924; J. P. Smith, 1927; Kutassy, 1931, p. 415; Marwick, 1953) and also after that date (Wen & others, 1976; Sha, Chen, & Qi, 1990). Most of these species were doubtfully referred to *Cardiomorpha*. Sepkoski (2002) assigned it a Carboniferous–Upper Triassic (Carnian) range, based on Morris (1967). In line with Pojeta and others (1971), we should be careful with studies at lower taxonomic levels of poorly known taxa, such as *Cardiomorpha*, because the evolutionary history of major lineages can give us a better overview of a particular group. They especially referred to *Cardiomorpha* records from the Ordovician–Devonian and the Triassic. Furthermore, its patchy distribution is very suspicious. We do not include the Triassic records, and we consider *Cardiomorpha* to be a Carboniferous (see discussion in Pojeta & others, 1971, p. 146; Simões & others, 1997; Waller & Stanley, 2005) and lower Permian (Runnegar, 1965; Runnegar & Newell, 1974) genus.

CARDITA Bruguière, 1792 in 1789–1792, p. 401

No occurrences from Induan–Sinemurian interval are considered; according to Chavan in Cox and others (1969), *Cardita* has a Paleocene–Holocene range. Although it was frequently quoted from the Triassic in papers prior to Cox and others (1969), after the *Treatise*, it was mentioned from the Triassic by Kollarova & Kochánova (1973) and from the Jurassic by Accorsi-Benini (1981). Cox and others (1969) did not comment on all the species attributed to *Cardita* in classical papers (e.g. Stoppani, 1860–1865; Winkler, 1861;

Goldfuss, 1863; Laube, 1865, among others). It is beyond the scope of this paper to review each of these species to determine in what other genera should they be included. This situation is repeated for many Recent genera, such as *Mytilus*, *Nucula*, and *Corbula*, which had traditionally been used as a mixed bag where all similar forms were included.

CERATOMYA Sandberger, 1864, p. 16

Cox and others (1969) assigned it a Lower–Upper Jurassic range. *Ceratomya* was reported from the Sinemurian of Europe (Etheridge, 1864; Hallam, 1976, 1977, 1987; Liu, 1995). The probable Sinemurian species are: *C. petricosa* (Simpson, 1855) (Hallam, 1976) and *C. gibosa* (Etheridge, 1864) (Damborenea in Damborenea & González-León, 1997), but, although Etheridge (1864) figured the specimens, he did not specify the age of the sediments. On the other hand, there are several papers where the genus is discussed systematically and figured from Pliensbachian beds (e.g., Damborenea in Damborenea & González-León, 1997; Delvene, 2003; Aberhan, 2004; Scholz, Aberhan, & González-León, 2008).

CHAENOCARDIA Meek & Worthen, 1869, p. 170

No occurrences in the study interval are considered; although it was mentioned from the upper Permian of southern China (L. Li, 1995), this will not be taken into account, because it is not a systematic treatment and does not mention the original data source. *Chaenocardia* is regarded as a typical Carboniferous genus (Cox & others, 1969; Newell & Boyd, 1995).

CHIRON Astafieva, 1997, p. 27

Chiron was replaced by *Chironopecten* Astafieva, 2001. Astafieva (1997) proposed *Chiron*, but this name had already been used for an insect, *Chiron* MacLeay, 1819, p. 107 (Astafieva, 2001).

CHULUARIA Waterhouse, 2000, p. 175

Chuluarina is not considered here, because the reasons to separate this genus from *Claraia* are insufficiently justified. Waterhouse (2000) proposed this new genus to accommodate specimens similar to *Claraia* but with differences in form and size of the right anterior auricles, being inequivalve, and the form of byssal notch. These differences are considered by most authors as species-level features (e.g., F. Yang, Peng, & Gao, 2001; He, Feng, & others, 2007).

CINGENTOLIUM Yamani, 1983, p. 6

Cingentolium Yamani, 1983 is a junior objective synonym of *Costentolium* Freneix, 1980, as they are based on the same type species, *Pecten cingulatum* Goldfuss, 1835 in 1833–1841 (see discussion for *Costentolium* and *Neoentolium* Romanov, 1985, below).

CLARAIOIDES Fang, 1993, p. 653, 660

Claraioides is regarded as a junior synonym of *Claraia* Bittner, 1901a (Newell & Boyd, 1995; F. Yang, Peng, & Gao, 2001; He, Feng, & others, 2007). Z. Fang (1993) proposed *Claraioides* to accommodate the upper Permian specimens that were assigned to *Claraia primitiva* Yin, 1983, and *Claraia diana* Guo, 1985, and he also proposed a new species, *Claraioides guizhouensis*. The proposal of this new genus was based on: “. . . the existence of a subcircular

byssal embayment in the right valve (lower valve), by which it may be readily distinguished from the comparable *Claraia* and *Pseudo-claraia*” (Z. Fang, 1993, p. 660). Newell and Boyd (1995) and F. Yang, Peng, and Gao (2001) considered it to be a junior synonym of *Claraia*, based on the lack of a quantitative, comparative study of local populations before proposing the new genus (Newell & Boyd, 1995) and the use of species-level features to discriminate at genus level, in this case the size, shape, and direction of the byssal sinus and the size and shape of the auricles (see discussion in F. Yang, Peng, & Gao, 2001, p. 800–801). Z. Fang (2003) disagreed with F. Yang, Peng, and Gao (2001) and again reaffirmed the validity of *Claraioides*; however, he did not provide further arguments. Kotlyar, Zakharov, and Polubotko (2004), according to Z. Fang (1993), decided to keep *Claraioides* separate from *Claraia*, and they referred the upper Permian specimens similar to *Claraia* to *Claraioides* (see discussion in Kotlyar, Zakharov, & Polubotko, 2004, p. 524). Delving into the discussion about the supposed synonymy, He, Feng, and others (2007) analyzed the variation in the ornamentation and shape of the byssal sinus in all species included in *Claraia* with their stratigraphic and paleogeographic distribution (He, Feng, & others, 2007, table 1, p. 1016 and discussion), showing that there is a progressive morphological change in *Claraia* from Changhsingian to Induan, indicating that the shape, size, and orientation within the byssal sinus are not suitable criteria for discrimination at generic level. Z. Fang and others (2009, p. 32) did not agree and provided a list of species included in *Claraioides*.

COMATAHALOBIA Polubotko in Polubotko, Payevskaya, & Repin, 2001, p. 100

Polubotko, Payevskaya, and Repin (2001), pursuing their revolutionary concept of the “*Halobia*” group (see discussion for the family Halobiidae in Included Genera, p. 91), used once again criteria such as shape and position of the anterior auricle and the ornamentation type to propose a new genus similar to, but separate from, *Halobia*. We follow McRoberts’s (1993) criteria and do not take into account this genus.

COSTENTOLIUM Freneix, 1980, p. 89

Entolium (*Costentolium*) Freneix, 1980, *Cingentolium* Yamani, 1983, and *Neoentolium* Romanov, 1985, were proposed for the same species group, which Staesche (1926) called the group of *E. cingulatum* (Goldfuss, 1835 in 1833–1841) (see Damborenea, 2002a, p. 44). The type species of the three taxa is the same, *Pecten cingulatum* Goldfuss, so even if it is regarded as a separate genus, it should be called *Costentolium* Freneix, 1980, by priority. Freneix (1980) also included in *E.* (*Costentolium*) the following species: *E. discites* (Schlotheim), *E. frontalis* (Dumortier), *E. proeteum* (d’Orbigny), *E. renievieri* (Oppel), *E. spathulatum* (Roemer), *E. partitum* (Sowerby), (?) *E. lackeyi* Quilty, and (?) *E. territorianum* Skwarko. Waller (2006) indicated that *Neoentolium* is a junior synonym of *Cingentolium*, but he did not mention the existence of *Costentolium*. In this paper, we follow a conservative view and regard all these species as belonging to *Entolium* in its original sense (see discussion for the family Entoliidae in Included Genera, p. 103).

COSTIGERVILLIA Cox & Arkell, 1948 in 1948–1950, p. 9

No occurrences are recorded in the study interval, although Muster (1995) indicated the possible record of *Costigervillia* from the Upper Triassic. The oldest reliable occurrences of *Costigervillia* are from the Upper Jurassic, with two species, *C. crassicoستا* (Morris & Lycett, 1853 in 1851–1855, p. 23) and *C. quincarinata* (Fischer, 1969) (Fürsich & Werner, 1988). Guo (1985) proposed *C. guibaoensis* Guo, 1985, from the Upper Triassic of China, but we were unable to locate information about this species. Apart from this mention, *Costigervillia* was only reported from the Upper Jurassic.

CULTRIOPSIS Cossmann, 1904, p. 510

Following Cox and others (1969, p. 308), *Cultriopsis* is regarded as a subgenus of *Gervillia*, although some authors assigned it a genus rank without justification (e.g., Komatsu, Chen, & others, 2004; Komatsu, Akasaki, & others, 2004).

CUSPIDARIA Nardo, 1840, p. 50

No occurrences from Induan–Sinemurian interval are considered, although there are several mentions of the genus from the Triassic and Jurassic. Prior to Cox and others (1969), *Cuspidaria* was reported from the Triassic (Diener, 1923, p. 243; Kutassy, 1931, p. 425; Leonardi, 1943; Rossi Ronchetti, 1959; Allasinaz, 1964) and from the Jurassic (Hayami, 1958c, 1959). Cox and others (1969, p. 854) assigned it a Cretaceous–Holocene range, disregarding those mentions. Subsequently, not all authors followed these guidelines when assigning a stratigraphic range to *Cuspidaria*; Skelton and Benton (1993, p. 260) and Sepkoski (2002) considered *Cuspidaria triassica* (Stoppani, 1865 in 1860–1865), from the Ladinian of Austria, as the oldest occurrence of the family Cuspidariidae; the original source is Morris (1967). Also, Runnegar (1974) suggested a possible Triassic origin for *Cuspidaria*; other authors assigned to this genus both Triassic species (Hayami, 1975; Lu & Chen, 1986) and Jurassic species (Hallam, 1976, 1977; Palmer, 1979; Fozy, Kázmér & Sente, 1994; J. D. Hudson & others, 1995; Liu, 1995). These are not taken into account here, since most were based only on general morphology and the presence of a typical, elongated so-called rostrum, as in cuspidarids (also observed in other bivalve families) and, furthermore, in none of them could the microstructure, musculature, and/or hinge be proven to be actually attributable to this family (Harper, Palmer, & Hudson, 2002). In addition, Allasinaz (1966, p. 641) indicated that, from the Triassic species referred to *Cuspidaria*, the only one that bears some resemblance to the living *Cuspidaria* is *C. alpiscivicae* Bittner, 1895. Allasinaz (1966) transferred all Triassic species attributed to *Cuspidaria* to *Solenomorpha*, but he did not sufficiently justify this decision (see discussion for *Solenomorpha* in this section, p. 170). Guo (1985) proposed the subgenus *Cuspidaria* (*Dianocuspidaria*) from the Carnian (lower Upper Triassic), based on only two specimens (Z. Fang & others, 2009). For all these reasons, we agree with Harper, Palmer, and Hudson (2002, p. 766–767) that the fossil record of the family Cuspidariidae was wrongly extended back by the inclusion of doubtful species.

**CYCLOPELLATIA Cossmann
in Cossmann & Pellat, 1907, p. 32**

Cyclopellatia is not considered in the study interval because the stratigraphic range assigned by Cox and others (1969) [L. Jurassic (Barr.)] is a mistake, the Barremian being a Lower Cretaceous stage.

DESIDERINECTES Kasum-Zadeh, 2003, p. 50

This genus was proposed by Kasum-Zadeh (2003) from the Upper Triassic of Europe with *Pecten* (*Chlamys*?) *desideri* Bittner, 1901b as type species, and including other species that the author did not name. Furthermore, he did not compare or justify the genus proposal. The type species was assigned to *Camptonectes* (*Annulinectes*) by Allasinaz (1972), and this is followed here.

DIETRICHIA Reck, 1921, p. 434

No occurrences from Induan–Sinemurian interval are considered, although both Cox and others (1969) and Sepkoski (2002) assigned it to have a Jurassic range. *Dietrichia* was only reported from the Oxfordian of Europe and Callovian–Oxfordian of Tunisia (Holzapfel, 1998), so its stratigraphic range is Middle–Upper Jurassic. The same name was used for a Linyphiidae spider genus by Crosby and Bishop (1933) but was recently replaced by *Neodietrichia* (Özdikmen, 2008).

**DIMYODON Munier-Chalmas
in Fischer, 1886 in 1880–1887, p. 937**

Dimyodon is considered a junior synonym of *Atrreta* Etallon, 1862 (Fürsich & Werner, 1988, p. 143; Malchus, 2000; Hautmann, 2001a, 2001b). According to Fürsich and Werner (1988), *Dimyodon* and *Atrreta* were only distinguished because *Dimyodon* had two muscle scars and internal radial ribs, which are lacking in *Atrreta*. However, in their study of the fauna from the Upper Jurassic of Portugal, they reported some specimens attributed to *Atrreta* that have these features and concluded that those differences are due to taphonomic processes: specimens with aragonitic inner shell layer replaced by calcite retained these internal structures (muscle and internal radial ribs) and were assigned to *Dimyodon*, while other specimens in which the inner shell layer was dissolved, removing such structures, were assigned to *Atrreta*.

DIOTIS Simonelli, 1884, p. 125

It is a junior homonym of *Diotis* Schmarada, 1859 (flatworm Turbellaria). *Diotis* Simonelli, 1884, was replaced by *Caenodiotis* Monari, 1994 (Monari, 1994).

ENANTIOSTREON Bittner, 1901c, p. 70

Checa and others (2003) and Márquez-Aliaga and others (2005) studied the syntypes of *Enantiostreon* and considered it to be an invalid genus. *Enantiostreon* was proposed by Bittner (1901c) to include Triassic ostreid bivalves (see Giebel, 1856) that were attached by their right valves, as observed by Noetling (1880). The type species is *Enantiostreon hungaricum* Bittner, 1912, from the Carnian of Hungary, with unknown hinge, the lower valve is clearly more convex than the upper valve, and specimens attached themselves by their right valves. Cox and others (1969) based their reference on a specimen of *Terquemia difformis* Goldfuss. According to the authors, *E. hungaricum* should be considered as a possible plicatulid

of uncertain generic relations. Some species traditionally included in *Enantiostreon*, such as *E. cristadiformis* Schlotheim, 1823 in 1822–1823, and *E. spondyloides* Schlotheim, 1823 in 1822–1823, clearly belong to Ostreidae, since they attached by the left valve and had a hinge without diagnostic structures (Checa & Jiménez-Jiménez, 2003b); they are included in *Umbrostrea* Hautmann, 2001a (Márquez-Aliaga & others, 2005).

ENOSOLEN Guo, 1988, p. 128

Junior synonym of *Tulongella* Chen & J. Chen in Wen & others, 1976 (Z. Fang & others, 2009, p. 143).

EOMONOTIS Grant-Mackie, 1978a, p. 102

Eomonotis is considered to be a subgenus of *Monotis* (Grant-Mackie, 1978a, 1980a; Grant-Mackie & Silberling, 1990; Silberling, Grant-Mackie, & Nichols, 1997), although some authors, without justification, regarded it as an independent genus (e.g., Kurushin, 1990; Klets, 2006; Wignall & others, 2007).

EOSCHIZODUS Cox, 1951, p. 369

No occurrences from the Induan–Sinemurian interval are considered. Cox (1951) proposed *Eoschizodus* to accommodate Paleozoic myophoriids (Devonian, Carboniferous, and Permian), and the same range was assigned in Cox and others (1969, p. 473): Devonian–Permian. Sepkoski (2002) assigned it a Devonian (Givetian)–Triassic (?lower Anisian) range, based on another database: Skelton and Benton (1993). The only information that Skelton and Benton (1993, p. 254) offered about this genus is “*Eoschizodus truncatus* (Goldfuss, 1837 in 1833–1841), *Strigocephalus* zone, Rhineland, Germany (Newell & Boyd, 1975)” and “Permian specimens are reported (Cox & others, 1969, p. 473).” The *Strigocephalus* zone corresponds to upper Middle Devonian (Newell & Boyd, 1975). According to these authors, *Eoschizodus* was rare and limited to its type species and only recorded from the *Strigocephalus* zone in Germany, so no Permian and Triassic records are here considered.

EPICLARAIA Gavrilova, 1995, p. 132

Epiclاراia is not considered here, because the reasons to separate this genus from *Claraia* are insufficiently justified. Gavrilova (1995) proposed this new genus to accommodate specimens similar to *Claraia* but with a differently shaped right auricle and byssal sinus. These characters were used at the species level within *Claraia* and are not enough to distinguish generic taxa in the group (F. Yang, Peng, & Gao, 2001; He, Feng, & others, 2007) (see discussion for *Claraioides* in this section, p. 159).

FENGJIACHONIA Wu, 1981, p. 377

Junior synonym of *Kija* Lebedev, 1959 (Ma, 1989, p. 611). S. Wu (1981) proposed *Fengjiachonia* from the Jurassic of China, and it was subsequently placed in synonymy by Ma (1989), because he considered both genera as identical in form, external ornamentation, and internal characters.

FILAMUSSIUM Waller, 2006, p. 342

Filamussium is not considered here, because we regard its proposal as unnecessary. The type species, *Pecten schaffh utli* Winkler,

1859, is best accommodated within *Parvamussium* Sacco, 1897, following its original concept (see discussion for *Parvamussium* in Included Genera, p. 95). Waller (2006) separated *Filamussium* from other propeamussiids by “having a filus structure on its left valve and in having internal ribs that were probably originally aragonitic rather than calcitic.” However, although the author compared his new genus with *Propeamussium*, he did not do a direct comparison with any *Parvamussium* species. Moreover, the presence or absence of the filus structure may be due to diagenetic processes, and it is observed in other bivalve groups as well (see Hautmann, 2001b, p. 62). Within the Propeamussiidae, genera are recognized by other characters, such as the presence or absence of internal ribs on the right valves or the presence or absence of lateral aperture and byssal notch in the adult stage.

FIMBRIA Megerle von M hlfeld, 1811, p. 52

Although Hallam (1977, 1990) mentioned *Fimbria* from the Hettangian, we did not find any record until the Pliensbachian. Monari (2003) considered that *Fimbria* had its origin during lower Pliensbachian times in the western Tethys, showing a diversity maximum during the Late Jurassic.

GEMMELLARODUS Di Stefano, 1912, p. 81

Junior synonym of *Neomegalodon* G mbel, 1862 (H. Yao & others, 2007). Allasinaz (1965) included *Gemmellarodus* and *Rossiodus* Allasinaz, 1965, as subgenera of *Neomegalodon*, and, although in Cox and others (1969), *Neomegalodon* was considered as a subgenus of *Megalodon*, both *Rossiodus* and *Gemmellarodus* continued to be used in different ways, as subgenera of *Neomegalodon* (Tichy, 1975, 1980a; V gh-Neubrandt & others, 1976; Sha, Chen, & Qi, 1990) or as independent genera (Allasinaz & Zardini, 1977; V gh-Neubrandt, 1982; Yancey & Stanley, 1999; H. Yao & others, 2003). H. Yao and others (2007) argued that neither *Gemmellarodus* nor *Rossiodus* were sufficiently well known to be useful concepts. Also, they stressed that the hinges of *Neomegalodon*, *Rossiodus*, and *Gemmellarodus* are similar, and, frequently, small-sized megalodontids were attributed to *Rossiodus* and very inequivalve ones to *Gemmellarodus*, using characters that are not systematically significant (see discussion in H. Yao & others, 2007, p. 1337).

GIBBOCONCHA De Gregorio, 1930a, p. 30

No occurrences from the Induan–Sinemurian interval are considered, although Cox and others (1969) mentioned *Gibboconcha* from the Lower Jurassic of Sicily, indicating that the description of the genus was made by De Gregorio based on a small fragment possibly belonging to a juvenile specimen of *Cardinia* or *Astarte*, and its internal characters were unknown. No more information about *Gibboconcha* was found, and, taking into account the doubts raised, we did not include it.

GLYPTOLEDA Fletcher, 1945, p. 293, 298

Glyptoleda is considered a subgenus of *Veteranella* Patte, 1926. Puri in Cox and others (1969) regarded *Glyptoleda* as a subgenus of *Veteranella*, and distinguished *V. (Veteranella)* and *V. (Glyptoleda)* by their posterior part not being constricted and constricted, respectively; the first from the Upper Triassic and the second from the Permian.

Other authors considered *Glyptoleda* as a junior synonym of *Veteranella* (see Waterhouse, 1980a), but Waterhouse (1980a, 1983, 1987) disagreed and regarded them as valid and independent genera, based primarily on differences in ornamentation. Subsequently, some authors followed Waterhouse in this regard (e.g., J. Chen, Lui, & Lan, 1983; Biakov, 1998, 2006; Zakharov & others, 2006; Z. Fang & others 2009). However, Z. Fang and Cope (2004) warned that the type of ornamentation is of low taxonomic significance, and it may even be variable at the intraspecific level. Biakov (1998, p. 132) mentioned that the ornamentation of *Glyptoleda* is an adaptation to the environment, and therefore is not useful as a taxonomic character. Following Puri in Cox and others (1969) and Z. Fang & Cope (2004), *Glyptoleda* is included as a subgenus of *Veteranella* (see discussion for *Nucundata* in this section, p. 166).

GONILIA Stoliczka, 1871 in 1870–1871, p. 278

No occurrences from the Induan–Sinemurian interval are considered, although Cox and others (1969) assigned it a Jurassic–Holocene range. The Jurassic record was referred to *Gonilia* (*Ensio*) Cox, 1962. The genus *Ensio* was proposed by Cox (1962), including three species: *Ptychomya agassizii* (holotype) from the Inferior Oolite of England (with a Toarcian–Bajocian range [West, 2007]), *Astarte divaricata* (junior synonym of *Ptychomya agassizii*) from the Bajocian of Lincolnshire Limestone of Santon, and *Astarte eastonii* from the Upper Jurassic of Borneo. Therefore the oldest record of *Gonilia* dates from the Toarcian. Sepkoski (2002) assigned it a Pliocene–Holocene range (see table in Jablonski & others, 2003).

GRYPHELLINA Newell, 1940, p. 289

Newell (1999, p. 4) rejected it because its type species, *Capulus sellardsi* Beede, 1907, is a gastropod.

GUICHELLA Li & Ding, 1981, p. 329

According to J. Chen and Komatsu (2002), *Guichiella* is considered a subgenus of *Claraia* Bittner, 1901a.

HABONUCULA Singh & Kanjilal, 1977, p. 189

No occurrences from Induan–Sinemurian interval are considered. The Zoological Record assigned it a Jurassic range and those data were incorporated into Sepkoski's database (2002). The original source is Singh and Kanjilal (1977), who proposed the genus from the lower Callovian. Therefore *Habonucula* is not included here. In addition, Jaitly, Fürsich, and Heinze (1995) regarded *Habonucula* as a junior synonym of *Nuculoma* Cossmann in Cossmann & Thiéry, 1907.

HEMIMENION Guo, 1988, p. 117

Junior synonym of *Aviculomyalina* Assmann, 1916 (Z. Fang & others, 2009). Guo (1988) proposed *Hemimenion* (family Myalinidae) and included two new species: *H. cuneatum* (type species) and *H. triangulare* from the Anisian of southwestern China. Z. Fang and others (2009) included it as a synonym under *Aviculomyalina*, and we follow this decision.

HUNANONECTES Fang, 1978, p. 465

Junior synonym of *Radulonectites* Hayami, 1957c (Damborenea, 2002a). Z. Fang (1978) proposed *Hunanonectes* as a subgenus of

Camptonectes from the Jurassic of China and included three new species: *C. (H.) sanduensis*, *C. (H.) parachlamys*, and *C. (H.) yizhangensis*). He indicated that it might also be a subgenus of *Chlamys*, because it was intermediate between *Camptonectes* and *Chlamys*. He interpreted the so-called *Camptonectes* striations as being radial ribs, and thus included it in *Camptonectes*. Subsequently, Damborenea (2002a) considered it to be a junior synonym of *Radulonectites*, since the species described by Z. Fang (1978) “have small faintly ornamented shells but are otherwise similar in general shape and other morphological aspects to both North and South Pacific species of *Radulonectites*.” Stiller (2006), although taking into account Damborenea's (2002a) research, decided to keep the two genera separate, but he considered that the three species described by Z. Fang (1978) were intraspecific variations and retained only the type species (*H. sanduensis* Fang, 1978). This was also done by Z. Fang and others (2009), but no mention of Stiller's paper was made. Stiller compared the type species with other species of *Radulonectites* (*R. japonicus* Hayami, 1957c; *R. exsertus* J. Chen, 1982b) from the Lower Jurassic of China (see discussion and synonym list in Stiller, 2006, p. 23–31), and the only difference he found was that the radial ornamentation was more pronounced in the latter species. We follow Damborenea (2002a) and regard *Hunanonectes* and *Radulonectites* as synonyms.

IMPOSIDONIA Waterhouse, 2008, p. 66

Waterhouse (2000, p. 181) described a new species, *Posidonia elegantula*, and, later, Waterhouse (2008) proposed a new genus based on this species. According to Waller and Stanley (2005, p. 19), “species of ‘*Posidonia*’ described by Waterhouse (2000, p. 181) from the Lower Triassic of the Himalayas also appear to be clariids.”

INDIGIROHALOBIA Polubotko, 1984, p. 42

Polubotko (1984) distinguished *Indigirohalobia* by the shape and position of the anterior auricle, by the ornamentation, and the presence of a strong ligament (H. J. Campbell, 1994), features considered by McRoberts (1993) and most authors as being diagnostic at the specific level (see H. J. Campbell, 1994, for a review on the discussion of this topic). Although many authors considered *Indigirohalobia* to be a valid genus (Okuneva, 1985, 1987; Kurushin, 1990; Polubotko, Payevskaya, & Repin, 2001, among others), we regard it as a junior synonym of *Halobia*, following McRoberts (1993) (see discussion of family Halobiidae in Included Genera, p. 91).

INOCERAMUS J. Sowerby in Anonymous, 1814, p. 448

Inoceramus was reported from the Early Jurassic on many occasions (e.g., A. F. Leanza, 1942; Cox & others, 1969; Escobar, 1980). Most of these specimens were attributed to *Inoceramus sensu lato*, and they would be better accommodated in other genera like *Parainoceramus*. According to Harries and Crampton (1998), the true inoceramids did not appear until the Late Jurassic.

IRANOPECTEN Repin in Polubotko, Payevskaya, & Repin, 2001, p. 118

Repin (in Polubotko, Payevskaya, & Repin, 2001) erected *Iranopecten* based on the type species *Indopecten glaber* Douglas, 1929. We are not taking into account this new genus, because we follow

the original assignation (Douglas, 1929; and Hautmann, 2001b) and refer this species to *Indopecten* Douglas, 1929.

ISOCARDIOIDES Fan, 1963, p. 523 [540]

Probably a junior synonym of *Schafhaeutlia* Cossmann, 1897 (Gu & others, 1976; Z. Fang & others, 2009).

JURASSICARDIUM Cossmann, 1906, p. 294

There are some reports from the Sinemurian of South America (Damborenea, 1996a; Damborenea & Manceñido, 2005b), but no systematic treatment of specimens was made. *Jurassicardium* was reported from the Upper Jurassic (Schneider, 1995). He noted that the specimens of the type species are lost and he excluded the genus from his analysis.

KRUMBECKIA Diener, 1915, p. 131

Junior synonym of *Schafhaeutlia* Cossmann, 1897 (see Hautmann, 2001b, p. 124). Diener (1915, p. 131) distinguished *Krumbeckia* from *Schafhaeutlia* by “oblique-oval shape of the shell and because the tooth of the hinge was more isolated;” according to Hautmann (2001b), these criteria do not allow separation of the two genera.

LAEVITRIGONIA Lebküchner, 1932, p. 68

No occurrences from the Induan–Sinemurian interval are considered. Cox and others (1969) mentioned it had its origin in the Lower Jurassic. Venzo (1942) noted that the oldest species assigned to this genus is *Trigonia* (*Laevitrigonia*) *oviedensis* Lycett, 1881, from the Hettangian of Oviedo (Asturias, Spain). Later, Dubar and others (1971) considered this species as a *Trigonia* and from Kimmeridgian age in Asturias, so we have serious doubts about the affinities of this record, whether it can be attributed to *Laevitrigonia* and even if the sediments from Oviedo referred by Venzo (1942) can be assigned to a Hettangian age. Several authors (Hallam, 1976, 1977; Francis & Hallam, 2003) indicated its origin in the Upper Jurassic of Europe.

LATERNULA Röding in Bolten, 1798, p. 155

Cox and others (1969) assigned it an Upper Cretaceous–Holocene range. *Anatina* Lamarck, 1818 is considered to be a junior synonym of *Laternula*, and this is the source of the problem about Triassic species attributed to *Laternula*. *Anatina* was widely reported from the Triassic, and, with the establishment of the synonymy discussed, most of the species were referred to other genera, but some remained in an indeterminate state. Some of these species, especially those reported from the Upper Triassic (e.g., Allasinaz, 1962; Sirna, 1968; Linck, 1972; Márquez-Aliaga, Plasencia, & Ros, 2005; Damborenea & Manceñido, 2012), are *L. rhaetica* (Gümbel, 1861), *L. zannonii* (Stoppani, 1860–1865), *L. amicii* (Stoppani, 1863 in 1860–1865), or *L. suessi* (Oppel, 1857 in 1856–1858). Most of them were based on specimens preserved as internal molds in which key characters were not observed. According to Runnegar (1974), the first laternulid could be *Cercomya* Agassiz, 1843 in 1840–1845, regarded originally as a subgenus of *Anatina* (Diener, 1923). A review of these Triassic species is necessary to determine if the range of *Laternula* should be extended or if they can be accommodated better in other genera. Following Cox and others (1969), we do not consider occurrences of *Laternula* from the Induan–Sinemurian interval.

LECOMPTEUS Poel, 1959, p. 13

According to Cox and others (1969), the type species designated by Poel (1959) is *Mytilus ornatus* Münster, 1837, in Goldfuss, 1833–1841, and it had a Jurassic range, as well as Cretaceous according to Sepkoski (2002). We could not see the original paper in which the genus was proposed, but all subsequent records reported it from the Lower Cretaceous of Japan (Hayami, 1975, among others). According to Kauffman and H. A. Leanza (2004), Münster (1837, in Goldfuss, 1833–1841) proposed the type species based on specimens from the Upper Cretaceous (Campanian) of Europe. The available information suggests that the presence of *Lecompteus* in the Lowest Jurassic is improbable. Kauffman and H. A. Leanza (2004, p. 1190) proposed to include *Mytilus ornatus* in their new genus *Nodomytilus*, but they did not mention *Lecompteus*, unaware of the position of this species (H. A. Leanza, personal communication, 2007).

LEVICONCHA Waagen, 1907, p. 149

Although Cox and others (1969) considered *Leviconcha* to be a junior synonym of *Neoschizodus* Giebel, 1855, several authors considered it to be a valid genus with different systematic relations: subgenus of *Neoschizodus* (Kobayashi & Tamura, 1968b), subgenus of *Myophoria* (Wen & others, 1976; C. Chen, 1982), or at genus level (Ling, 1988; Sha, Chen, & Qi, 1990). In this paper, we follow Kobayashi and Tamura (1968b), in the absence of a modern revision, because it adequately justifies the position of *Leviconcha*.

LUPHERELLA Imlay, 1967, p. 8

Lupherella was erected as genus by Imlay (1967). Following Damborenea (1987b), *Lupherella* is considered to be a subgenus of *Otapiria* Marwick, 1935. Damborenea found that adults of *Lupherella boechiformis* (Hyatt, 1894) (type species of *Lupherella*) were extremely similar to juveniles of *Otapiria originalis* Kiparisova, 1960, and *Otapiria neuquensis* Damborenea, 1987b (see discussion in Damborenea, 1987b, p. 156). J. Chen (1988) also noticed that the separation between *Otapiria* and *Lupherella* at generic level was not well founded. However, other authors (e.g. Aberhan, 1998a; J. Yin, Yao & Sha, 2004) considered *Lupherella* to be a separate genus.

LYRIOMYOPHORIA Kobayashi, 1954, p. 66

Junior synonym of *Elegantinia* Waagen, 1907 (Kobayashi & Tamura, 1968b; Boyd & Newell, 1999). Cox and others (1969) considered *Lyriomyophoria* to be a valid genus and *Elegantinia* to be a junior synonym of *Gruenewaldia* Wöhrmann, 1889. However, shortly before the publication of Cox and others (1969), Kobayashi and Tamura (1968a, p. 91) decided, following McLearn (1942), to keep both genera as valid, and, subsequently, they considered *Lyriomyophoria* to be a junior objective synonym of *Elegantinia*, because they share the same type species, *Lyriodon elegans* Dunker, 1851, p. 300; this was followed years later by Boyd and Newell (1999, p. 547).

MACTROMYOPSIS Chavan, 1959, p. 506

No occurrences from the Induan–Sinemurian interval are considered. Chavan (1959) proposed *Mactromyopsis* and assigned it a Bajocian–Callovian range. Cox and others (1969, p. 511) assigned it a Jurassic (Charmouthian–Callovian) range in Europe [Charmouthian is an old name that corresponds

to Pliensbachian (Morris, 1967; Vera, 1994)]. Interestingly, Sepkoski (2002) assigned it a Jurassic (Hettangian–Callovian) range, based on data provided by Skelton and Benton (1993). However, these last authors assigned a Hettangian–Holocene range to the family Mactromyidae, pointing out that the oldest record for the family was *Mactromyopsis* (*Mactromyella*) *inflata* (Thevenin, 1909), from the Charmouthian of France and England. Monari (2003) quoted the same species from the Bajocian of northwestern France. We consider the first record of *Mactromyopsis* to be Pliensbachian.

MAGNOLOBIA Kurushin & Truschelev, 2001, p. 244

Kurushin and Truschelev (2001) reviewed the taxonomy of the genus *Daonella* and proposed a new genus, *Magnolobia* (type species: *Halobia premium* Kiparisova & Popov, 1946, *vide* Kurushin & Truschelev, 2001), a genus close to *Daonella* that differs from it mainly because “ribs are recurved, the anterior elevation is well-developed in the presence of the triangular posterior filed from the valve, in the large number of umbonal crurae, and in the presence of the intercalating ribs in the inter-rib spaces and in the accessory ribbing.” Following McRoberts (1993), these differences are not considered to be sufficient to separate two genera (see discussion for the family Halobiidae in Included Genera, p. 91).

MALLETIA Des Moulins, 1832, p. 85

Although *Malletia* is a genus with an accepted range from the Cretaceous to the Holocene (Sepkoski, 2002), there are some Triassic and Jurassic records. Dagys and Kurushin (1985) reported *Malletia pseudopraecursor* Kurushin (in Dagys & Kurushin, 1985, pl. V, 5–8) and *Malletia* sp. (pl. V, 9 and pl. VI, 1) from the Anisian and Ladinian of northern Siberia, but in our opinion, these specimens, especially on the basis of their hinge teeth, belong to *Palaeoneilo elliptica* var. *praecursor* (Frech, 1904). This last species was compared with *M. pseudopraecursor* by Kurushin (in Dagys & Kurushin, 1985), and the only difference between them is that the latter is more elongated than the former. Frech (1904, p. 12, fig. 9) figured three specimens from different ages and localities, showing the species variability in shell elongation. The oldest mention from the Jurassic is ?*Malletia* sp. from the Pliensbachian of South America (Damborenea, 1987a). Zhakarov and others (2006) also mentioned *Malletia* from the Pliensbachian of the Boreal region, but they did not treat the genus systematically and did not indicate the original source of data. Therefore *Malletia* is not considered here because it is not recorded with certainty before the Pliensbachian.

MARTESIA G. B. Sowerby, 1824 in 1821–1825, pl. 23

No occurrences from the Induan–Sinemurian interval are considered. Cox and others (1969) assigned it a ?Carboniferous, Jurassic–Holocene range, and Sepkoski (2002) assigned a Cretaceous (Cenomanian)–Holocene range, based on data offered by Kelly (1988). However, Kelly (1988) considered *Martesia* as a valid genus from the Paleocene to the Recent, since the Mesozoic records were not confirmed and the Carboniferous ones were unfounded (see discussion in Kelly, 1988, p. 366–367).

MCLEARNIA Crickmay, 1930b, p. 45

Mclearnia is not included here, because all quotes from the Lower Jurassic are doubtful, and it is considered to be a subgenus of *Camptonectes* (Kelly, 1984; Kelly, Dhondt, & Zakharov, 1984; Fürsich & Thomsen, 2005). Cox and others (1969) mentioned it as a doubtful genus from the Lower Cretaceous and indicated the need for further investigation. The genus was not widely mentioned, as the type specimens are poorly preserved and it is difficult to compare them with others. Therefore, most species were included in *Boreionectes* Zakharov, 1965, now considered to be a junior synonym of *Mclearnia* (Kelly, Dhondt, & Zakharov, 1984). *Mclearnia* was reported from the Hettangian of northeastern Asia (Kurushin, 1990), but nevertheless, Zakharov and others (2006) reported that its oldest record is from the Aalenian of northern Siberia and the Arctic region. The mention of Kurushin (1990) is not taken into account and considered to be unjustified.

MEGALODON J. de C. Sowerby, 1827, p. 131

Although there are numerous records of *Megalodon* from the Triassic (e.g., Parona, 1888, 1889; Tommasi, 1890; Bittner, 1895; Wurm, 1913; Trechmann, 1918; Schmidt, 1935; Dechaseaux, 1940; Leonardi, 1943; Marwick, 1953; Kiparisova, 1954; Terranini, 1958; Virgili, 1958; R. Hudson & Jefferies, 1961; Allasinaz, 1962, 1964, 1965; Brinkmann, 1966; Encheva, 1972; Fürsich & Wendt, 1977; Hallam, 1981; Lu & Chen, 1986) and from the Jurassic (e.g., Fraser, Bottjer, & Fischer, 2004); following Végh-Neubrandt (1982), we consider *Megalodon s.s.* as a typically Paleozoic genus, specifically restricted to the Devonian. This genus is closely related to *Neomegalodon* and *Triadomegalodon* (Végh-Neubrandt, 1982). The first was originally proposed as subgenus of *Megalodon*, and this is the origin of many of the Triassic quotes. Cox and others (1969), Hallam (2002), and Sepkoski (2002) considered it to be extinguished in the Rhaetian.

MESOMILTHA Chavan, 1938, p. 231

In recent years, *Mesomiltha* was reported from the Upper Triassic (e.g., Ivimey-Cook & others, 1999; Guex & others, 2003, 2004; Lucas & Tanner, 2004), although we could not confirm these records nor those from the lower Jurassic. Ivimey-Cook and others (1999) included specimens from the Rhaetian of England with some doubts, since the diagnostic features were not observed. In the other three papers mentioned above, *Mesomiltha* is listed from the Rhaetian of Nevada, but no systematic treatment was offered. Reports from the Hettangian of Japan (Z. Huang, 1986) are also questionable, because the species were only doubtfully attributed to *Mesomiltha*.

MOLUKKANA Krumbeck, 1923a, p. 219

Cox and others (1969) treated *Molukkana* as doubtful and noticed that it was poorly known and possibly indistinguishable from *Pachymya* (*Pachymya*). It is a monospecific genus; the type species, *M. seranensis* Krumbeck, 1923a, was reported by Krumbeck (1923a) and Cox and others (1969) from the Norian of Indonesia. No reports after 1969 were found, and everything suggests that all the old records originated with Krumbeck (1923a).

MUSCULUS Röding in Bolten, 1798, p. 156

No occurrences from the Induan–Sinemurian interval are considered. Cox and others (1969) assigned it a Jurassic–Holocene range; Sepkoski (2002) specified its origin in the upper Sinemurian [data from Hallam (1977), who mentioned the species *Musculus subcancellata* (Buvignier) from the Sinemurian of Europe, North America, and South America]. We are not taking this quote into account, because it is impossible to corroborate it and we have doubts about its validity. No reports were located in any paper after or before Cox and others (1969). In reviews by Damborenea (1987a, 1987b, 2002a) and Aberhan (1994a) of South American Jurassic bivalves of the Andean Cordillera, *Musculus* was not mentioned, but they included *Modiolus*, a genus with similar external morphology, which can be confused if specimens are not well preserved.

MYTILOIDES Brongniart, 1822, p. 320

Cox and others (1969) regarded *Mytiloides* as a subgenus of *Inoceramus* and assigned it a Jurassic–Upper Cretaceous range. Sepkoski (2002), without indication of the source, considered its origin in the Sinemurian. No mention of *Mytiloides* from the Lower Jurassic was located. Kauffman and Powell (1977) emended the diagnosis of *Mytiloides* and considered it to be a separate genus from *Inoceramus*. Harries and others (1996) noticed that *Mytiloides* had a Cretaceous origin and that all Jurassic species assigned to *Mytiloides* belong to other genera.

MYTILUS Linnaeus, 1758, p. 704

Although Cox and others (1969) assigned it an Upper Jurassic–Holocene range, *Mytilus* was mentioned repeatedly from the Triassic. The species most frequently mentioned for this period is *Mytilus eduliformis* Schlotheim, 1820 (e.g., Zorn, 1971; Busse 1972; Z. Yang & Yin, 1979; Dagens & Kurushin, 1985; Warth, 1990; Budurov & others, 1991; Gou, 1993). Márquez-Aliaga (1983, 1985) mentioned “*Mytilus*” from the Hispanic Muschelkalk, with the quotation marks indicating that it was not a Triassic genus. Waller (in Waller & Stanley, 2005) proposed a new genus, *Promysidiella* (type species: *Mysidiella cordillerana* Newton in Newton & others, 1987), and included several species, among them *Mytilus eduliformis* and *Mytilus otiosus* McLearn, 1947; the author also indicated that “some species described as ‘*Mytilus*’ from the European Muschelkalk may prove to be members of this genus.” Therefore we consider that the *Mytilus* range started in the Jurassic.

NEOENTOLIUM Romanov, 1985, p. 37

Romanov (1985) gave generic names to the four groups recognized by Staesche (1926) within *Entolium s.l.* (see discussion in Damborenea, 2002a, p. 42–44). The *Entolium cingulatum* Goldfuss group was referred to the new genus *Neoentolium* (type species: *Pecten cingulatus* Goldfuss, 1835 in 1833–1841), and he added other species [*N. cingulatum* (Goldfuss), *N. renevieri* (Oppel), *N. masticonense* (Lissajons), *N. partitum* (Cox), *N. radiatum* (Andreeva)]. Romanov (1985) assigned it a Hettangian–Kimmeridgian range in Europe and Asia. Two other authors, Freneix (1980) and Yamani (1983), proposed two new genera for Staesche’s group, *Costentolium* Freneix, 1980, and *Cingentolium* Yamani, 1983. Waller (2006) considered *Neoentolium*

to be a junior synonym of *Cingentolium* and questioned the validity of the latter, as Yamani confused the right and left valves, and several diagnostic features described by him were actually diagenetic marks. But Waller (2006) did not take into account Freneix (1980), who described *Entolium* (*Costentolium*) Freneix, 1980, based on the same type species as the other two genera, and thus has priority over them.

In the absence of a recent review on the *Entolium* group, we follow a conservative attitude and consider *Neoentolium* to be within *Entolium*, following Staesche (1926) (see discussion for the family Entoliidae in Included Genera, p. 103).

NEOPECTEN Bychkov, 1985, p. 11

Neopeecten is not considered here, because we lack information about it, and none of the databases consulted mention it. The only information was provided by the Zoological Record: “*Neopeecten* Gen nov of Aviculopectinidae, Type species *N. oxytomaeformis*, p. 11, Upper Triassic, *Neopeecten damesi* (Böhm, 1903) Comb nov Transferred from, *Pecten*, p. 11 *Neopeecten oxytomaeformis* sp. nov., Russia, Upper Triassic, p. 11 (Bychkov, N. 1985. [Upper Triassic molluscs of the Kenkeren Range (Koryak Plateau)]. Pokhialainen, V.P. [Eds]. [Mesozoic Bivalvia and Cephalopoda from northeastern Russia. Collected scientific articles.] Akademiya Nauk SSSR, Magadan. 1985: 1–153. Chapter pagination: 5–24.” It was mentioned from the Norian by Polubotko and Repin (1990) and Zakharov, Kurushin, and Pokhialainen (1996).

NEPTUNELLA Astafieva, 1997, p. 24

Neptunella was replaced by *Neptunopeecten* by Astafieva (2001). Astafieva (1997) proposed *Neptunella*, unaware that the name had already been used three times for different mollusks: *Neptunella* Gray, 1854, *Neptunella* Meek, 1864, p. 38, and *Neptunella* Verrill, 1873, p. 639 (Astafieva, 2001).

NUCULA Lamarck, 1799, p. 87

No occurrences from the Induan–Sinemurian interval are considered, following Cox and others (1969), who assigned it a Cretaceous–Holocene range, although many later authors still used the name for Triassic and Jurassic specimens (e.g., Encheva, 1972; Bachmann, 1973; Quintero & others, 1977; Harper, Forsythe, & Palmer, 1998).

NUCULOOPSIS Girty, 1911, p. 133

Although *Nuculopsis* was reported from the Triassic (e.g., Hayami, 1975), it was always reported as *Nuculopsis* (*Palaeonucula*). These mentions are not taken into account, because *Palaeonucula* is considered here as a separate genus from *Nuculopsis*, although, prior to Cox and others (1969), *Palaeonucula* was regarded as a subgenus of *Nuculopsis* and even its junior synonym (Nakazawa & Newell, 1968). Carter (1990a, p. 149–150) stated that they were different and distinct genera: *Nuculopsis* possessed a nacreous inner shell layer, while the inner shell layer of *Palaeonucula* was homogeneous, but when internal characters are observed, they can be confused. The range of *Nuculopsis* is emended with respect to Sepkoski (2002), who considered its extinction to have been in the Early Triassic (early Induan). Presumably this datum was taken from Cox and others (1969), although a Carboniferous–Permian range was assigned there.

NUCUNDATA Waterhouse, 1964, p. 641

Nucundata is not taken into account here, because it is considered to be a subgenus of *Veteranella* Patte, 1926. Waterhouse (1964, p. 641) described *Nucundata* based on its ornamentation and distinguished it from *Glyptoleda* by: "A minor change in ornament occurred in a New Zealand stock of Phestiinae, comparable to but less drastic than that shown by the Australasian genus *Glyptoleda*, and probably equally short-lived. The change simply emphasized tangential instead of concentric ornament." Subsequently, Puri in Cox and others (1969) considered it to be a subgenus of *Veteranella*, together with *Glyptoleda* (see discussion for *Glyptoleda* in this section, p. 161). This author distinguished *V. (Glyptoleda)* from *V. (Nucundata)*, because the latter had less prominent ornamentation and *V. (Veteranella)* was distinguished from *V. (Nucundata)* by the non-constricted or constricted posterior part, respectively. The differences in ornamentation between the three subgenera of *Veteranella* (*Veteranella*, *Glyptoleda*, and *Nucundata*) were considered to be variations within the genus. However, Waterhouse (1980a, p. 102) noticed that "externally *Nucundata* and *Veteranella* are very similar and unaware of the internal characters of *Veteranella*, for example, the presence or absence of ribs on the escutcheon, or ribs on the umbonal internal part ... [characters to which Waterhouse (1964) gave considerable importance when describing *Nucundata* and several species of *Glyptoleda*] . . . the name *Nucundata* can be used." This was followed by Waterhouse (1987) and J. Chen, Liu, and Lan (1983), who also proposed a new subfamily, Veteranellinae, using the variation in the ornamentation as criteria. Z. Fang and Cope (2004, p. 1125) disagreed with this last decision, because they considered: "Clearly a factor that may be of lower taxonomic significance at specific level can hardly be significant at subfamilial level. For this reason we reject the subfamily Veteranellinae . . ." We follow Puri in Cox and others (1969) and consider *Nucundata* to be a subgenus of *Veteranella*, because variation in the ornamentation is a problematic criterion even at the specific level (Z. Fang & Cope, 2004).

OPISOMA Stoliczka, 1871 in 1870–1871, p. 276

No occurrences from the Induan–Sinemurian interval are considered. Cox and others (1969) assigned it a Jurassic (Infraliasic–Rauracian [equivalent to middle Oxfordian]) range; Sepkoski (2002), a Jurassic (upper Pliensbachian–upper Oxfordian) range based on Hallam (1981), but in this last paper, there is no mention of *Opisoma*. Although the genus was widely reported from the Pliensbachian (especially in "Lithiotis" facies) (Hallam, 1969, 1972, 1976, 1977; Accorsi Benini, 1981; Buser & Debeljak, 1994; Liu, 1995; Aberhan & Hillebrandt, 1999; Damborenea, 2002b; Saadi & others, 2003; Fraser, Bottjer, & Fischer, 2004), there is no evidence from the Sinemurian.

PACHYMYONIA Dun, 1932, p. 411

Pachymyonia is not considered here, because it is regarded as a subgenus of *Myonia*, following Cox and others (1969). Waterhouse (1969) argued that the differences in position and morphology of the adductor and retractor muscles between *Myonia* and *Pachymyonia* perfectly supported the separation of the two genera. This was followed in other papers (Waterhouse, 1987, 2002). However, other

authors preferred to keep it as a subgenus of *Myonia* (Astafieva-Urbaytis, 1976; Scarlato & Starobogatov, 1979).

PACIFIHALOBIA Polubotko, 1990, p. 131

According to McRoberts (1993), *Pacifihalobia* is considered to be a junior synonym of *Halobia* Bronn, 1830a, since the features used for proposing this genus are of specific level (see discussion for the family Halobiidae in Included Genera, p. 91). Polubotko, Payevskaya, and Repin (2001) considered it to be a valid genus.

PALAEONTOLIUM Romanov, 1985, p. 35

Palaeontolium is not considered here, because it was based on *Pleuronectites discites* Schlotheim, 1820, a species with some problems disregarded by Romanov (Waller, 2006, p. 325). Romanov (1985) included the following species: *P. microtis* (Wittenburg), *P. discites* (Schlotheim), *P. marginiplicatum* (Kittl), *P. liscaviense* (Giebel), *P. weissenbachense*, and *P. hallense* (Wohermann). We consider *Pleuronectites discites* Schlotheim, 1820, as an *Entolium* (see discussion for the family Entoliidae in Included Genera, p. 103).

PALAEOLOPHA Malchus, 1990, p. 102

Junior synonym of *Actinostreon* Bayle, 1878 (Hautmann, 2001a; Checa & Jiménez, 2003b; Márquez-Aliaga & others, 2005). The genus proposed by Malchus (1990) was placed in synonymy by Hautmann (2001a), basically for two reasons: first, the type species designated by Malchus, *Ostrea haidingeriana* Emmrich, 1853, has a shell microstructure that suggests it should be allocated to *Actinostreon*; second, Malchus (1990) figured the type species of *Actinostreon*, *Ostrea solitaria* J. de C. Sowerby, 1825, as *Palaeolopha solitaria* (Hautmann, 2001a). We follow Hautmann in this case, because the synonymy is more than justified.

PARAHALOBIA Yin & Hsu, 1938 in Chen, 1976, p. 224

Parahalobia was proposed as a subgenus of *Halobia* to accommodate *Halobia* forms lacking radial ornamentation from the Anisian and Ladinian of China (H. J. Campbell, 1994). Subsequently, several authors considered it at the genus level, but none of them justified this decision (e.g., C. Chen & Yu, 1976; Sha, Chen, & Qi, 1990). McRoberts (1993, p. 201) considered *Parahalobia* as a junior synonym of *Halobia* (see discussion for the family Halobiidae in Included Genera, p. 91). However, Sepkoski (2002) considered it in his compendium of genera, taking the data from H. Yin (1985), who regarded it as a subgenus of *Halobia*. H. J. Campbell (1994) indicated that *Parahalobia* could be relocated as a subgenus of *Halobia*, because it is similar in all respects except for the lack of radial ornamentation. For all these reasons, we do not regard *Parahalobia* as an independent genus.

PAULLIA (no author)

Schubert (1993) and Schubert and Bottjer (1995) mentioned *Paulia* as a new genus that would accommodate some species attributed to *Pernopecten*, but they did not formally describe it and mentioned it as a personal communication by Boyd in 1991; however, Boyd never published its description and therefore the name is invalid (*nomen nudum*), although it is taken into account in the PBDB (online).

PECTINULA A. F. Leanza, 1943, p. 244

Junior synonym of *Posidonotis* Losacco, 1942 (Damborenea, 1986, 1987b). Damborenea (1986, 1987b), after careful consideration of the type species of *Pectinula* (*Pectinula cancellata* A. F. Leanza, 1943) and *Posidonotis* (*Posidonotis dainelii* Losacco, 1942), concluded that the only difference between them was that the former had an anterior auricle, absent in the latter, a fact that was attributed by Damborenea to the poor preservation of Losacco's material, as in many specimens of *Pectinula cancellata*, the anterior auricle was not observed. Later, Hayami (1988), after studying his own well-preserved material, restored the validity of *Pectinula*. The author based his argument on the differences in auricle shape and in the lack of byssal notch in juvenile stages in his specimens. Very few later papers mentioned the name *Pectinula* (see Monari, 1994; Waller, 2006); most used *Posidonotis*, accepting the synonym proposed (see Damborenea, 1993, 2001; Aberhan, 1994a, 1998a, 2001; Aberhan & Pálffy, 1996; Fürsich & others, 2001).

PERAMPLIATA Arkell, 1936 in 1929–1937, p. xx

No occurrences from the Induan–Sinemurian interval are considered. Cox and others (1969) assigned it a Jurassic range, but there is no evidence of *Perampliata* until the Oxfordian (Hallam, 1976; Liu, 1995).

PERIBOSITRA C. Chen, 1981, p. 81

Junior synonym of *Claraia* Bittner, 1901a (Nakazawa, 1992; Z. Fang & others, 2009). C. Chen in Zhao and others (1981) proposed *Peribositra*, based on the type species *P. baoqingensis* Chen, 1981, and included it in the family Posidoniidae. Z. Fang and others (2009) placed it in synonymy with *Claraia*, according to, among others, Waller and Stanley (2005, p. 20), but the latter authors only stated that *Peribositra* was a clariid, not a posidoniid. We follow Z. Fang and others (2009) in this regard (Chuzhen Chen was the author of *Peribositra* and is a coauthor of Z. Fang and others [2009]).

PERIBOSITRIA Kurushin & Trushchelev, 1989, p. 59

Junior synonym of *Bositra* De Gregorio, 1886 (Waller & Stanley, 2005). *Peribositria* was proposed by Kurushin and Trushchelev (1989) from the Triassic of Siberia and is still used by Russian authors, particularly in biostratigraphic syntheses (e.g., Polubotko, Payevskaya, & Repin, 2001; Klets, 2006; Konstantinov, Sobolev, & Yaderkin, 2007). Waller and Stanley (2005) rejected all differences with *Bositra* mentioned by Kurushin and Trushchelev (1989) to separate the genera, since most of these were due to taphonomic issues (see discussion in Waller & Stanley, 2005, p. 20). However, McRoberts (2010) decided provisionally to retain the genus, because the ligamental system of the Triassic forms is not well known.

PERIHALOBIA Gruber, 1976, p. 192

Although *Perihalobia* was originally proposed as a subgenus of *Halobia*, later it was considered at the generic level, which is totally unjustified, according to several authors (McRoberts, 1993, 2000; H. J. Campbell, 1994), because they are indistinguishable (see discussion for Halobiidae in Included Genera, p. 91).

PHOLADOMYOCARDIA Szajnocha, 1889, p. 88

No occurrences from the Induan–Sinemurian interval are considered. Cox and others (1969) assigned it a Jurassic range in South America (Peru), based on the original description of the genus, but there is no more information about it. Moreover, *Pholadomyocardia* was considered to be a doubtful genus, because no internal characters are known (Cox & others, 1969).

PHYMODONUCULA Guo, 1988, p. 112

Phymodonucula was erected by Guo (1988) from the Carnian of southwestern China and included in the family Nuculidae. Z. Fang and others (2009, p. 6) considered *Phymodonucula* a dubious genus, because the ligament is not known, as none of the specimens have the ligament properly preserved. This is followed here.

PLACUNOPSIS Morris & Lycett, 1853 in 1851–1855, p. 5

Following Todd and Palmer (2002), we consider the origin of *Placunopsis* to be in the Middle Jurassic. There are several Triassic species attributed to *Placunopsis* (see discussion for the genus *Pseudoplacunopsis* in Included Genera, p. 70).

PLATYMYOIDEA Cox, 1964, p. 42

Cox and others (1969) assigned it a Lower Jurassic–Lower Cretaceous range. The oldest report dates from the Pliensbachian (Damborenea in Damborenea & González-León, 1997; Aberhan, 2004). Liu (1995) quoted the genus from the Sinemurian of Morocco, but we could not corroborate this information. Furthermore, Hautmann (2001b) attributed a single, fragmentary specimen from the Norian of Iran to *Platymyoidea* sp. We are not taking this into account, because it is necessary to check it with new and better material. For all of these reasons, we will not consider occurrences from the Induan–Sinemurian interval until reliable information is available.

PLESIOCYPRINA Fischer, 1887 in 1880–1887, p. 1072

Although several sources (Cox & others, 1969; Sepkoski, 2002; Gardner, 2005; J. Yin & Grant-Mackie, 2005) assigned an Upper Triassic (Rhaetian)–Upper Jurassic range, it seems that all data originated from Cox and others (1969). Nevertheless, *Plesiocyprina* was not reported for our study interval. Neither Diener (1923) nor Kutassy (1931) referred to it in their treatises. The oldest record is Toarcian (Gahr, 2002).

PLEUROMYSIDIA Ichikawa, 1954, p. 52

Junior synonym of *Otapiria* Marwick, 1935 (Zakharov, 1962). According to Ando (1988), Zakharov established the synonymy of *Pleuromysidia* with *Otapiria*, because he did not observe significant morphological differences between them, and this was followed by most authors (e.g., Hayami, 1975; Ando, 1983, 1988; Kobayashi & Tamura, 1983b; Okuneva, 1986; Damborenea, 1987b).

PLICATOSTYLUS Lupper & Packard, 1930, p. 204

Junior synonym of *Lithiotis* Gümbel, 1871 (Broglia-Loriga & Neri, 1976; Accorsi-Benini & Broglia-Loriga, 1977). This synonymy was accepted by most subsequent authors (e.g., P. L. Smith & Tip-

per, 1986; Nauss & Smith, 1988; Aberhan, 1998b, 2001; Fraser, Bottjer, & Fischer, 2004).

PLICATULA Lamarck, 1801, p. 132

Cox and others (1969) assigned *Plicatula* a Middle Triassic–Holocene range. Subsequently, it was consistently mentioned from both the Triassic and the Jurassic. The problem with this genus and its range is that many species attributed to *Plicatula* are now regarded as belonging to other genera, such as *Harpax* Parkinson, 1811, *Eoplicatula* Carter, 1990a, and *Pseudoplacunopsis* Bittner, 1895. Hautmann (2001a) did not consider *Plicatula* from the Triassic. Regarding the Jurassic specimens, in most of them, the hinge is not preserved, and it is difficult to know which species should be assigned to *Harpax* and which to *Plicatula*. Damborenea (2002a) believed that the genera coexisted in the early history of the group during the Upper Triassic, but no specific records were found. Following Hautmann (2001a), we do not consider *Plicatula* to be from the Triassic, and, although it may have been present in the lower Jurassic, we do not have enough evidence to decide.

POLIDEVCIA Chernyshev, 1951, p. 25

Since its proposal over 50 years ago, there has been an open debate about the validity of *Polidevcia*. According to different authors, it was considered to be a junior synonym of *Phestia* (McAlester in Cox & others, 1969), a junior synonym of *Culunana* Lintz, 1958, a subgenus of *Phestia* (Nakazawa & Newell, 1968; González, 1969; Carter, 1990a), or a valid and independent genus (Ciriacks, 1963; Waterhouse, 1964) (see discussions in Carter, 1990a, p. 153; Bradshaw, 1999, p. 70; and Anelli, Rocha-Campos, & Simões, 2002, p. 170–171). Here we follow the approach adopted by Carter (1990a), treating *Polidevcia* as a subgenus of *Phestia*.

POSIDONIA Bronn, 1828, p. 268

According to Waller and Stanley (2005), *Posidonia* is a Paleozoic genus. Most species described under the genus *Posidonia* from the Lower and Middle Triassic belong to *Bositra* De Gregorio, 1886 (as emended in Waller & Stanley, 2005).

PRAECHLAMYS Allasinaz, 1972, p. 340

Although some authors (Waller & Marincovich, 1992; Monari, 1994; Damborenea, 2002a) considered *Praechlamys* Allasinaz, 1972, at the generic level to be separate from *Chlamys*, Allasinaz (1972) described it as a subgenus of *Chlamys*. Taking into account the problems with the so-called *Chlamys*-like forms (see discussion for *Chlamys* in Included Genera, p. 97), we follow a conservative attitude and follow Allasinaz's original concept, even knowing the problems involved (see Damborenea, 2002a). Other authors, such as Posenato (2008b), followed this same position, and Hautmann (2001b) even questioned the validity of *Praechlamys*, since, in his opinion, the type of ornamentation is not an important taxonomic character at subgeneric level, and Allasinaz (1972) used this criterion when separating the subgenera *C.* (*Chlamys*), *C.* (*Praechlamys*), and *C.* (*Granulochlamys*).

PRIMAHALOBIA Polubotko, 1988, p. 98

Polubotko recognized *Primahalobia* as a new subgenus of *Indigirohalobia* Polubotko, 1984, based on the angular relationship of the anterior auricle (H. J. Campbell, 1994). Subsequently, Polubotko, Payevskaya, and Repin (2001) raised it to generic level. Following McRoberts (1993), we do not consider it to be valid, because the diagnostic criteria for *Primahalobia* are used by most authors at the specific level (see discussion for the family Halobiidae in Included Genera, p. 91).

PRONOELLA Fischer, 1887 in 1880–1887, p. 1087

No occurrences from Induan–Sinemurian interval are considered. Cox and others (1969) included two subgenera in *Pronoella*: *P.* (*Pronoella*) and *P.* (*Gythemon*); only the first one interests us because of its Lower Jurassic range. Nevertheless, no records were located from Hettangian or Sinemurian beds, although it was widely mentioned from the Pliensbachian (Hallam, 1972, 1976, 1977, 1987; Fürsich, 1982; Liu, 1995; Holzapfel, 1998; Gahr, 2002).

PROPEAMUSSIUM De Gregorio, 1884, p. 119

Following Damborenea (1998), we consider that *Propeamussium* ranges from the Upper Cretaceous to the Recent. Following the original concept of *Parvamussium* and *Propeamussium*, Triassic and Jurassic *Propeamussium* records are better accommodated in *Parvamussium* Sacco, 1897 (see discussion for *Parvamussium* in Included Genera, p. 95).

PROSPONDYLUS Zimmermann, 1886, p. 105

Prospondylus was considered to be a junior synonym of *Pseudomonotis* von Beyrich, 1862, by Newell (1937), and this was followed in Cox and others (1969). Newell and Boyd (1970) reestablished the validity of *Prospondylus*. Although *Prospondylus* was reported from the Triassic, those records are not considered, since it is regarded as a Paleozoic genus (Newell & Boyd, 1970; Márquez-Aliaga & others, 2005). Hautmann (2001a, 2001b) pointed that it may be present in Triassic sediments ("*Hinnites*" *comptus* Bittner, 1898), but this is not proven.

PROTODICERAS G. Böhm, 1892, p. 51

Although *Protodiceras* was reported from the Sinemurian, no occurrences from the Induan–Sinemurian interval are considered. Cox and others (1969) reported it from the lower Lower Jurassic. Hallam (1976) quoted *Protodiceras pumilum* (Guembel) from the Sinemurian and Pliensbachian of Europe, data incorporated by Sepkoski (2002) in his database. However, Hallam (1977) only reported it from the Pliensbachian of Europe. No undoubted Sinemurian records were found.

PSEUDOCLARAIA Z. Zhang, 1980, p. 443

Junior synonym of *Claraia* Bittner, 1901a (Newell & Boyd, 1995; F. Yang, Peng, & Gao, 2001; He, Feng, & others, 2007; Z. Fang & others, 2009). Z. Zhang (1980) proposed *Pseudoclaraia* and designated *Claraia wangi* (Patte, 1935) as type species. He considered *Pseudoclaraia* to be very close to *Claraia* and argued that it differed from it by the larger right anterior auricle and by differences in shape and orientation of the byssal sinus. Nakazawa

(1996) included it as a subgenus of *Claraia*, since differences were not great and often their differentiation was very difficult. Newell and Boyd (1995) considered *Pseudoclaraiia* to be a junior synonym of *Claraia*, because no quantitative and comparative studies of local populations were made before the proposal of the new genus. F. Yang, Peng, and Gao (2001) reached the same conclusion about the synonymy after carrying out a comparative study between *Claraioides*, *Claraia*, and *Pseudoclaraiia*; they concluded that the only differences between these three genera were: 1) right anterior auricle shape, and 2) byssal sinus shape. These differences, in their opinion, were not reliable to separate the genera, because the byssal sinus shape is due to the adaptation of *Claraia* to different environments, and, on the other hand, the diagnosis of *Claraia* states nothing about the size and shape of the byssal sinus; therefore, this character can only be used as diagnostic at the specific level. For all these reasons, F. Yang, Peng, and Gao (2001) considered *Pseudoclaraiia* to be a junior synonym of *Claraia*. Kotlyar, Zakharov, and Polubotko (2004) argued for the validity of *Pseudoclaraiia* but did not provide new arguments. He, Feng, and others (2007), following Boyd and Newell (1995) and F. Yang, Peng, and Gao (2001), reached the same conclusion regarding the synonymy of *Pseudoclaraiia* after studying the variation in ornamentation and byssal sinus shape of all species included in *Claraia* in relation to their stratigraphic ranges and paleogeographic distribution (see He, Feng, & others, 2007, table 1, p. 1016 and discussion). The authors showed there was a gradual morphological change from the early Changhsingian to Induan, indicating that the shape, size, and orientation of the byssal sinus was not a valid criterion for discrimination at the generic level in this group.

PSEUDOMONOTIS von Beyrich, 1862, p. 10

Although *Pseudomonotis* is frequently mentioned from the Triassic and Jurassic (see section PBDB age range for example, online), we follow Cox and others (1969), Newell and Boyd (1970, 1989, 1995), and Hautmann (2001a, 2001b) in the idea that it was an exclusively Paleozoic genus. Newell and Boyd (1970, 1989, 1995) showed the external morphological similarity between *Pseudomonotis* and *Gryphaea* (see Newell & Boyd, 1995, fig. 47). In many cases, these genera can only be distinguished by the shell microstructure and the attachment valve (right in *Pseudomonotis* and left in *Gryphaea*) (Newell & Boyd, 1995). In the words of Newell and Boyd (1989, p. 2): “*Pseudomonotis* is not an oyster. It is an aberrant scallop, an aviculopectinacean with an oysterlike habit of fixation.” Because of this external resemblance, *Pseudomonotis* is commonly confused with Triassic and Jurassic ostreids.

PSEUDOPACHYMYTILUS Krumbeck, 1923b, p. 87

No occurrences from the Induan–Sinemurian interval are considered, although both Cox and others (1969) and Sepkoski (2002) assigned it a Lower Jurassic range, because only Pliensbachian records were reported (e.g., Hallam, 1972; Liu, 1995, 1999; Posenato & Avanzini, 2004).

PSEUDOPIS Cox, 1946, p. 44

No occurrences from Induan–Sinemurian interval are considered, although Cox and others (1969) assigned it a Lower Jurassic range,

the same age indicated by Cox (1946) when proposing *Pseudopis*. The oldest record is Pliensbachian (Hallam, 1976, 1977, 1987; Liu, 1995).

PTEROCLARAIA Guo, 1985, p. 266

Waterhouse (2000, p. 167) raised *Pteroclaraiia* to genus level (Guo [1985] had proposed it as a subgenus of *Claraia*), arguing that “the size and definition of the posterior wing are distinctive and easily recognised features.” Nevertheless, together with J. Chen and Komatsu (2002) and Z. Fang and others (2009), we consider *Pteroclaraiia* to be a subgenus of *Claraia*, since this character is not regarded as diagnostic at the genus level (He, Feng, & others, 2007).

PTEROHALOBIA Guo, 1985, p. 266

Z. Fang and others (2009) placed *Pterohalobia* in synonymy with *Daonella* Mojsisovics, 1874. Their reasons were: “The anterior auricle of the figures of the holotype were not appropriately clipped off by Guo (1985, pl. 16, 4b) and its ornamentation is very similar to that of *Daonella boeckhi* Mojsisovics.” Guo (1985) erected *Pterohalobia* based on *P. productalata* Guo, 1985, from the Anisian of southwestern China. The material figured by Guo (1985) is very poor.

PTEROPERNA Lycett, 1850, p. 421

Fürsich and Werner (1988, p. 106) considered *Pteroperma* as a junior synonym of *Pteria* Scopoli, 1777, because, in their view, “the main diagnostic feature of *Pteroperma*, the presence of 1 to 4 external longitudinal grooves on the exterior of the posterior wing, does not justify separation at the generic level. Such grooves occasionally are also present in individuals of Recent species of *Pteria*. Furthermore, populations from the Kimmeridgian of Consolação show that the number and distinctness of such grooves varies greatly.” Hautmann (2001b) provisionally considered it to be a subgenus of *Pteria*, as his specimens are similar to the type species of *Pteroperma*. We judge it to be more appropriate to keep it as a subgenus of *Pteria*, because, although they are very similar, *Pteroperma* is a useful concept and easily recognized in the Upper Triassic and Jurassic.

PTEROPIRIA Waterhouse, 2008, p. 169

This genus was proposed by Waterhouse (2008, p. 169) with *Otapiria taillieuri* Imlay, 1967, p. 3, as type species. It was diagnosed as “characterized by presence of well developed posterior wing on left and right valve.” Within the range of morphological variability accepted within *Otapiria*, *O. taillieuri* Imlay is extremely similar to the type species of *Otapiria*, *O. marshalli* (Trechmann), see Imlay (1967, pl. 1) for figures of both species.

PTYCHOSTOLIS Tullberg, 1881, p. 14

No occurrences from the Induan–Sinemurian interval are considered, although both Cox and others (1969) and Sepkoski (2002) assigned it a Jurassic range. Even though it was impossible to see Tullberg (1881), where *Ptychostolis* was proposed and which is also the only record located, we know the author assigned it a Tithonian range. However, it is difficult to know the exact age of the specimens studied by Tullberg (1881), because they come from two different localities and four different lithological units; the author reported the species *Ptychostolis nordenskiöldii* from the Kalkstein of Skodde Bituminoeser Bay, where only *Ammonites okensis* (d’Orbigny) (now

Craspedites okensis) was found, which is an index Tithonian taxon [if Tullberg's identification is correct, since he did not figure the specimen (Kaim, personal communication, 2004)].

PULVINITES Defrance in Blainville, 1824, p. 316

Palmer (1984) considered that *Pulvinites* had its origin in the Middle Jurassic, but Damborenea (1987b) assigned some Pliensbachian South American specimens to this genus and noted that some Hettangian specimens of France could be included in *Pulvinites*. A review of these specimens is needed in order to include *Pulvinites* in our study interval.

QUADRATIA Yin, 1974, p. 25

It is a junior homonym of *Quadratia* Muir-Wood & Cooper, 1960, p. 161 (Brachiopoda; family Productellidae) (Z. Fang, 2009). The name was replaced by *Guizhoumyophoria*, new name, based on the same type species, *Quadratia quadrata* Yin (Z. Fang, 2009).

RETROCERAMUS Koschelkina, 1957, p. 29

No occurrences from the Induan–Sinemurian interval are considered, although a doubtful mention from the Sinemurian in PBDB (online) was located. This is from Aberhan's (1995) unpublished material, and it is only doubtfully attributed to this genus (?*Retroceramus* sp). In addition, J. Chen (1982a) proposed a new species, *Retroceramus? xiaoshuiensis* Chen from the Upper Triassic of southern China; this uncertain mention is not taken into account. Throughout the consulted literature, the origin of *Retroceramus* is regarded as Middle Jurassic (Hallam, 1976, 1977; Crampton, 1988; Damborenea, 1996b; N. Hudson, 2003; Damborenea & Manceñido, 2005a; Zakharov & others, 2006) or Toarcian at the earliest (Hallam, 1987; J. Yin & Grant-Mackie, 2005).

RHYNCHOPTERUS Gabb, 1864, p. 31

Junior synonym of *Pteria* Scopoli, 1777 (see Silberling & Nichols, 1982, p. 66). *Rhynchopterus* Gabb, 1864, is a junior homonym of *Rynchopterus* Shrank, 1798, a beetle genus. The name proposed by Shrank was a mistake, because surely he meant *Rhynchophorus* (Silberling & Nichols, 1982), but even so, it is a valid name and therefore *Rhynchopterus* Gabb should not be used for a bivalve. Instead of proposing a new name for the poorly known bivalve genus, it is more appropriate to leave it as a probable synonym of *Pteria s.l.*

ROSSIODUS Allasinaz, 1965, p. 120

Junior synonym of *Neomegalodon* Gümbel, 1862 (H. Yao & others, 2007). See discussion for *Gemmellarodus* in this section (p. 161).

RUGICLARAIA Waterhouse, 2000, p. 179

Waterhouse (2000) proposed *Rugiclararaia* with *Claraia aurita* (Hauer, 1850) as type species. Waterhouse (2000, p. 179) indicated that *R. aurita* differs from the type species of *Claraia*, *Claraia clarae* (Hauer, 1850) by the absence of radial ornament, but He, Feng, and others (2007) attributed a concentric and radial ornamentation to both species. Another feature mentioned by Waterhouse (2000) for his new genus is the auricle size and shape, characters used to discriminate species by most authors (F. Yang, Peng, & Gao, 2001).

For all these reasons, we do not consider *Rugiclararaia* to be a valid genus and include its type species in *Claraia*.

SATURNELLA Astafieva, 1994, p. 16

Name replaced by *Saturnopecten* Astafieva, 2001. Astafieva (1994) proposed *Saturnella* without knowing that the name was already being used for a Jurassic foraminiferan, *Saturnella* Hedinger, 1993, p. 33 (Astafieva, 2001).

SATURNOPECTEN Astafieva, 2001, p. 557

According to Newell and Boyd (1995, p. 85), *Saturnopecten* was not taken into account, because it was based on very few specimens, mostly broken or poorly preserved, and no studies of microstructure and/or hinges were carried out.

SEPTIFER Recluz, 1848 in 1848–1849, p. 275

Although both Cox and others (1969) and Sepkoski (2002) assigned it a Triassic–Holocene range; Carter (1990a) argued that the Triassic specimens attributed to *Septifer* were not related to the type species (*Mytilus bilocularis* Linnaeus, 1758, p. 705), and they differed in shell microstructure, mineralogy, and other features, such as the position of the ligament. The Triassic species attributed to *Septifer* are: *S. eduliformis* (Schlotheim, 1820) (Ürlich, 1992; Posenato, 2002; Posenato & others, 2002); *S. rugulosus* (Bittner, 1895) (Zardini, 1981); *Mytilus (Septifer) praeacutus* Klipstein, 1843 in 1843–1845 (Diener, 1923); and *Mytilus (Septifer) praeacutiformis* Wilckens, 1909 (Diener, 1923); all are mentioned from Ladinian and Carnian. No more records of the genus are known until the Cretaceous. The species *eduliformis* was included in *Promysidiella* Waller & Stanley, 2005, based on the study of collections in various museums (Waller & Stanley, 2005). Carter (1990a) showed that *rugulosus* did not match *Septifer* due to substantial differences with its type species. And *praeacutus* and *praeacutiformis* were originally described in the genus *Mytilus*, being included in the subgenus of *Septifer* by Diener (1923). Sente and Vörös (in Budai & others, 2003) mentioned *Septifer?* sp. from the Middle Triassic, but this record is not taken into account, because its generic attribution is doubtful. Although this topic requires a major review, it seems that *Septifer* has not been recorded from the Triassic.

SICHUANTRIGONIA Gou, 1993, p. 24

Sichuantrigonia was placed in synonymy with *Acanomyphoria* Guo, 1985, by Z. Fang and others (2009), because the ornament is very similar in both genera and that is practically the only difference.

SOLENOMORPHA Cockerell, 1903, p. 559

Solenomorpha is a typically Paleozoic genus. Cox and others (1969) assigned it a Lower Devonian–upper Permian range. However, Allasinaz (1966) mentioned it from the Carnian when he transferred the species *Cuspidaria gladius* Laube, 1865, to *Solenomorpha*. Allasinaz (1966) also considered that all Triassic species (without mentioning them) attributed to *Cuspidaria* should be included in "*Solenopsis*" (junior synonym of *Solenomorpha*). We have no opinion on the subject. The only species mentioned by Allasinaz (1966) was *C. gladius*, and in the figures (pl. 41, 1–2), the characters he discussed in the text are not observed. If we compare these figures with those

offered by Cox and others (1969, p. 821, fig. F3, 2) or by some others on Paleozoic specimens (e.g., LaRocque, 1950, pl. 17,8–11; Hoare, Heaney, & Mapes, 1989, fig. 7.9), they do not seem to have much in common. *Solenomorpha gladius* was subsequently mentioned from the Carnian following Allasinaz (1966) (Jelen, 1988; Jurkovsek, 1993). We follow Cox and others (1969) in the range considered for this genus.

SOMAPTERIA Tamura, 1960, p. 224

No occurrences from the Induan–Sinemurian interval are considered. According to Cox and others (1969), *Somapteria* was reported from the Upper Jurassic of Japan. *Somapteria* is a monospecific genus limited to the Kimmeridgian of Japan (Hayami, 1975). Tëmkin (2006) assigned it a Middle Triassic range, but this must be a mistake, because none of the sources mentioned in his table offered this information.

SPONDYLUS Linnaeus, 1758, p. 690

No occurrences from the Induan–Sinemurian interval are considered. The oldest specimen attributable to Spondylidae was reported from the Bajocian of France (Harper in Waller, 2006); according to Skelton and Benton (1993), the first species attributable to this family should be *Spondylus consobrinus* Deslongchamps. Malchus (2004) extended the family range back to the upper Permian, but he did not justify it. *Spondylus* is rarely mentioned from the Jurassic, and it is often mistaken for *Eopecten* Douvillé, 1897 (Waller, 2006). Cox and others (1969) assigned it a Jurassic–Holocene range, but in previous papers, it was widely quoted from the Triassic. Frequently, these specimens could be referred to the Triassic *Newaagia* Hertlein, 1952 (Waller, 2006). Moreover, there is another similar genus with which it may be mistaken: *Spondylopecten* Röder, 1882. Johnson (1984) stated that *Spondylopecten* ranged from the Middle Jurassic, but Waller (2006) reported it from the Upper Triassic, referring to some specimens in the Mesozoic Stratigraphy collections of the Smithsonian Institution from Nevada, attributed to *Spondylopecten*. However, Waller (2006) did not describe or figure the material, and we are not taking this record into account.

STREBLOCHONDRIA Newell, 1938, p. 80

Although *Streblochondria* is considered to be a Paleozoic genus (Newell, 1938; Newell & Boyd, 1995), several Triassic records were located (e.g., Nakazawa, 1971; Tamura, 1973; Hayami, 1975; Tamura & others, 1975; Fraiser & Bottjer, 2007a), but none of them proved its occurrence after the upper Permian. Nakazawa (1971) tentatively included his specimens from the Triassic of Japan in “*Streblopteria*“ *matsushitai* Nakazawa, 1971, because they were referable to the subfamily Streblochondriniinae Newell, 1938, and he preferred this genus over others of this subfamily. Hayami (1975) simply repeated Nakazawa’s data (1971). Tamura (1973) tentatively referred his specimens from the Middle Triassic of Malaysia to this genus (*Streblochondria?* sp.), because, although they showed the typical ornamentation of *Streblochondria*, the ligament was not observed in the three deformed specimens (two external molds and the upper part of internal mold). Tamura and others (1975) repeated Tamura’s data (1973). Finally, Fraiser and Bottjer (2007a) assigned four valves from the Triassic of Japan to *Streblochondria*, but they

neither figured nor described the specimens, and we are not taking this record into account.

STREBLOPTERINELLA [Kurushin, 1998]

The generic name *Streblopterinella* was introduced by N. I. Kurushin (1998) in his unpublished doctoral thesis. The genus *Streblopterinella* Kurushin comprised seven species: *Streblopteria newelli* Kurushin, 1982; *Streblopteria jakutica* Kurushin in Dagys & Kurushin, 1985; *Streblopteria egorovi* Kurushin, 1984, as well as four further species which are *nomina nuda* (described in Kurushin, 1998). Unfortunately, the generic name *Streblopterinella* has never been officially published (in accordance with ICZN rules, 1999) by the author, and it is considered *nomen nudum* (Konstantinov, personal communication, 2011).

TAIMYRODON Sanin, 1973, p. 92

Taimyrodon was originally described from the Upper Cretaceous of northern Siberia (Sanin, 1973). Subsequently, it was mentioned from Triassic (Dagys & Kurushin, 1985; Kurushin, 1990; Klets, 2006) and Lower Jurassic deposits (Meledina & Shurygin, 2001; Zakharov & others, 2006). Most of these records did not figure the specimens, and specimens in the others do not show the hinge features and therefore could belong to *Palaeoneilo*.

TEINONUCULANA

Zhang in Zhang, Wang, & Zhou, 1977, p. 9

R. Zhang in R. Zhang, Wang, and Zhou (1977) proposed *Teinonuculana* (Lower Jurassic of China), based on the type species *T. guangdongensis* Zhang in Zhang, Wang, & Zhou, 1977, with special emphasis on ornamentation. According to J. Yin and McRoberts (2006), the diagnostic features of the type species of *Teinonuculana* (elongate form, taxodont dentition, and characteristic rostrum) fit perfectly with those of *Ryderia* Wilton, 1830, and the external ornamentation of *Teinonuculana* is the same as in English specimens of *Ryderia texturata* (Terquem & Piette, 1865) from the Lower Jurassic (see J. Yin & McRoberts, 2006, p. 106). For those reasons, J. Yin and McRoberts (2006) included *Teinonuculana* as a subjective synonym of *Ryderia*, and this is followed here. These authors also warned about the difficulties of studying the ornamentation of these species, since conmarginial or V-shaped ribs are often destroyed or deformed by taphonomic processes.

TOMMASINA Cox, 1964, p. 44

Cox (1964) proposed the name *Tommasina* to replace *Mytiliconcha* Tommasi, 1911, p. 35 (*non Mytiliconcha* Conrad, 1862, p. 290, as *Mytiliconcha* [erroneously] on p. 579). Almost all authors regarded this name change as valid, but Stiller and Chen (2006) defended the validity of *Mytiliconcha* as an unnecessary replacement, following Vokes (1980). In our opinion, the name is indeed unnecessary, because the name proposed by Conrad was *Mytiliconcha*, and therefore it is not a homonym of *Mytiliconcha* (ICZN Art. 56.2, 1999). Moreover, *Mytiliconcha* is not included here, because it is a junior synonym of *Protopsis* Kittl, 1904 (see Waller & Stanley, 2005, p. 9). These authors considered *Tommasina* [= *Mytiliconcha*] to be a junior synonym of *Protopsis*, because they have the same diagnostic features, although the hinge structure

of *Protopsis* is unknown. Hautmann (2008) believed both genera show significant differences on external morphology, but the poor knowledge of *Tommasina* [= *Mytiliconcha*] makes it difficult to establish its taxonomic relationships.

TRICHITES Voltz in Thurmann, 1833, p. 13

No occurrences from the Induan–Sinemurian interval are considered. Cox and others (1969) assigned it to have a Middle Jurassic (Bajocian)–Lower Cretaceous range, but Sepkoski (2002) considered *Trichites* to be from the Norian, based on Hallam (1981). We could not locate the original quotation nor any other reference that substantiates the datum in the references mentioned by Hallam (1981) for the Norian of North America, where the genus was supposedly reported. *Trichites* was frequently mentioned from the Middle and Upper Jurassic (Fürsich, 1980; Damborenea, 1987a; Aberhan, 1994b; Liu, 1995; Fürsich & Hautmann, 2005; Sano & others, 2010) and also from the Lower Jurassic, but the oldest record is from the Pliensbachian of South America (Pérez, 1982; Damborenea, 1987a; Liu, 1999), and the Toarcian of Europe (Gahr, 2002).

VENTALIUM De Gregorio, 1930a, p. 23

Cox and others (1969) considered it to be a doubtful genus, and no later mention of *Ventalium* was found. The range assigned was Jurassic, but it was impossible to corroborate its occurrence within the range of study. Furthermore, Cox and others (1969, p. 371) stated: “Type imperfect, characters not fully known but considered by De Gregorio to be related to *Pecten*.” Damborenea (1987b, p. 198) considered it to be a junior synonym of *Eopecten* Douvillé, 1897: “This genus [*Ventalium*] from the lower Jurassic of Sicily was based on incomplete specimens that are in all aspects comparable with fragments of *Eopecten*, especially in ornamentation pattern.”

VIETNAMICARDIUM Vu Khuc, 1977a, p. 678

Junior synonym of *Tulongocardium* Chen, Chen, & Zhang in Wen & others, 1976 (Schneider, 1995). Vu Khuc (1977a) proposed *Vietnamicardium* based on Upper Triassic specimens from Vietnam, with *V. vietnamicum* (Vu Khuc in Vu Khuc & others, 1965) as type species. A year earlier, Chen and others (in Wen & others, 1976) had proposed the subgenus *Cardium* (*Tulongocardium*), and *Cardium vietnamicum* Vu Khuc was one of its listed species. For this reason, *Vietnamicardium* was considered a synonym of *C.* (*Tulongocardium*) (Schneider, 1995, p. 322). On the other hand, Hautmann (2001b, p. 146), although discussing the possible synonymy, considered *Vietnamicardium* to be a distinct genus and included in it some species previously assigned to *Cardium* (*Tulongocardium*). Sepkoski (2002), by mistake, called it *Tulongocardium*. Since the synonymy proposed by Schneider seems sufficiently justified, we follow him, and we also agree to regard *Tulongocardium* at the generic level.

VOKESSELLA Chavan, 1952, p. 97

No occurrences from the Induan–Sinemurian interval are considered. Both Cox and others (1969) and Sepkoski (2002) assigned it a Jurassic range without further discussion. Liu (1995) reported it from the Kimmeridgian.

WALLEROBIA Waterhouse, 2008, p. 176

Junior synonym of *Enteropleura* Kittl, 1912 (J. Chen & Stiller, 2010). Waterhouse (2008) proposed *Wallerobia* based on *Enteropleura jenksi* Hopkin & McRoberts, 2005, p. 797 as type (= *Enteropleura* sp. A of Waller in Waller & Stanley, 2005). J. Chen and Stiller (2010, p. 526) rejected it and regarded it as a junior synonym of *Enteropleura* because “the morphological features emphasized by Waterhouse (2008) to distinguish *Wallerobia* from *Enteropleura* are only of species-level significance, and the character of the morphological differences does not justify the formal erection of a new genus-level taxon.” We are not taking into account this new genus, because we follow Hopkin and McRoberts (2005), Waller (in Waller & Stanley, 2005), J. Chen and Stiller (2007, 2010), and McRoberts (2010), and include the type species in the genus *Enteropleura* Kittl, 1912.

XINANOPECTEN Feng, Cui, & Liu, 1992, p. 512

Feng, Cui, and Liu (1992) proposed *Xinanopecten* from the upper Permian of southern China, based on the type species *X. orbicularis* n. sp. In its diagnosis, they especially referred to the ornamentation, the only feature that differentiates it from the genus *Streblochondria* Newell, 1938. According to the diagnosis, this ornament consists of “Radial costae wide and clear, concentric lines very weak in the middle and posterior parts of the shell body; but radial costae narrow and weak, concentric lines clear in the anterior part of the shell body. Costae growing bifurcately on the left and right valves.” To begin with, the poor preservation of the figured specimens could be the cause of the observed differences between the anterior and posterior parts; moreover, if we compare the diagnosis of *Xinanopecten* with the diagnosis given by Newell (1937) for *Streblochondria*, *Xinanopecten* could be easily included in *Streblochondria*, since the variation on ornamentation is used by Newell (1937) and by other authors (Ciriacks, 1963; Newell & Boyd, 1985, 1995) as a diagnostic criterion at specific level; and, finally, the diagnosis of *Xinanopecten* is based on three poorly preserved specimens, which is not enough to characterize the population variation. For all these reasons, we do not include it here.

YOKOYAMAINA Hayami, 1958b, p. 23

Yokoyamaina is considered to be a subgenus of *Integricardium* Rollier, 1912 in 1911–1918 (Hayami, 1975). Hayami (1958b) proposed it from the Lower Jurassic of Japan. Later, Hayami (1975), after reviewing the type species, decided that *Yokoyamaina* fits better as a subgenus of *Integricardium*, and this is followed by most authors (Hallam, 1977; Matsukawa & Nakada, 2003; Kondo & others, 2006). However, some databases and other authors have not discussed the issue, and they considered it to be at the genus level (Vokes, 1980; Schneider, 1995; Sepkoski, 2002; PBDB, 2005).

ZANDAIA Yin & Nie, 1990, p. 106 [255]

Junior synonym of *Praeotapiria* Kurushin in Dagys & Kurushin, 1985 (Z. Fang & others, 2009). Yin and Nie (1990) proposed *Zandaia*, based on *Z. angusta* Yin & Nie, 1990, from the upper Lower Triassic of the Himalayan region (China), but Z. Fang and others (2009) placed it in synonymy with *Praeotapiria*. Kurushin (in Dagys & Kurushin, 1985) proposed *Praeotapiria* as a subgenus of *Otapiria* Marwick, 1935. According to Ando (1988), this new

subgenus is unnecessary, since morphological differences with other species of *Otapiria* are very subtle. *Zandaia* is better placed in synonymy with *Otapiria*.

ZITTELIHALOBIA Polubotko, 1984, p. 42

Polubotko distinguished *Zittelihalobia* from *Halobia*, based on the shape and position of the anterior auricle and ligament (H. J. Campbell, 1994). *Zittelihalobia* was considered to be a junior synonym of *Halobia* by McRoberts (1993), while H. J. Campbell (1994) preferred to keep it as a subgenus of *Halobia*. However, many authors had a different concept of this group and considered it to be a genus (Okuneva, 1987; Kurushin, 1990, 1991; Vu Khuc & Tran Huyen, 1998; Polubotko, Payevskaya, & Repin, 2001; Klets, 2006; Konstantinov, Sobolev, & Yaderkin, 2007). We follow here a conservative approach, considering that this taxon should be maintained at subgenus level at the most.

Other doubtful genera

There are several genera that were included in *Incertae sedis* in Cox and others (1969), and no more information about them was found. These genera are: *Bleta* De Gregorio, 1930b, p. 17; *Carnidia* Bittner, 1901c, p. 6; *Cruciella* Koken, 1913, p. 35; *Ensia* De Gregorio, 1930b, p. 21; *Gerlus* De Gregorio, 1930b, p. 21; *Gingillum* De Gregorio, 1930a, p. 27; *Psammoconcha* Tommasi, 1896, p. 61; *Rebusum* De Gregorio, 1930a, p. 27; and *Taeniodon* Dunker, 1848, p. 179 (see Vokes, 1945, for some information about *Taeniodon*).

Also, there are several genera considered by Sepkoski (2002) in our study interval that we do not consider, because no records in this interval are found: *Cyrtopinna* Mörch, 1853, p. 51; *Atomodesma* von Beyrich, 1865, p. 71; *Cyrtorostra* Branson, 1930, p. 44; *Etheripecten* Waterhouse, 1963, p. 193; *Lopha* Bolten, 1798, p. 168; *Eoschizodus* Cox, 1951, p. 369; *Astartellopsis* Beurlen, 1954, p. 128; *Cowperesia* Mendes, 1952, p. 86; *Mactromya* Agassiz, 1843 in 1840–1845, p. 187; *Terraia* Cox, 1934, p. 269; *Unicardium* d'Orbigny, 1850, p. 218; and *Panopea* Menard, 1807.

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