


New Triassic Aviculopectinoidea (Bivalvia), with notes on the taxonomic concept of the superfamily

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Abstract.—We describe two new genera of Triassic Aviculopectinoidea: *Cristaflabellum* n. gen., which is biconvex and has a strongly plicate shell, and *Globodiscus* n. gen., which is equiconvex and externally smooth or nearly so. *Globodiscus* contains the new species *G. kiliani* n. gen. n. sp. and *G. vinzenti* n. gen. n. sp. In order to make the taxonomic concept of the superfamily Aviculopectinoidea more consistent with that of its sister group Pectinoidea (scallops), we use tribes rather than families or subfamilies for accommodating the new taxa. *Cristaflabellum* is placed in the tribe Antijanirini (previously family Antijaniridae), whereas *Globodiscus* is made the type genus of the new tribe Globodiscini. Both tribes are placed within the family Aviculopectinidae, which is revised to include both equiconvex and inequiconvex taxa. We suggest that tribes are a more appropriate taxonomic rank for many of the previously erected species-poor families and subfamilies of Aviculopectinoidea.

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Introduction

The Triassic was a time of major evolutionary transitions in bivalves, which occurred at least partly in response to increased ecological opportunities after the end-Permian mass extinction (Gould and Calloway, 1980; Hautmann, 2007; Ros et al., 2011; Friesenbichler et al., 2019). Some of the most species-rich extant bivalve taxa have their roots in that time, such as the oysters (Hautmann, 2001; Hautmann et al., 2017) and the scallops (Hautmann, 2010). Scallops in the strict sense (Pectinoidea) are characterized by an alivincular-alate ligament system and a ctenolium (Waller, 1978, 1984; Hautmann, 2004, 2010; Serb, 2016), and first appeared in the fossil record in the Anisian (early Middle Triassic; Hautmann, 2010). In their gross morphology, scallops are similar to the geologically older Aviculopectinoidea, from which they likely evolved (Newell and Boyd, 1995; Hautmann, 2010). Ancestral Aviculopectinoidea co-existed with descent Pectinoidea at least until the end of the Triassic (Newell and Boyd, 1995). This situation provides opportunities for the study of the ecological and evolutionary processes that operate when one clade is displaced by an ecologically similar sister taxon over geologic time, but it is also a challenge for taxonomists. The starting point and main purpose of this study is the description of some new Triassic taxa of Aviculopectinoidea. Thereby, we faced the problem that the current taxonomic concept of this superfamily is rather different from that of its sister taxon Pectinoidea, which is scientifically obviously unsatisfying. We therefore embed the description of

the new taxa in a discussion of the different taxonomic approaches in these two superfamilies and possible routes towards a more coherent classification.

Outline and problems in the taxonomy of scallops and their ancestors

We herein refer to scallops in the strict sense all taxa that were included in the superfamily Pectinoidea by Carter et al. (2011). The synapomorphies of this superfamily are the presence of an alivincular-alate ligament system and a ctenolium (Waller, 1978, 1984; Hautmann, 2004, 2010). The Carter et al. (2011) classification accepts Waller's (2006) hypothesis that the absence of a ctenolium in Spondylidae is due to secondary reduction; the family Spondylidae is therefore included in the Pectinoidea.

Aviculopectinoidea are characterized by pectiniform shells with a deep byssal notch in the right valve and an alivincular-areate ligament. Our concept of the superfamily Aviculopectinoidea is equivalent to the hyporder Aviculopectinoidei Starobogatov, 1992, as used in Carter et al. (2011), excluding Pterinopectinoidea Newell, 1938, which have a duplivincular ligament, and Deltopectininae Dickins, 1957 and Chaenocardidae Miller, 1889, which have a transitional ligament and articulating teeth. Aviculopectinoidea probably gave rise to Pectinoidea through genera such as *Guizhoupecten* Chen, 1962 (Newell and Boyd, 1985) or *Leptochondria* Bittner, 1891 (Hautmann, 2010). The alternative hypothesis that scallops derived from the entoliid *Pernopecten* Winchell, 1865 (Waller,

2006) is less likely, given that the geologically oldest scallops lack all derived character states of entoliids (Hautmann, 2010; Carter et al., 2011).

Whereas there is a clear morphological concept of Pectinoidea and Aviculopectinoidea, the hierarchical arrangement of taxa within these superfamilies is complicated by random iteration of forms and structures (Hertlein, 1969, p. N348; Newell and Boyd, 1995, p. 22). For that reason, Hertlein (1969) arranged scallop genera in informal groups rather than in subfamilies, and this practice was maintained for some time (e.g., Waller, 1991, fig. 8). More recently, however, Pectinidae have been subdivided into several subfamilies, but the composition of these subfamilies differs between authors, and each subfamily still comprises a considerable number of lower-rank taxa (Serb, 2016, tab. 1.1).

In contrast to the integrative concepts of pectinoid families/subfamilies, Aviculopectinoidea have been split into a huge number of families/subfamilies, most of which contain only few genera and species. This approach started with Newell and Boyd (1995), who divided the Aviculopectinoidea into nine families, each containing only few genera. Once established, it proved difficult to include new genera within these narrowly defined families, which resulted in the erection of even more families (e.g., Waterhouse, 2008). The current state of classification is summarized in Carter et al. (2011), who listed 23 families/subfamilies for the Aviculopectinoidea, as understood in this paper (see above).

The effect of these two different approaches is a strong bias of apparent richness at different taxonomic levels. Waller (1991, p. 2) reported ~7000 described fossil and recent species for the Pectinoidea, 80% of which were placed in one of only five genera. Pectinoidea currently contains eleven families and subfamilies (Carter et al., 2011), thus the ratio of the number of (sub) families to the number of described species is roughly 1:640 in this superfamily.

Because a complete survey of all described aviculopectinoid species is not available, we estimated the family to species ratio for Aviculopectinoidea from the number of described species listed in the Paleobiology Database for the families and genera treated in Newell and Boyd (1995). Accordingly, the nine families recognized in that paper contain 18 genera with 322 described species (121 of which have been assigned to *Aviculopecten*), resulting in a family to species ratio of 1:35.

We note that the number of described species is likely much larger than the number of “true” species, but this bias applies to both superfamilies and therefore cancels out if the two ratios are compared. We also note that including the 16 mostly species-poor (sub)families that were added since the Newell and Boyd (1995) study would make the difference in the family to species ratios even more pronounced.

Taking the estimations from above, it becomes clear that there is a pronounced discrepancy between the species richness of Aviculopectinoidea and Pectinoidea at different taxonomic levels. Pectinoidea have ~20 times more (described) species than Aviculopectinoidea, and a (sub)family of Pectinoidea contains on average 18 times as many species as a (sub)family of Aviculopectinoidea. However, Aviculopectinoidea have more than twice as many families/subfamilies as Pectinoidea (23 versus 11). An analysis of subfamily-level diversity would therefore indicate a significant decrease in richness between

ancestral Aviculopectinoidea and descendent Pectinoidea, even though there is actually a huge increase at the species level.

It is a commonplace that all taxa above the species level are arbitrarily defined units and that no strict criteria exist how groups of phylogenetically related species are to be classified at different taxonomic levels (genus, family, order etc.). Usually, however, there is at least some intuitive agreement among specialists about the appropriate taxonomic rank of such groups, usually based on the number of morphological differences between and the taxonomic richness within them. Without such an agreement, it would not make sense to label supraspecific taxa at all. At least in bivalves, the case of Pectinoidea versus Aviculopectinoidea is an extreme exception, especially because these superfamilies are genealogically related and share comparable morphological traits. A revision of these two superfamilies with a coherent taxonomic concept is therefore overdue, but unfortunately not on the horizon.

As a first step to the solution of this dilemma, we suggest lowering the rank of taxon-poor families and subfamilies of Aviculopectinoidea to the level of tribes, and avoiding nested hierarchies where the phylogenetic relationships are not well established. Tribes are increasingly used for taxon-poor groups in the Pectinoidea (e.g., Serb, 2016, tab. 1). Transferring this concept to the Aviculopectinoidea would clearly help to make the taxonomy of these two superfamilies better comparable. We apply this idea in the context of the new taxa introduced below, but we do not propose further revisions of the Aviculopectinoidea because we have not studied a sufficient amount of material from other families within this superfamily, particularly not from the Paleozoic. However, we hope that this discussion will serve as a starting point for a comprehensive revision in the future.

Materials and methods

Geologic setting.—Specimens from the Anisian of North Dobrogea (Romania) were collected by E.G. in a limestone quarry south of the village of Mahmudia (45°03012.41′N, 29°03034.52′E). The fossils were associated with a *Tubiphytes*-microbial buildup within the Caerace Formation, located in the northeastern part of the quarry. Further details on the fossil locality, stratigraphy, and environmental context are given in Friesenbichler et al. (2019).

Material from the Early Triassic of West Timor stems from highly fossiliferous blocks up to a few meters thick that have been interpreted as olistoliths embedded in the Cenozoic Bobonaro Formation (Charlton et al., 2009). However, a more recent interpretation suggests that these blocks have been brought up to the surface by mud volcanoes linked with oil seepage (Tim Charlton, personal communication, 2019; see also Rothpletz, 1891 for a similar, yet forgotten interpretation). Regardless of the question of their origin, the geologic age of the fossil material is precisely known thanks to co-occurring ammonoids, which indicate a Spathian (late Early Triassic) age for the bivalves studied herein.

Repositories and institutional abbreviations.—The specimens from the Anisian of Romania that were examined in this study are deposited in the collections of the Museum of the

Laboratory of Palaeontology in the University of Bucharest (LPB), Romania. The material from the Early Triassic of West Timor is part of the “John Snyder collection” (SNY) housed in the collection of the Paläontologisches Institut und Museum of the University of Zurich (PIMUZ), Switzerland.

Systematic paleontology

Family Aviculopectinidae Meek and Hayden, 1864

2000 Hayasakapectinidae Boyd and Newell, p. 534.

Revised diagnosis.—Shell equiconvex or inequiconvex, auriculate, with deep byssal notch in right valve and byssal sinus in left valve; discs plicate; ligament alivincular-areate; hinge teeth absent.

Remarks.—Valve convexities were regarded as a diagnostic character of this family, but it was debated whether the shell was equi- or inequiconvex. Newell and Boyd (1995) considered Aviculopectinidae as equiconvex, but Fang and Morris (1999) have shown that the type species of *Aviculopecten* M’Coy, 1851 is inequiconvex, having a nearly flat right valve. Boyd and Newell (2000) accepted this finding and revised Aviculopectinidae accordingly. For equiconvex taxa that are otherwise morphologically comparable with Aviculopectinidae, they introduced the new family Hayasakapectinidae Boyd and Newell, 2000. The confusion about valve convexity arose from the coexistence of equiconvex and inequiconvex species in M’Coy’s (1844, 1851) collection and their close morphological resemblance with regard to their left valves (inequiconvex *A. planoradiatus* M’Coy, 1851 versus equiconvex *A. flexuosus* M’Coy, 1844 and *A. americanus* Newell and Boyd, 1995). We assume that the differential valve convexity among otherwise similar species is an indication of morphological plasticity with regard to this character, which therefore does not indicate phylogenetic relationships among genera. We therefore treat Hayasakapectinidae as a synonym of Aviculopectinidae.

Tribe Antijanirini Hautmann in Carter et al., 2011

Remarks.—We lower in rank here the family Antijaniridae Hautmann in Carter et al., 2011 to a tribe. A full diagnosis of this taxon is given in Hautmann in Carter et al. (2011, p. 19). Antijanirini differ from other aviculopectinids among other things in having (sub)orbicular discs with short hinge margins; moreover, the posterior auricle is not alate. Antijanirini is a Triassic taxon that is similar in many morphological aspects to contemporaneously evolving Pectinidae (e.g., orbicular discs, tendency towards a more convex right valve, relatively short hinge margin, well-differentiated anterior auricles); however, it maintains primitive traits, such as an alivincular-areate ligament and the lack of a ctenolium.

Genus *Cristaflabellum* new genus

Type species.—*Pecten volaris* Bittner, 1902.

Other species.—*Pecten interstriatus* Münster, 1841.

Diagnosis.—Shell small to medium sized, equi- or slightly inequiconvex; discs acline, nearly orbicular, strongly plicate; hinge margin shorter than overall length; right valve with short anterior auricle with deep byssal notch lacking a ctenolium; posterior auricle of right valve blunt, rectangular or with very shallow sinus, similar in size to anterior one; auricles of left valve subequal.

Occurrence.—Anisian to Carnian, western Tethys.

Etymology.—Combination of *crista* (Lat.) = comb, and *flabellum* (Lat.) = fan, referring to the fan-like appearance of the ornamentation.

Remarks.—The shell interior and the ligament area of *Cristaflabellum* are not known. However, placement of the new genus in Aviculopectinidae implies that its ligament system was alivincular-areate. This assumption seems justified because the alternative ligament condition (the pectinoid alivincular-alate condition; Hautmann, 2004) evolved in conjunction with a ctenolium (Hautmann, 2010), which is lacking in *Cristaflabellum*.

Bittner (1902, p. 635) suggested that the high convexity of the right valve of his new species, *Pecten volaris*, was a diagnostic difference to the otherwise similar *Pecten interstriatus*, and that this difference was possibly of phylogenetic significance because a more convex right valve might indicate ancestry to Jurassic “*Vola*” (= *Pecten*). We agree that the morphology of *Pecten volaris* is reminiscent of some geologically younger pectinids, and that differences in the convexity of the right valve may serve as a criterion for the separation of the two species *volaris* and *interstriatus*. However, we do not assume that different convexity of the right valves is of generic importance; rather, we interpret the difference in valve convexity between these two otherwise similar species as an indication of morphological plasticity of *Cristaflabellum* with respect to this character.

Allasinaz (1972) assigned *Pecten volaris* and *P. interstriatus* to *Chlamys* Röding in Boltzen, 1798, but our material of *Pecten volaris* demonstrates clearly the absence of a ctenolium (Fig. 1.2), which excludes an assignment to *Chlamys*. The plicate shells and the morphology of the auricles are in accordance with the diagnosis of the Aviculopectinidae, as revised herein. Within the Aviculopectinidae, *Cristaflabellum* shows typical traits of other genera of the tribe Antijanirini (*Antijanira* Bittner, 1901; *Amphijanira* Bittner, 1901; *Oxypteria* Waagen, 1907). *Cristaflabellum* differs from these genera by a high number of plicae that are equal in strength; additionally it differs from *Antijanira* in being equiconvex.

Cristaflabellum volare (Bittner, 1902)

Figure 1

*1902 *Pecten volaris* Bittner, p. 634, pl. 27(10), fig. 32.

1972 *Chlamys* (*Chlamys*) *volaris*; Allasinaz, p. 339, pl. 44, fig. 9; pl. 45, figs 1, 2.

1981 cf. *Chlamys volaris*; Zardini, pl. 18, figs 8a, b.

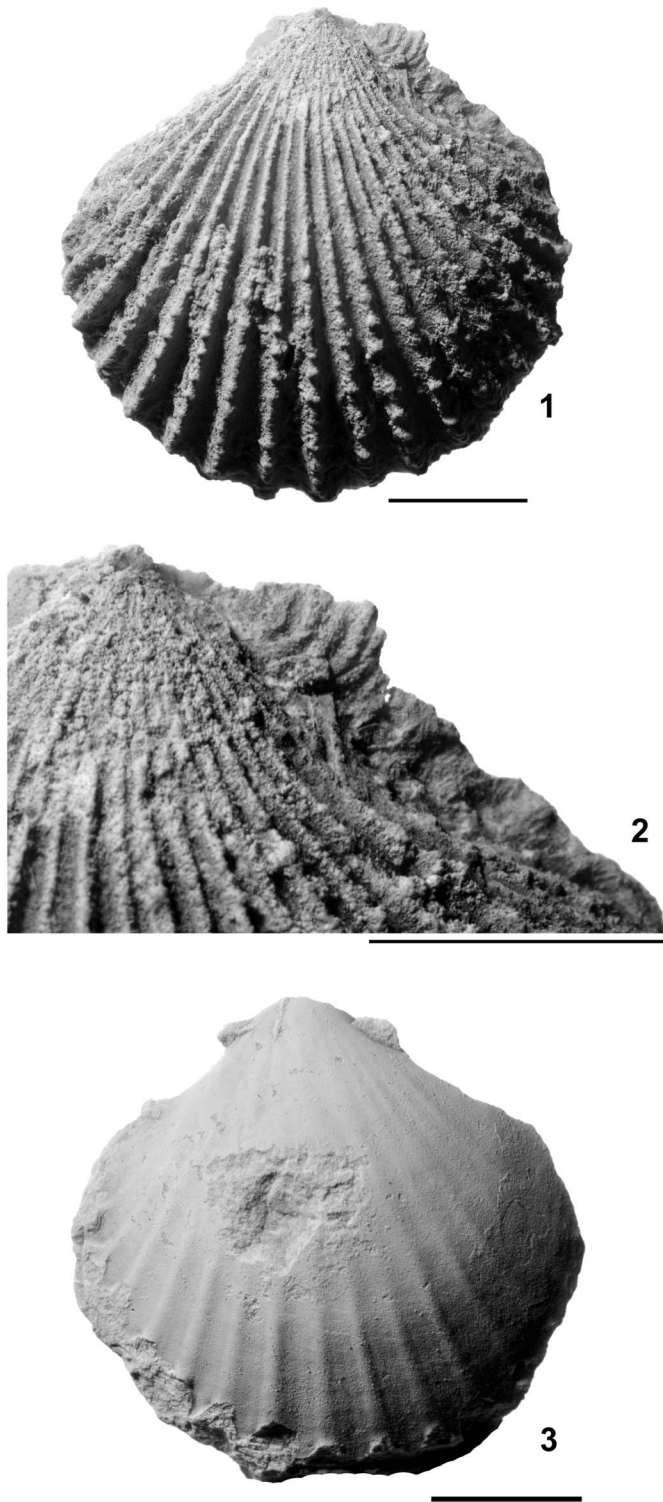


Figure 1. (1–3) *Cristaflabellum volare* (Bittner, 1902). (1, 2) LPB IIIIL 2019, exterior of right valve; (2) detail of (1), showing right anterior auricle and anterior disc margin; note the absence of a ctenolium; (3) LPB IIIIL 2020, internal mold, valve orientation uncertain. Scale bars represent 5 mm.

2019 ‘*Pecten*’ *volaris*; Friesenbichler et al., p. 12, fig. 4H.

Lectotype.—Right valve illustrated in Bittner (1902, pl. 27, fig. 32), designated by Allasinaz (1972, p. 339).

Description.—See Friesenbichler et al. (2019). We add here that this species is probably equiconvex, based on our material and the figures in Allasinaz (1972, pl. 44, figs. 1, 2). We refigure (Fig. 1) the superbly preserved right valve (erroneously indicated as a left valve in Friesenbichler et al., 2019) and an internal mold from the Anisian of Dobrogea (Romania).

Remarks.—*Cristaflabellum volaris* differs from the otherwise similar *C. interstriatus* by having a more convex right valve (Bittner, 1902, p. 635).

Tribe Globodiscini new tribe

Type genus.—*Globodiscus* n. gen.

Diagnosis.—Shell equiconvex or nearly so; discs orbicular to slightly procoscent; ligament alivincular-areate; crura absent.

Right valve.—Umbo centrally placed, orthogyrate; anterior auricle well differentiated, large, anteriorly elongated, dorsally not projecting above hinge line; byssal notch deep; posterior auricle blunt and small or ill defined; ornamentation lacking or with fine, regularly spaced commarginal riblets.

Left valve.—Umbo centrally placed, orthogyrate; anterior auricle with shallow sinus; posterior auricle blunt and ill defined; shell exterior smooth or with weak, regularly spaced commarginal riblets.

Remarks.—This new taxon exemplifies the problems of classification within a clade that is characterized by the prevalence of plesiomorphic traits and iterative evolution. Globodiscini n. tribe has an equiconvex shell with weak commarginal ornamentation and an alivincular-areate ligament, lacks hinge teeth or crura, and has an obtuse posterior extremity in both valves. It thus differs from Aviculopectinidae, which are plicate and have rectangular to acuminate posterior auricles, from Heteropectinidae, which are costate, have a flat right valve and an acuminate posterior auricle, and from Hunanopectinidae, which are inequiconvex and have crura. Therefore, the Globodiscini n. tribe cannot be accommodated within either of these families. However, none of its traits is unique within Aviculopectinoidea.

Genus *Globodiscus* new genus

Type species.—*Globodiscus kiliani* n. sp.

Other species.—*Globodiscus vinzenti* n. sp.

Diagnosis.—As for the tribe.

Occurrence.—Early to Middle Triassic, Tethys.

Etymology.—Combination of globus (Lat.) = sphere and discus (Lat.) = disc, referring to the spherical shell with two virtually circular discs.

Remarks.—See remarks on the tribe Globodiscini n. tribe.

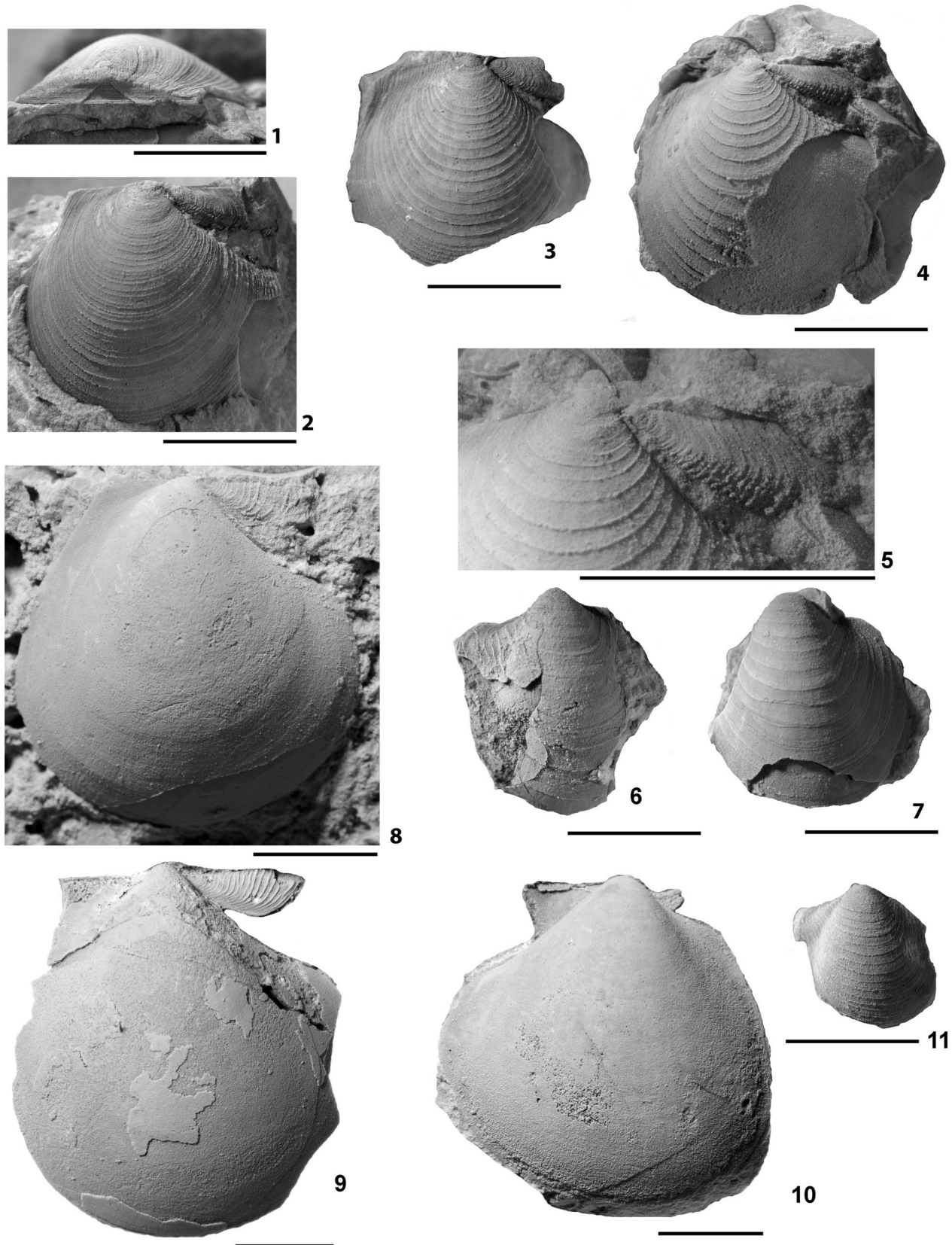


Figure 2. (1–7, 11) *Globodiscus vinzenti* n. gen. n. sp. (1, 2) PIMUZ 37585, holotype, right valve from SNY 14A: (1) ligament area, (2) shell exterior; (3) PIMUZ 37586, right valve from SNY 11A; (4, 5) PIMUZ 37587, right valve from SNY 9A: (4) shell exterior, (5) details of anterior auricle; (6) PIMUZ 37588, left valve from SNY 13B; (7) PIMUZ 37589, left valve from SNY 11A; (11) PIMUZ 37590, left valve (locality unknown). (8–10) *Globodiscus kiliani* n. gen. n. sp. (8) LPB IIIIL2023, right valve; (9) LPB IIIIL 2021, holotype, right valve; (10) LPB IIIIL 2022, left valve. Scale bars represent 5 mm.

Globodiscus kiliani Hautmann, new species
Figure 2.8–2.10

2019 Aviculopectinoidea, gen. et sp. nov.; Friesenbichler et al., p. 13, figs. 4E–G.

Holotype.—LPBIII 2021, original of Friesenbichler et al., 2019, fig. 4E; right valve from the Anisian of Dobrogea, Romania, refigured in Figure 2.9.

Diagnosis.—Right anterior auricle without carina; greatest length of anterior auricle coincides with dorsal margin; discs externally smooth.

Occurrence.—Middle Triassic, Romania.

Description.—Shell medium-sized, biconvex; discs higher than long, slightly prorescent, externally smooth; umbones orthogyrate; posterior auricles small and blunt; anterior auricle of right valve elongated, dorsally straight, ventrally curved to form a deep byssal notch towards the disc, externally covered with weak commarginal ribs (Fig. 2.8, 2.9); anterior auricle of left valve with faint byssal sinus (Fig. 2.10); internal structures not observed.

Etymology.—Named for my oldest son, Kilian.

Materials.—Two right valves and one left valve.

Remarks.—The only comparable species is the new species described in the following.

Globodiscus vinzenti Hautmann, new species
Figure 2.1–2.7, 2.11

Holotype.—PIMUZ 37585 (Fig. 2.1, 2.2) from SNY 14A.

Diagnosis.—Right anterior auricle flexed in dorso-ventral cross section producing an external carina that marks the line of maximum length; incremental lines becoming stronger below carina; anterior margin of auricle angulated, distal end below dorsal margin; ornamentation with faint commarginal riblets.

Occurrence.—Spathian (Early Triassic), Timor.

Description.—Shell small (length of largest specimens ~15 mm); equiconvex; hinge without teeth or crura; ligament alivincular-areate (Fig. 2.1).

Right valve.—Disc orbicular; umbo orthogyrate, scarcely projecting above hinge margin; anterior auricle elongated, distally extending up to anterior limit of disc, with medial carina that defines the maximum length that is reached below the dorsal margin, incremental lines increasing in strength below carina (Fig. 2.5); posterior hinge margin not well differentiated from disc; ornamentation consisting of regularly spaced commarginal riblets (~20 for an individual of 10 mm length).

Left valve.—Anterior auricle separated from disc by shallow depression (Fig. 2.11); other characters as in the opposite valve.

Etymology.—Named for my second son, Vinzent.

Materials.—Three right and five left valves from the Spathian (Early Triassic) of Timor.

Remarks.—*Globodiscus vinzenti* n. gen. n. sp. differs from *G. kiliani* n. gen. n. sp. by the morphology of its anterior auricle, the presence of commarginal riblets on the discs, and in being nearly circular in outline (rather than being slightly higher than long as in *G. kiliani* n. gen. n. sp.).

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References

- Allasinaz, A., 1972, Revisione dei Pettinidi Triassici: Rivista Italiana di Paleontologia e Stratigrafia, v. 78, p. 189–428.
- Bittner, A., 1891, Triaspetrefakten von Balia in Kleinasien: Jahrbuch der k. k. Geologischen Reichsanstalt, v. 41, p. 97–116.
- Bittner, A., 1901, Lamellibranchiaten aus der Trias des Bakonyer Waldes: Resultate der wissenschaftlichen Erforschung des Balatonsees, Anhang: Palaeontologie der Umgebung des Balatonsees II, v. 3, p. 1–107.
- Bittner, A., 1902, Brachiopoden und Lamellibranchiaten aus der Trias von Bosnien, Dalmatien und Venetien: Jahrbuch der k. k. Geologischen Reichsanstalt, v. 52, p. 495–646.
- Bolten, J.F., 1798, Museum Boltenianum sive Catalogus Cimeliorum e Tribus Regnis Naturae quae olim Collegerat Joa. Fried. Bolten. Pars Secunda. Continens Conchylia sive Testacea Univalvia, Bivalvia, & Multivalvia: Hamburg, Johan Christi Trappli, 199 p.
- Boyd, W.D., and Newell, N.D., 2000, The importance of recently reported specimens of the Late Paleozoic bivalve *Aviculopecten planoradiatus* McCoy, 1851: Acta Palaeontologica Sinica, v. 39, p. 533–534.
- Carter, J.G., Altaba, C.R., Anderson, L.C., Araujo, R., Biakov, A.S., et al., 2011, A synoptical classification of the Bivalvia (Mollusca): Paleontological Contributions, University of Kansas, v. 4, p. 1–47. <https://doi.org/10.17161/PC.1808.8287>
- Charlton, T.R., Barber, A.J., McGowan, A.J., Nicoll, R.S., Roniewicz, E., Cook, S.E., Barkham, S.T., and Bird, P.R., 2009, The Triassic of Timor: lithostratigraphy, chronostratigraphy and palaeogeography: Journal of Asian Earth Sciences, v. 36, p. 341–363.
- Chen, C.C., 1962, Lamellibranchiata from the Upper Permian of Ziyun, Guizhou (Kueichow): Acta Palaeontologica Sinica, v. 10, p. 199–205 [in Chinese].
- Dickins, J.M., 1957, Lower Permian pelecypods and gastropods from the Carnarvon Basin, Western Australia: Commonwealth of Australia, Bureau of Mineral Resources, Geology and Geophysics, Bulletin, v. 41, p. 1–75.
- Fang, Z.J., and Morris, N.J., 1999, On the genera *Aviculopecten* and *Heteropecten*: Acta Palaeontologica Sinica, v. 38, p. 147–154.
- Friesenbichler, E., Hautmann, M., Grädinaru, E., and Bucher, H., 2019, A highly diverse bivalve fauna from a Bithynian (Anisian, Middle Triassic) *Tubiphytes*-microbial buildup in North Dobrogea (Romania): Papers in Palaeontology. doi: 10.1002/spp2.1286
- Gould, S.J., and Calloway, C.B., 1980, Clams and brachiopods—ships that pass in the night: Paleobiology, v. 6, p. 383–396.
- Hautmann, M., 2001, Taxonomy and phylogeny of cementing Triassic bivalves (Families Propondylidae, Plicatulidae, Dimyidae and Ostreidae): Palaeontology, v. 44, p. 339–373.
- Hautmann, M., 2004, Early Mesozoic evolution of alivincular bivalve ligaments and its implications for the timing of the “Mesozoic marine revolution”: Lethaia, v. 37, p. 165–172.
- Hautmann, M., 2007, Steuerungsfaktoren globaler Biodiversifizierungsmuster am Beispiel frühmesozoischer Muscheln: Beringeria, v. 37, p. 61–74.
- Hautmann, M., 2010, The first scallop: Paläontologische Zeitschrift, v. 84, p. 317–322.
- Hautmann, M., Ware, D., and Bucher, H., 2017, Geologically oldest oysters were epizoans on Early Triassic ammonoids: Journal of Molluscan Studies, v. 83, p. 253–260.

- Hertlein, L.G., 1969, Family Pectinidae Rafinesque, 1815, *in* Moore, R.C., ed., Treatise on Invertebrate Paleontology, Part N, Mollusca 6, Volume 1: Geological Society of America and University of Kansas Press, Boulder CO and Lawrence, KS, p. N348–N373.
- M'Coy, F., 1844, A Synopsis of the Characters of the Carboniferous Limestone Fossils of Ireland: Dublin, Dublin University Press, 207 p.
- M'Coy, F., 1851, Descriptions of some new Mountain Limestone fossils: The Annals and Magazine of Natural History (series 2), v. 7, p. 167–175.
- Meek, F.B., and Hayden, F.V., 1864, Palaeontology of the Upper Missouri: Smithsonian Contributions to Knowledge, v. 14, p. 1–135.
- Miller, S.A., 1889, North American Geology and Palaeontology for the use of Amateurs, Students and Scientists: Cincinnati, Western Methodist Book Concern, 664 p.
- Münster, G.G. zu, 1841, Beiträge zur Petrefacten-Kunde. IV. Beschreibung und Abbildung der in den Kalkmergelschichten von St. Cassian gefundenen Versteinerungen: Bayreuth, Buchner'sche Buchhandlung, 152 p.
- Newell, N.D., 1938, Late Paleozoic Pelecypods: Pectinacea: State Geological Survey of Kansas Publications, v. 10, p. 1–123 [for 1937].
- Newell, N.D., and Boyd, D.W., 1985, Permian scallops of the pectinacean family Streblochondriidae: American Museum Novitates, v. 2831, p. 1–13.
- Newell, N.D., and Boyd, D.W., 1995, Pectinoid bivalves of the Permian–Triassic crisis: American Museum of Natural History Bulletin, v. 227, p. 1–95.
- Ros, S., De Renzi, M., Damborenea, S.E., and Márquez-Aliaga, A., 2011, Coping between crises: Early Triassic–Early Jurassic bivalve diversity dynamics: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 311, p. 184–199.
- Rothpletz, A., 1891, The Permian, Triassic, and Jurassic Formations in the East-Indian Archipelago (Timor and Rotti): The American Naturalist, v. 25, p. 959–962.
- Serb, J.M., 2016, Reconciling morphological and molecular approaches in developing a phylogeny for the Pectinidae (Mollusca: Bivalvia): Developments in Aquaculture and Fisheries Science, v. 40, p. 1–29.
- Starobogatov, Y.I., 1992, Morphological basis for phylogeny and classification of Bivalvia: Ruthenica, v. 2, p. 1–25.
- Waagen, L., 1907, Die Lamellibranchiaten der Pachycardientuffe der Seiser Alm nebst vergleichend paläontologischen und phylogenetischen Studien: Abhandlungen der k. k. geologischen Reichsanstalt, v. 18, p. 21–180.
- Waller, T.R., 1978, Morphology, morphoclines and a new classification of the Pteriomorpha (Mollusca: Bivalvia): Philosophical Transactions of the Royal Society of London, Ser. B, v. 284, p. 345–365.
- Waller, T.R., 1984, The ctenolium of scallop shells: functional morphology and evolution of a key family-level character in the Pectinacea (Mollusca: Bivalvia): Malacologia, v. 25, p. 203–219.
- Waller, T.R., 1991, Evolutionary relationships among commercial scallops (Mollusca: Bivalvia: Pectinidae), *in* Shumway, S.E., ed., Scallops: Biology, Ecology and Aquaculture: Elsevier, New York, p. 1–73.
- Waller, T.R., 2006, Phylogeny of families in the Pectinoidea (Mollusca: Bivalvia): importance of the fossil record: Zoological Journal of the Linnean Society, v. 148, p. 313–342.
- Waterhouse, J.B., 2008, Aspects of the evolutionary record for fossils of the bivalve subclass Pteriomorpha Beurlen: Earthwise, v. 8, p. 1–219. [published by the author]
- Winchell, A., 1865, Descriptions of new species of fossils from the Marshall Group, and its supposed equivalent in other states: Proceedings of the Academy of Natural Sciences of Philadelphia, v. 1865, p. 109–133.
- Zardini, R., 1981, Fossili Cassiani (Trias Medio-Superiore). Atlante dei Bivalvi della Formazione di S. Cassiano raccolti nella regione Dolomitica attorno a Cortino d'Ampezzo: Edizione Ghedina, Cortina d'Ampezzo, p. 1–14.

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