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Unusual brachiopod fauna from the Middle Triassic algal meadows of Mt. Svilaja (Outer Dinarides, Croatia)

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Abstract.—Ladinian deposits at Mt. Svilaja in Dalmatia (Outer Dinarides, Croatia) yielded an abundant brachiopod fauna of low diversity interpreted as a parautochthonous assemblage representing an ecosystem of dasycladacean submarine meadow. The fauna consists of four named species and one left in open nomenclature. The most common is the spiriferinide *Flabellocyrtia flabellulum* Chorowicz and Termier, 1975 (Spiriferinida) accounting for more than 70% of the material. The athyridide *Cassianospira humboldtii* (von Klipstein, 1845) is the only species known from elsewhere (Anisian of Southern Alps). The new species of Spiriferinida *Thecocyrtella dagysii* Halamski, Bitner, Kaim, Kolar-Jurkovšek, and Jurkovšek n. sp. differs from other representatives of the genus in having a deep ventral sulcus. *Albasphe albertimagni* Halamski, Bitner, Kaim, Kolar-Jurkovšek, and Jurkovšek n. gen. n. sp. is a new brachiopod that possesses a dorsal septum with an intra-septal cavity and dorsal submarginal ridges, both features in common with Aalenian *Zellania* Moore, 1855 from which it differs in lack of the ventral septum and of ventral submarginal ridges. They are interpreted as members of a sparsely recorded paedomorphic evolutionary line of terebratulides with secondarily lost loop, described formally herein as Gwyniidina Halamski and Bitner n. subordo and subdivided into newly emended Dispheniidae Grant, 1988 (Dispheniinae Grant, 1988 with the only genus *Disphenia* and Albasphinae Halamski and Bitner n. subfam. with *Albasphe* and *Zellania*) and Gwyniidae MacKinnon, 2006 (including Recent *Gwynia* and *Simpliciforma*). In contrast to previous interpretations, the trocholophe lophophore of *Gwynia* is interpreted herein as secondarily simplified.

Introduction

Despite severe losses during the great extinction event at the Permian–Triassic boundary, brachiopods were still a major component of the faunas of the latter period (Kummel, 1979). The recovery of brachiopods began in the mid- to late Induan (early Early Triassic) and pre-extinction diversity levels are reported to have been attained in the Anisian (early Middle Triassic; Chen et al., 2005, 2010), much later than for ammonoids (late Induan; Zakharov and Popov, 2014). Early Triassic brachiopod faunas are globally poor (19 genera all over the world after Vörös, 2010; according to Clapham et al., 2013, 45 genera are present already in the Induan but even this number is quite low if compared with Permian faunas, cf. *infra*), while Middle Triassic ones are distinctly richer (84 Anisian and 91 Ladinian genera; Vörös, 2010); the acme of Triassic brachiopod diversity was in the Norian (133 genera). However, unlike Anisian (Sun et al., 2009) and Late Triassic brachiopods, Ladinian (late Middle Triassic) brachiopod faunas are poorly known (Sun, 1980, p. 1181; Dagys, 1993, p. 82). The complete absence of Ladinian brachiopods in the Caucasus sections in which both Anisian and Carnian representatives of this phylum are known and with neither major lithological shifts nor changes in abundance of other faunal groups led Ruban (2006a, b) to postulate that an “enigmatic Ladinian crisis” took place during the aforementioned stage. Ladinian brachiopod faunas in South China are also distinctly less diverse than Anisian ones but it is uncertain whether this is due to global or local causes (Shen et al., 2006).

The aims of the present study are: (1) to document a hitherto poorly known Ladinian brachiopod fauna from Mt. Svilaja (Dinarides, Croatia), including the description of one new genus and two new species, as well as the redescription of an inadequately described genus and species, all three unknown outside the studied locality; (2) to show that a sparsely recorded evolutionary line, a representative of which is present in the studied material, may be traced from the Permian to Recent times, including reinterpretation of systematic position of one Permian and one Recent brachiopod genus as well as a formal description of a new suborder of the Terebratulida.

History of research

Ladinian brachiopods from the Svilaja range were first mentioned by von Kerner (1908, p. 283) who reported two unpublished identifications by Schloenbach, ‘*Retzia* (?) *quadricostata*’ and ‘*Spiriferina hirsuta*’, and two (also unpublished) by Bittner, ‘*Spirigera* cf. *trigonella*’ and ‘*Rhynchonella vivida* var. *dalmatina*'. This material, however, came from other outcrops in the same mountain range. Silicified faunas from the section at Svilaja dealt with herein were first described by Chorowicz and Termier (1975); however, only a small fraction of the total diversity (e.g., a single brachiopod species compared to five described herein, a single anthozoan compared to nine present in the fauna, and two gastropod taxa compared to several dozen known in the locality; J. Stolarski and A. Kaim, unpublished data) was revealed. Silicified brachiopods from Svilaja were also the subject of a preliminary communication by Jaecks et al. (2003); however, his interpretation of the brachiopod described here as *Thecocyrtella dagysii* n. sp. as a post-Paleozoic productide is rejected by the present authors.

Geologic setting

In terms of present geography, the study area (Fig. 1.1) is situated in the Dinarides, a mountain belt belonging to the southern branch of the Alpine chain (Ager, 1980), occupying the northeastern coast of the Adriatic Sea. More precisely, Svilaja is an isolated mountain range in central Dalmatia, situated ca. 30 km north from the city of Split; it is separated from the main chain of the Dinarides by the valley of Cetina with the Peruča Lake (Peručko jezero). The Mt. Svilaja section is located along the Mijići–Zelovo Sutinsko road at approximately 43°42'51" N 16°32'8" E (between the towns of Muć and Sinj; Fig. 1.2).

In terms of geology, the Dinarides represent the collision chain between the northeastern edge of the Apulia (= Adria) microplate and Europe (Tari, 2002). The south-western part of this mountain range, called Outer (or External) Dinarides, represents a complex set of carbonate platforms referred to collectively as the Adriatic-Dinaridic Carbonate Platform (Vlahović et al., 2002). In the Middle Triassic this area was an epicontinental sea situated at the western edge of the Tethys (Adriatic continental margin; Fig. 1.4) subject to rifting processes without, however, any apparition of oceanic crust until the Norian (middle Late Triassic) (Pamić et al., 1998; but see Sudar et al., 2013). The considered area belongs to a geological unit called the Dalmatian-Herzegovinan Composite Terrane (Karamata, 2006) and in the Middle Triassic was situated in the equatorial zone (15° N paleolatitude according to Dercourt et al., 1993 and Stampfli et al., 2002; 5° N according to Szulc, 2000, and Golonka et al., 2006; 10° S paleolatitude according to Karamata, 2006 and references therein; Fig. 1.3). Details of paleogeographic reconstructions of the area considered are still debated (e.g., Channell and Kozur, 1997 and references therein; compare also slight differences in paleogeographic maps in Fig. 1.3 and 1.4).

The Middle Triassic of the studied section at Mt. Svilaja starts with Anisian dolomitic Otarnik Breccia. Late Anisian to early Ladinian vitrocrystallic tuffs ('pietra verde') are conformably overlain by cherty limestones and dolomites (the horizon with the fauna studied) with abundant calcareous algae [the most common species being *Diplopora annulata* Schafhäutl and *Teutloporella herculea* (Stoppani) Pia (Grgasović et al., 2007)], foraminifers, radiolarians, serpulids, gastropods, bivalves, ammonoids, brachiopods, crinoids, and conodonts. The ammonoid assemblage is composed of both leiostraca (*Proarcestes* sp.) and trachyostraca: *Alkaites dinaricus* Balini, Jurkovšek and Kolar-Jurkovšek, 2006, *Detoniceras svilajanus* Balini, Jurkovšek and Kolar-Jurkovšek, 2006, and *Argolites trinodosus* Balini, Jurkovšek and Kolar-Jurkovšek, 2006 (Balini et al., 2006). Based on conodont fauna this interval is attributed to the Ladinian *hungaricus* Assemblage Zone (Jelaska et al., 2003). This interval is followed by well bedded pelagic limestone with sporadic marl laminae which are attributed to *mungoensis* (Ladinian) and *murchianus* (upper Ladinian to ?lower Carnian) conodont zones. A paleokarstified emersion surface can be observed at the top of these limestones (Bucković and Martinuš, 2010).

Material and methods

Preservation and taphonomy.—The described fauna is silicified and has been extracted from limestone through etching in acetic acid. The faunal content of the rock is quite rich; brachiopods and gastropods are the most abundant, corals and algae are abundant, echinoderms are frequent, whereas bivalves and ammonoids are rare. The present sample (1791 specimens; see Table 1) has been obtained after dissolving ca. 100 kg of rock; a minor part thereof consists of specimens naturally weathered from the rock.

The silicification process does not affect all parts of the shell equally. It was observed that shells of *Flabellocyrtia flabellulum* and of *Thecocyrtella dagysii* sometimes possess a deltidium and sometimes not (compare Figs 4.12, 4.24 and 4.14, 4.17, 4.25–4.29, 4.34 as well as 6.1, 6.2, 6.5, 6.7 and 6.3, 6.13, 6.18, 6.32, 6.34–6.37; specimens lacking the deltidium are more frequent). This is best interpreted as resulting from selective silicification; a very similar situation (pseudodeltidium lacking or more seldom present due to selective silicification) was described by Pope (1982, p. 4; see also Holdaway and Clayton, 1982). Hollow spaces appearing inside the shell are also an artifact explained by the silicification either proceeding from the external surfaces towards the internal layers and often remaining incomplete (for an example of a list of artifacts caused by silicification, see Caruthers and Stanley, 2008, p. 155) or occurring preferentially along certain layers of the shell (Crowley, 1988; Carson, 1991, p. 462). In some cases, concentric rings (beekite) typical of silicification obscure the original surface of the valves (Fig. 4.31). Although most of original microstructure gets indeed lost during the silicification process (Brenchley and Harper, 1998, p. 78), by no means should it be understood that all microstructural information is lost during diagenesis. In several cases, punctae are preserved (*Thecocyrtella*: Fig. 4.4, *Flabellocyrtia*: Fig. 4.3, *Albasphe*: Fig. 4.2) and sometimes the same may be said even about the axial cavity of the spines of the spiralium in *Flabellocyrtia*. Overall, however, the silicification in the material studied may be described as intermediate in character between two extreme types referred to in a description of silicified Carboniferous brachiopods by Sun and Baliński (2008, p. 491), namely preserving very fine details including some information on microstructure on one hand and obliteration of original patterns up to the apparition of a secondary "spongy" texture on another hand.

The percentage of disarticulated valves in the material amounts to about 33% (see Table 1 for details). Referring to a

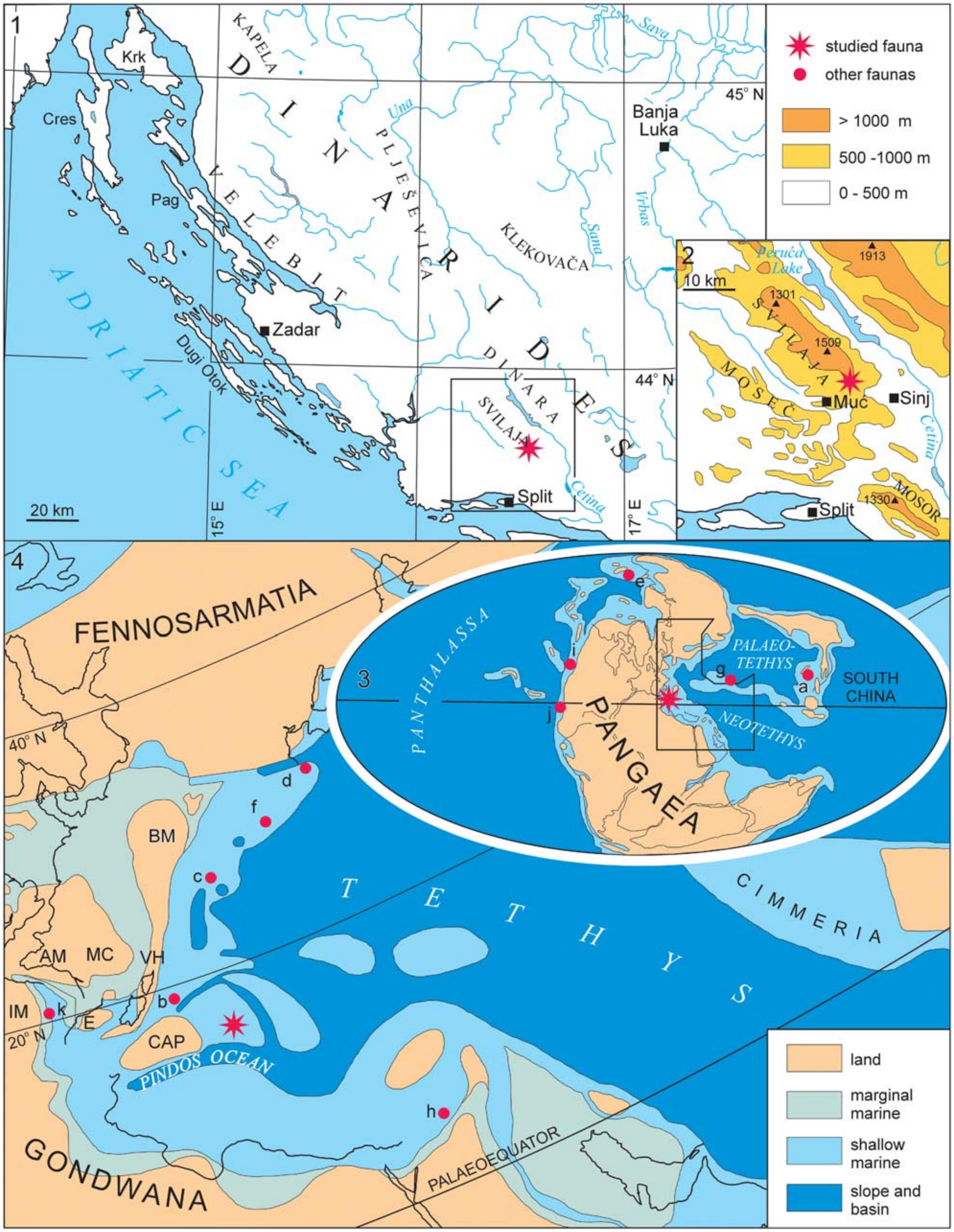


Figure 1. Geological setting of the studied fauna. (**1**) General map showing the position of the Svilaja range within the Dinarides. The rectangle shows the area enlarged in (**2**). (**2**) Hypsometric map showing the position of the studied section in the Svilaja range. Mountain ranges in full capitals; Towns in Roman typeface; rivers and lakes italicized. (**3**) Global paleogeography in the Middle Triassic. The polygon shows the area enlarged in (**4**). (**4**) Paleogeographical reconstruction of the western edge of the Tethys in the Late Anisian (supposed not much different to the situation in the Ladinian). Simplified and redrawn after Jawecka et al. (1987), Dercourt et al. (1993). AM = Armorican Massif; BM = Bohemian Massif, CAP = Central Apennine Plateau, E = Ebro Massif, IM = Iberian Massif, MC = Massif Central, VH = Vindelician High. Minuscules a–k denote approximate localizations of Ladinian brachiopod faunas all over the world; see text for explanation.

Table 1. Numerical characteristics of the material studied.

		Ventral Valves		Dorsal Valves		
Taxon	Articulated Shells		Isolated Valves		Total	Total Corrected
Cassianospira humboldtii	27 79.4%	4 11.8%	20.6%	3 8.8%	34 1.9%	31 2.0%
Thecocyrtella dagysii	133 54.1%	101 41.0%	44.9%	12 4.9%	246 13.7%	234 14.9%
Flabellocyrtia flabellulum	872 66.8%	192 14.7%	33.2%	241 18.5%	1305 72.9%	1113 71.0%
Albasphe albertimagni	161 79.3%	17 8.4%	20.7%	25 12.3%	203 11.3%	186 11.9%
Terebratulidina? indet.	3 100%				3 0.1%	3 0.2%
Total	1196 66.8%	314 17.5%	33.2%	281 15.7%	1791	1567 1791

"Total corrected" stands for the sum of articulated shells and of those of either isolated valves which are more numerous; the percentages referred to the "total" (next to last column) are then these in the studied material, whereas those referred to the "total corrected" are an approximation (minimum number of individuals) of the original biocoenosis.

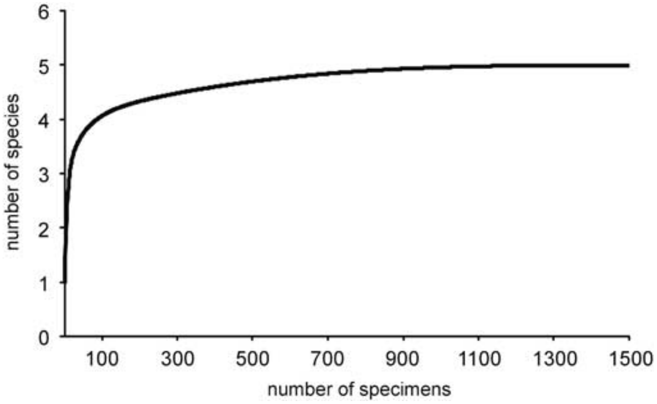


Figure 2. Rarefaction curve for the brachiopod sample from Svilaja.

paleoecological analysis of Middle Triassic brachiopod assemblages with different percentages of disarticulated valves (Pálfy, 1991), the value for Svilaja assemblage corresponds approximately to "reasonable 'background' disarticulation under average circumstances," i.e., without much postmortem transport. However, the ratios of ventral versus dorsal valves are somewhat different from the value 1:1 expected if there is no postmortem bias (Chen et al., 2010 and references therein). This is especially the case for the spiriferinide *Thecocyrtella dagysii* in which ventral valves are over eight times more numerous than dorsal ones; this, however, is best explained as expressing their different preservational qualities (Alexander, 1986, 1990)—the ventral valve is massive, whereas the dorsal one is fragile—or perhaps some kind of differential sorting. For the other species the value of the discussed ratio is between 1.26 and 1.46; this seems to indicate a moderate bias. The assemblage is thus interpreted as parautochthonous (perhaps even autochthonous).

The sample is of low diversity (Shannon index = 0.88) and relatively medium dominance (Simpson D index = 0.54). Rarefaction analysis (Fig. 2) suggests that the present collection is fully saturated and additional sampling is rather unlikely to result in a discovery of additional species. Very small differences between percentages of species referred to the total material and corrected values (minimum number of individuals; Zuschin et al., 2003 and references therein) allow to consider that the biocoenosis structure is reflected more or less accurately in the material.

Methods.—Internal features of described brachiopods have been investigated by X-ray microtomography (Zeiss XRadia MicroXCT-200) at the NanoFun laboratory at the Institute of Paleobiology; this method was applied to single specimens of *Flabellocyrtia flabellulum*, *Thecocyrtella dagysii*, and *Albasphe albertimagni*. Results concerning these three species were not the same. In *F. flabellulum* and *T. dagysii* the optical densities of silicified shell and silicified matrix fragments are quite different (on CT images shell is grey and rock is white), wherefore sections are easy to interpret, with the obvious reservation that absence of an anatomic structure in the selectively silicified material (see above) does not disprove its presence *in vivo*. On the contrary, in the analyzed specimen of *A. albertimagni* the optical densities of various parts of the shell are not so different, hence there was no clear limit between the rock matrix and the shell (on CT scans, shell showed a continuous intergrading of grey to white half-tones and in some cases it was impossible to decide if a white spot corresponds to the brachiopod or to the matrix).

The self-evident advantages of the X-ray tomography method, above all, its non-destructive character and the possibility of obtaining sections along several series of planes from a single specimen (Figs 5, 7, and 10), have been widely discussed in a number of contributions (Hamada et al., 1991; Błażejowski et al., 2011; Zapalski and Dohnalik, 2013; and references therein). A disadvantage of this method is, however, that it produces only images based on difference in density between shell and the surrounding rock (or the air in case of our etched material). The classic method of obtaining sections from acetate peels allows visualising the internal structure of the shell with growth lines and crystallite orientation, which is not possible using X-ray microtomography. For example, Kozłowski (1929) who studied Devonian and Triassic representatives of Cyrtinidina (*Cyrtina* and *Hirsutella*) by means of serial sections and acetate peels was able to show that in both the median septum was composed of three distinct lamellae. This character could not be checked in *Flabellocyrtia* (Bittnerulidae, Cyrtinoidea). Nonetheless, in the case of our material the X-ray microtomography is the only way to investigate the internal structures as it is impossible to make acetate peels from silicified material.

Due to the small size of the studied brachiopods, photographs were taken mostly under a scanning electron microscope. Selected specimens were mounted on stubs, coated with platinum, and examined using a Philips XL-20 microscope at the Institute of Paleobiology in Warsaw. Larger brachiopods (Figs 3.12–3.16, 4.30–4.34, 6.4–6.7, 6.9–6.18, 8.22–8.31) were photographed in visible light after coating with ammonium chloride, although some shell regions were refractory to coating, probably due to their extraction from the rock by acid etching. Medium-sized specimens were photographed under Nikon SMZ 1500 binocular equipped with Nikon D5200 digital camera; some photographs were assembled from a series of up to five frames using the Helicon Focus programme. The largest ones were photographed with a Nikon D-1X digital camera with a Nikkor micro 55/2.8 lens.

The main collection is housed at the Jurkovšek Palaeontological Collection that has been registered with the Slovenian National History Museum in Ljubljana and abbreviated BJ. Representative collections of species studied is also kept at the Institute of Paleobiology of the Polish Academy of Sciences in Warsaw (collection number ZPAL Bp 72).

Systematic paleontology

Phylum Brachiopoda Duméril, 1805

Remarks.—The classification framework and the authorship of the names follow the revised *Treatise on Invertebrate Paleontology*, *Part H* (Williams et al. 2000), except for the superfamily Zeillerioidea, the authorship of which is to be attributed to Schuchert (*in* Schuchert and LeVene, 1929, p. 24) who introduced the subfamily Zeilleriinae by Latinising the vernacular (invalid) name “Zeilleriidés” used by Rollier (1915). Allan (1940), credited with the authorship in the *Treatise*, was in fact only the first to use the name at family level. The first use at superfamily level was by Kyansep (1961) (personal communication, M. Manceñido, 2014).

Synonymy lists are established with short comments by means of special signs following the system described by Halamski (2009, p. 46–47; further references therein). For species published in monographs issued during a several years’ period, the full citation follows the model proposed by Halamski and Baliński (2013, p. 265).

Subphylum Rhynchonelliformea Williams et al., 1996
Class Rhynchonellata Williams et al., 1996
Order Athyridida Boucot, Johnson and Staton, 1964
Suborder Retziidina Boucot, Johnson and Staton, 1964
Superfamily Retzioidea Waagen, 1883
Family Neoretziidae Dagys, 1972
Genus *Cassianospira* Dagys, 1972

Type species.—*Retzia loczyi* Bittner, 1900; Carnian.

Remarks.—This genus has been reported from the Upper Triassic (Carnian and Norian) up to now (Dagys, 1974, p. 288; Alvarez and Rong, 2002, p. 1591). This is the first report from the Middle Triassic (Ladinian).

Cassianospira humboldtii (von Klipstein, 1845 *in* 1843–45 [‘1843’])
Figure 3.1–3.16

*1845 Spirifer *Humboldtii* von Klipstein, p. 233; pl. 15, fig. 17.

1853 *Waldheimia? Humboldtii*; Gray, p. 85.

1889 *Retzia Humboldtii Klipst. sp.*; Bittner, p. 168.

1890 Retzia Humboldtii Klipst. spec.; Bittner, p. 88; pl. 2, fig. 33.

Type material.—Articulated shell from the Carnian of San Cassian (southern Alps) figured by Klipstein (1845, pl. 15, fig. 17) NHMUK PI OR 30635, holotype by monotypy.

Description.—Shell teardrop-shaped, wider than long when young, about as wide as long in larger individuals due to the growth of the ventral umbo, markedly to very strongly ventribiconvex, up to 4.1 mm in width; maximal width about the midlength of the dorsal valve or slightly anteriorly. Hinge line and anterior commissure straight. Ventral valve high; interarea apsacline, nearly flat near the hinge line, markedly incurved in umbonal region; a rather narrow delthyrium closed by a symphytium bordered by low rounded rims (Fig. 3.11); foramen submesothyrid. Dorsal valve weakly convex.

Ornamentation of stout, high, rounded plicae, beginning at umbo, separated by narrower furrows; up to five pairs on the ventral valve, a median one and up to four pairs of lateral ones on the dorsal valve. Growth lines not observed.

Dorsal interior: cardinal flange thick, supported by a high and thin (Fig. 3.10) or moderately thick (Fig. 3.9) median septum, the length of the septum equaling approximately two-thirds of that of the valve; spiralium not preserved. Ventral interior (Fig. 3.7, 3.8) poorly preserved.

Material.—Twenty-seven mostly subcomplete articulated shells, four ventral, and three dorsal valves.

Dimensions.—ZPAL Bp 72/4/1: length 2.7 mm; width 2.5 mm; thickness 1.8 mm.

Remarks.—The publication date of *Cassianospira humboldtii* requires a comment. The *Beiträge zur geologischen Kenntniss der östlichen Alpen* by A. v. Klipstein are dated 1843 at the title page (in the reference list of the *Treatise on Invertebrate Paleontology*, *Part H*, *Revised*, confounded with *Beiträge zur*

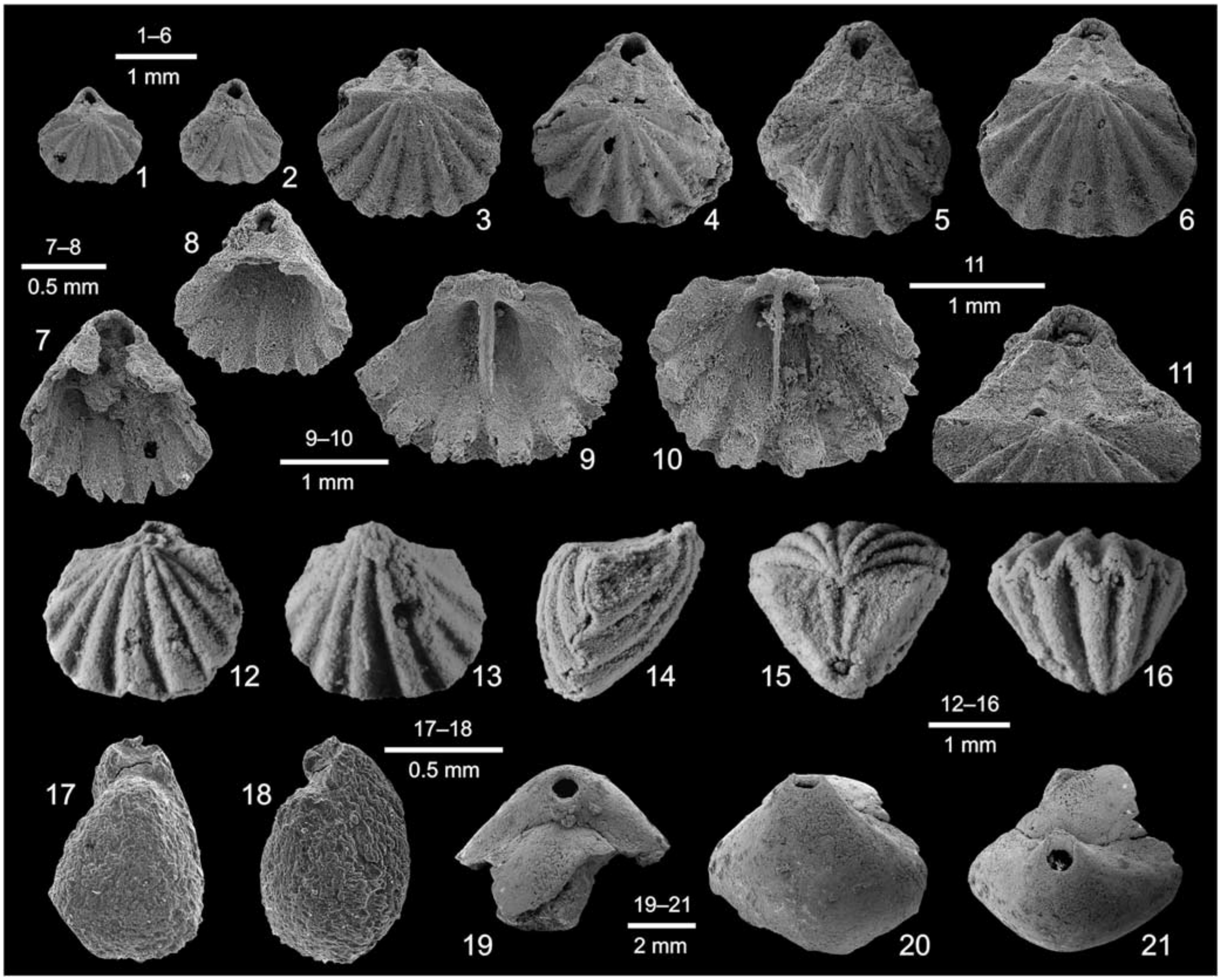


Figure 3. *Cassianospira humboldtii* (von Klipstein, 1845). (**1–6, 11**) Six articulated shells BJ 2281, 2292, 3057, 2293, 2382, ZPAL Bp 72/4/1 (**6, 11**) in dorsal views (**1–6**) and an enlargement of the interarea (**11**). (**7, 8**) Ventral valves BJ 2383, 2439. (**9, 10**) Dorsal valves BJ 2440, 3054. (**12–16**) Articulated shell ZPAL Bp 72/4/1 in dorsal, ventral, lateral, posterior, and anterior views. (**17–21**) Terebratulidina? gen. et sp. indet. (**17, 18**) juvenile articulated shell BJ 3056 in dorsal and lateral views. (**19–21**) Fragment of an adult shell BJ 3055 in dorsal, ventral, and posterior views. (**1–11, 17–21**) SEM micrographs; (**12–16**) images taken in visible light.

geologischen und topographischen Kenntnis der östlichen Alpen by the same author printed in three parts between 1871 and 1883). However, "*Spirifer humboldtii*" (our *Cassianospira humboldtii*; not to be confounded with *Spirifer humboldtii* d'Orbigny, 1842, which comes from the Silurian of Bolivia; Schuchert, 1897, p. 287; Bassler, 1915, p. 892) is dated 1844 by Gray (1853, p. 85), whereas Bittner (1889, p. 159) and Sherborne (1927, p. 3053) give the date 1845. As often in the nineteenth century, the monograph by Klipstein was apparently printed during several years; the date given by the *Index Animalium* (Sherborne, 1927) is accepted here.

Cassianospira humboldtii is known from the Carnian of the Alps. It differs from *Cassianospira loczyi* (Bittner, 1900) in having the median plica on the dorsal valve of the same height as the admedian pair of plicae (lower than the lateral ones in *C. loczyi*). *Cassianospira klipsteinii* (Bittner, 1889) is another similar species differing in higher interarea (Bittner 1890, pl. 2, figs 30–31; Zardini, 1988, pl. 10, fig. 13).

Order Spiriferidina Ivanova, 1972
Suborder Cyrtinidina Carter and Johnson *in* Carter et al., 1994
Superfamily Suessioidea Waagen, 1883
Family Bittnerulidae Schuchert *in* Schuchert and LeVene, 1929
Subfamily Bittnerulinae Schuchert *in* Schuchert and LeVene, 1929
Genus *Thecocyrtella* Bittner, 1892

Type species.—*Cyrtotheca ampezzana* Bittner, 1890; Cortina d'Ampezzo, Alps; Carnian.

Remarks.—Carter (2006, p. 1889) included absence of fold and sulcus among diagnostic characters of *Thecocyrtella*. *T. dagysii* is similar to *T. ampezzana* in internal characters but possesses a ventral sulcus; we consider that this is not a character justifying separation at genus level but rather a reason for the emendation of the diagnosis; the discussed fragment should run “sulcus absent or present”.

Thecocyrtella dagysii new species
Figures 4.1, 4–34; 5

Type material.—Holotype, BJ 3083.0; illustrated paratypes, BJ 3081, 3084–3101; ZPAL Bp 72/3/1; type locality, Svilaja, Dinarides; cherty limestones and dolomites, Ladinian, Middle Triassic.

Diagnosis.—*Thecocyrtella* with a deep ventral sulcus.

Dimensions.—Holotype BJ 3083: length 2.7 mm; width 2.1 mm; thickness 2.2 mm.

Description.—Shell very strongly ventribiconvex. Dorsal valve medially indented, nearly flat, hinge line straight, postero-lateral extremities auriculate; maximal width at hinge line; a strong median rib present in some specimens (Fig. 4.28–4.30), sometimes situated in the middle of a faint sulcus (Fig. 4.30). Ventral valve pyramidal, beak incurved, with a narrow, deep V-shaped median groove originating at umbo; lateral slopes mostly smooth, seldom with faint plication. Interarea very high, apsacline, concave; delthyrium narrow (0.11–0.16 of the area width), with subparallel edges, covered by a wider (0.28–0.37 of the area width) deltidium (Fig. 4.9, 4.13, 4.19; rarely preserved, *cf. supra*). Shell substance punctate (Fig. 4.4).

Dorsal interior: crura subparallel (Fig. 4.7) or divergent (Fig. 4.5, 4.10), then coalescing to form a jugum (Figs 4.11; 5.1, section at 0.918 mm; 5.2, section at 1.557 mm); spiralium continuing quite far towards the ventral beak but less than one entire whorl is preserved (Fig. 5.3). Ventral interior: median septum thin, moderately high, not very long; spondylium (Fig. 5.1, sections at 2.150 and 2.296 mm) present in umbonal region (0.4 mm long in a specimen 2.4 mm long); teeth small.

Etymology.—In honor of Algirdas Dagys (30.08.1932–7.01.2000), Lithuanian paleontologist, in recognition of his contribution to the study of Triassic brachiopods (name Latinised as *Dagysius*, then genitive *Dagysii*).

Material.—One hundred and thirty-three articulated shells, 101 ventral valves, and 12 dorsal valves (paratypes).

Remarks.—The described material is included in *Thecocyrtella* Bittner, 1892 on account on shape, minute size, (near) lack of radial ornamentation, and possession of a ventral septum and a spondylium. Dagys (1974, p. 149) showed that Bittner (1890) misinterpreted an incomplete beak of the type species *T. ampezzana* (Bittner, 1890) as representing an attachment scar (a similar condition is shown in Fig. 4.19); as a matter of fact, there is no such structure in the discussed genus. For the terminological question of deltidium vs. symphytium, cf. *infra*, remarks on *Flabellocyrtia flabellulum*.

T. dagysii n. sp. differs from *T. ampezzana* and from *T. orientalis* Ivanova *in* Dagys, 1965 [this species was sometimes cited as “*T. orientalis* Ivanova, 1960” but the original publication (Ivanova, 1960, p. 279, text-fig. 407, pl. 64: 9) was without either description or diagnosis; the first to provide a diagnosis was Dagys (1965, p. 107), so the name must be considered as validly introduced only in the latter publication] in having a deep ventral sulcus. *Bittnerula zitteli* (Bittner, 1890) (syn. *Spirifer buchii* von Klipstein, 1843; Dagys, 1974 considered *Bittnerula* as a synonym of *Thecocyrtella*) has a weaker ventral sulcus and a much higher interarea. *Thecocyrtelloidea tubulosa* Yang and Xu, 1966 from the Anisian of Guizhou has no spondylium and its spiralium has at least five whorls (Yang and Xu, 1966).

The interpretation of brachiopods described herein under *Thecocyrtella dagysii* n. sp. as post-Paleozoic productides was proposed in a preliminary communication by Jaecks et al. (2003) without knowledge of the internal structures, which are crucial for correct identification. Moreover, Jaecks et al. (2003) misinterpreted some poorly preserved unidentified epizoans in the umbonal region of some specimens as alleged productide spines.

Subfamily Hirsutellinae Xu and Liu, 1983
Genus *Flabellocyrtia* Chorowicz and Termier, 1975

Type species.—*Flabellocyrtia flabellulum* Chorowicz and Termier, 1975; Svilaja; Ladinian.

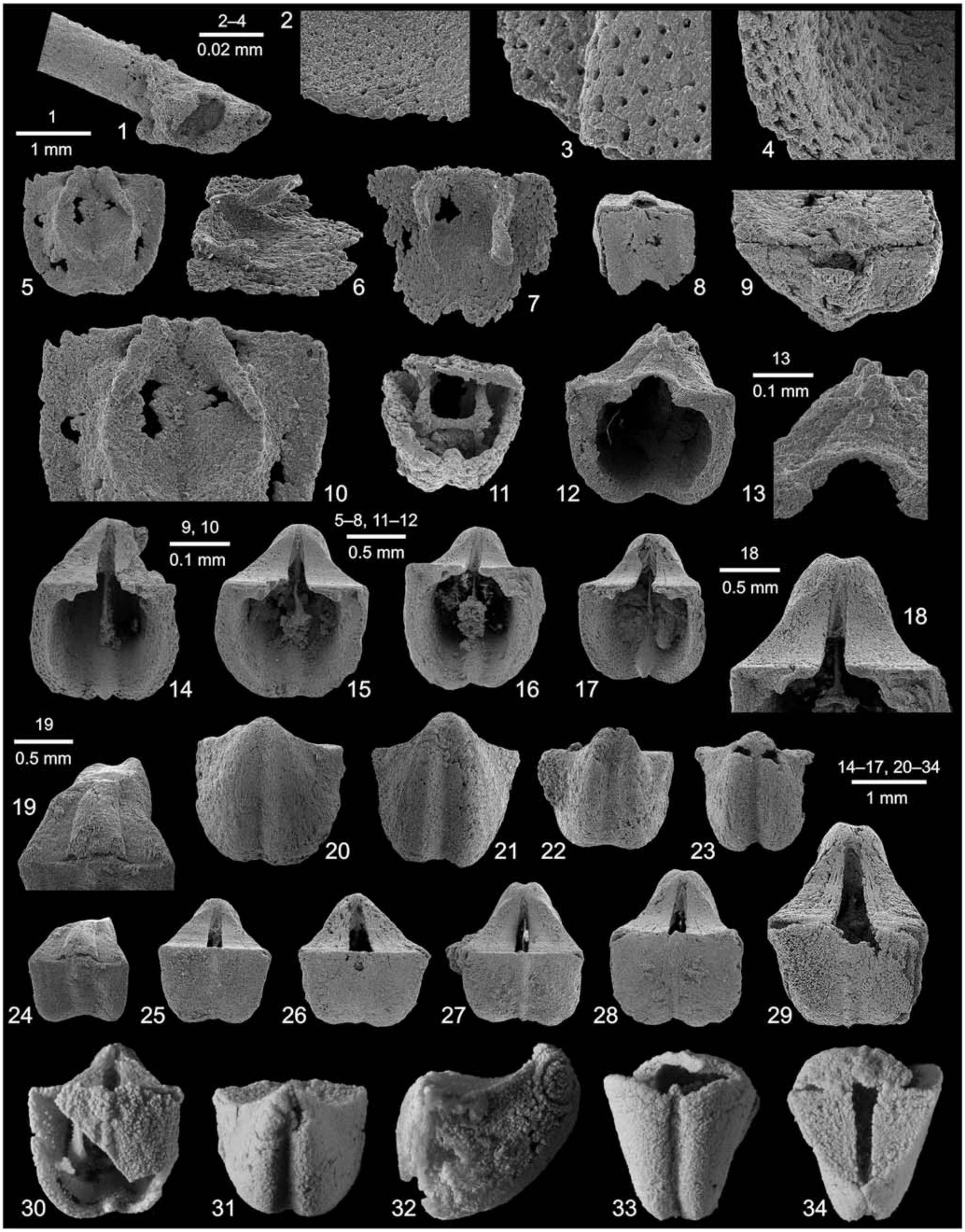
Flabellocyrtia flabellulum Chorowicz and Termier, 1975
Figures 4.3, 6, 7

*1975 *Flabellocyrtia flabellulum* Chorowicz and Termier, p. 235–237; text-fig. 4; pl. 20, figs 5–13.

Type material.—Specimens figured by Chorowicz and Termier (1975: text-fig. 4, pl. 20, figs 5–13), syntypes; repository unknown [not traced in UPMC, MNHN, FLS, and UCBL].

Description.—Shell up to 8.6 mm in width, wider than long, very strongly ventribiconvex. Anterior commissure weakly unisulcate. Dorsal valve weakly convex with a wide, triangular median sulcus to more seldom weakly concave; maximal width at hinge line or about the posterior third; hinge line straight; interarea sublinear. Ventral valve: interarea approximately catacline, high, incurved; delthyrium occupying about one sixth to one fifth of the interarea width, closed by a seldom preserved deltidium (Fig. 6.1, 6.2, 6.5, 6.7; incomplete in the umbonal region in all studied specimens). Ornamentation of strong, acute plicae separated by V-shaped furrows about as wide as the plicae; a median plica and 3(–4) lateral ones per flank on the dorsal valve; ventrally up to five pairs of plicae. Shell substance punctate (Fig. 4.3).

Dorsal interior: External plications reflected on the internal side on the valve. Cardinal process (ctenophoridium) multilobate (Fig. 6.25, 6.26), situated on a wide platform (Fig. 6.24–6.27) extending through the median third of the valve width, giving rise laterally to crura (Fig. 6.8) and narrow, posteriorly directed hinge plates (Fig. 6.25). Crura stout, wide, anteriorly directed (Figs 6.8; 7.2, section at 3.578 mm), diverging at 40°–70°, long, extending nearly to the antero-lateral margin. Radial traces of narrow mantle canals present in marginal region (Fig.6.28–6.30). Spiralium of about four whorls (Fig. 6.33; 7.1,


1
1 mm
1
2–4
0.02 mm
2
3
4
5
6
7
8
9
10
11
12
13
0.1 mm
13
9, 10
0.1 mm
5–8, 11–12
0.5 mm
18
0.5 mm
14
15
16
17
18
19
0.5 mm
19
20
21
22
23
14–17, 20–34
1 mm
24
25
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34

section at 3.377 mm); hollow spines can sometimes be observed on external sides of the first whorl (Fig. 6.31, 6.36; 7.2, section at 3.226 mm, enlargement; 7.3, section at 0.924 mm, enlargement).

Ventral interior: Teeth flat, relatively wide (Fig. 6.34, 6.35). Median septum posteriorly with a tichorhinum (Fig. 7.2, section at 0.465 mm), the canal thereof without a septum; anteriorly septum high, blade-like (Fig. 6.32, 6.37).

Material.—Eight hundred seventy-two articulated shells, 192 ventral valves, and 241 dorsal valves; collection numbers BJ 3058–3072, 3082, 3105–3106; ZPAL Bp 72/1.

Dimensions (in mm).—ZPAL Bp 72/1/3: length (l) 6.8, length of the dorsal valve (d) 5.3, width (w) 6.3, thickness (t) 5.7; ZPAL Bp 72/1/4: l 8.5, d 5.7, w 6.5, t 5.4; ZPAL Bp 72/1/1: l 6.0, d 4.8, w 7.3, t 5.4; ZPAL Bp 72/1/4: l 8.4, d 6.4, w 8.0, t 6.9.

Remarks.—The dorsal cardinalia were interpreted by Chorowicz and Termier (1975, p. 236) as consisting of a large cardinal process occupying one third of the valve length linked to short crura. As a matter of fact, the cardinal process (ctenophoridium, similarly as in *Hirsutella*, the type genus of the subfamily to which *Flabellocyrtia* belongs) is of usual size but situated on a wide platform and the crura are long (see description above). The structures closing the delthyrium of *Flabellocyrtia* and *Thecocyrtella* are called deltidium by Carter (2006); in the material studied no median line of junction could be observed, wherefore, following Williams and Brunton (1996), the term 'symphytium' would theoretically be more appropriate; the present authors decided to follow the general usage reflecting the fact that such a junction line is seldom preserved in the fossil material (R. Gourvennec, pers. comm., March 2014).

Order Terebratulida Waagen, 1883
Suborder Gwyniidina Halamski and Bitner, new

Diagnosis.—Terebratulida with secondarily lost loop; lophophore supported by submarginal ridges in some representatives.

Remarks.—Representatives of the order Terebratulida are characterized by the lophophore being supported by a loop (Cloud, 1942; Williams and Wright, 1961; Cooper, 1983; Boucot and Wilson, 1994; MacKinnon and Lee, 2006), originating either alone (suborder Terebratulidina) or in conjunction with the septal pillar (suborder Terebratellidina) (MacKinnon and Lee, 2006). The identification of an early-branching (Permian to Recent) lineage of terebratulides lacking a loop, even if such a simplification be not a strictly unique case among over six hundred genera belonging to this order (cf. *infra*, Gwynioidea, remarks), justifies the erection of a new suborder. Such a proposal is supported by results of molecular studies that place Recent *Gwynia* in an isolated position, namely as a basal branch of the terebratellidines (Cohen, 2007), although with relatively weak support (personal communication, B. Cohen, 2013).

Superfamily Gwynioidea MacKinnon, 2006

Diagnosis.—Shell minute, punctate, rounded to medially indented in outline. Loop absent. Submarginal ridges supporting the lophophore present in some representatives. Cardinal process weakly developed or absent. Dental plates absent. Septa with internal cavities, either ventral or dorsal, present in some representatives.

Families included.—Dispheniidae Grant, 1988; Gwyniidae MacKinnon, 2006 (*nomen translatum ex* Gwynioidea MacKinnon, 2006; herein).

Remarks.—The superfamily Gwynioidea MacKinnon, 2006 was introduced (MacKinnon 2006) for two related (Logan et al., 1997) genera of minute brachiopods characterized by presence of submarginal ridges supporting the lophophore, Recent *Gwynia* (Logan et al., 1997; Simon and Willems, 1999; Álvarez and Emig, 2005) and Jurassic *Zellania* (Baker, 1970). The latter is closely related to Triassic *Albasphe* n. gen. described herein, which in its turn appears to be an evolutionary descendant of Permian *Disphenia*. Bitner et al. (2013) described the Recent genus *Simpliciforma* in which the diagnostic submarginal ridges have been lost secondarily. The absence of submarginal ridges in the specimen described by Lüter (2008) as *Gwynia macrodentata* allows to transfer this species to the genus *Simpliciforma* (see also comments in Bitner et al., 2013, p. 287). The links between each pair of stratigraphically successive genera are clear but the entire evolutionary line defined in this way is much less easy to characterize. The superfamily Gwynioidea is redefined herein to include two families, Paleozoic to Mesozoic Dispheniidae Grant, 1988 and Pleistocene to Recent Gwyniidae MacKinnon, 2006 (for nomenclatural issue related to such a treatment, see Appendix). Baker (1970) convincingly showed that probable affinities of *Zellania* were with primitive terebratulides belonging to the superfamily Stringocephaloidea King, 1850; nonetheless, he refrained from formally proposing such a conclusion on account of the stratigraphic gap between Devonian Stringocephaloidea and Middle Jurassic *Zellania*. Discovery of Permian and Triassic predecessors of the latter genus eliminates this objection and the superfamily Gwynioidea can be interpreted as descending from a representative of the suborder Terebratulidina Waagen, 1883 (*incerti subordinis* in MacKinnon, 2006). The comparison of all

Figure 4. (**1, 4–34**) *Thecocyrtella dagysii* Halamski, Bitner, Kaim, Kolar-Jurkovšek, and Jurkovšek n. sp. (**1**) A poorly preserved shell BJ 3081 attached to a fragment of a thallus of a (dasyclad?) alga. (**4**) Punctae (seen from inside) of the shell ZPAL Bp 72/3/1. (**5, 10**) Dorsal interior BJ 3084, general view and enlargement of the cardinalia. (**6, 7**) Dorsal interior BJ 3085 in oblique and ventral views. (**8, 9**) Juvenile articulated shell BJ 3098, dorsal view and enlargement of the interarea. (**11**) Dorsal interior BJ 3104 showing crura. (**12, 13**) Ventral valve BJ 3087, dorsal view and enlargement of the deltidium. (**14–18**) Four ventral valves ZPAL Bp 72/3/1, BJ 3095, 3094, and 3093 in dorsal views and an enlargement of the interarea. (**19, 24**) Articulated shell BJ 3086 in postero-dorsal view and enlargement of the interarea. (**20–23**) Four ventral valves 3089, 3092, 3102, and 3103 in ventral views. (**25–29**) Five articulated shells BJ 3096, 3101, 3099, 3100, and 3097 in postero-dorsal views. (**30–34**) Holotype BJ 3083 in dorsal, ventral, lateral, anterior, and posterior views. (**2**) *Albasphe albertimagni* Halamski, Bitner, Kaim, Kolar-Jurkovšek, and Jurkovšek n. gen. n. sp.; punctae (seen from inside) of the shell ZPAL Bp 72/2/6. (**3**) *Flabellocyrtia flabellulum* Chorowicz and Termier, 1975; punctae (seen from inside) of the shell BJ 3082. (**1–29**) SEM micrographs; (**30–34**) images taken in visible light.

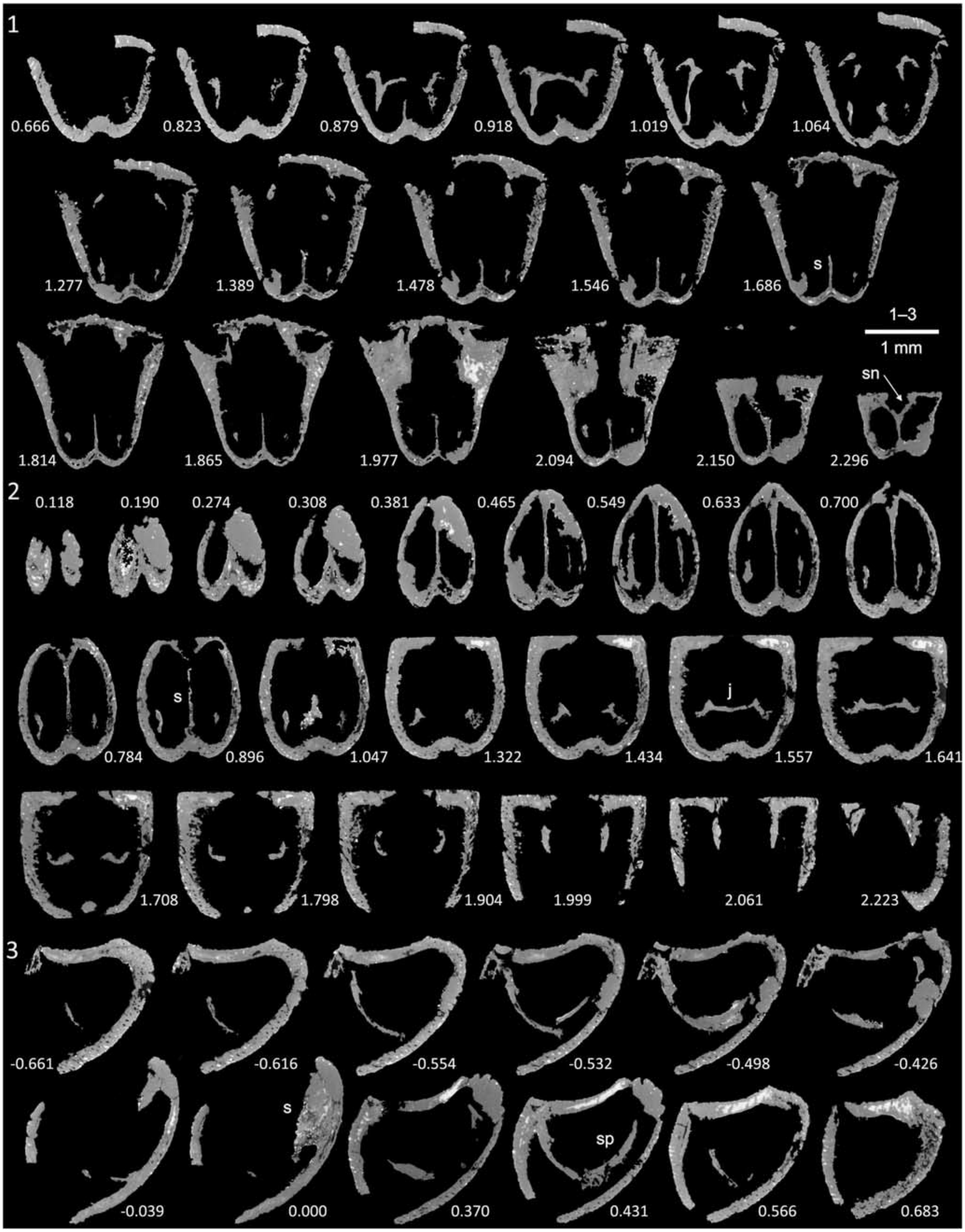


Figure 5. *Thecocyrtella dagysii* Halamski, Bitner, Kaim, Kolar-Jurkovšek, and Jurkovšek n. sp.: X-ray microtomograph sections of the holotype BJ 3083. (**1**) Sections parallel to the delthyrium, distances (in mm) measured from front; (**2**) sections parallel to the commissural plane, distances (in mm) measured from the tip of the ventral umbo; (**3**) sections parallel to the symmetry plane, distances (in mm) measured either side from the latter. J = jugum, s = septum, sn = spondylium, sp = spiralium.

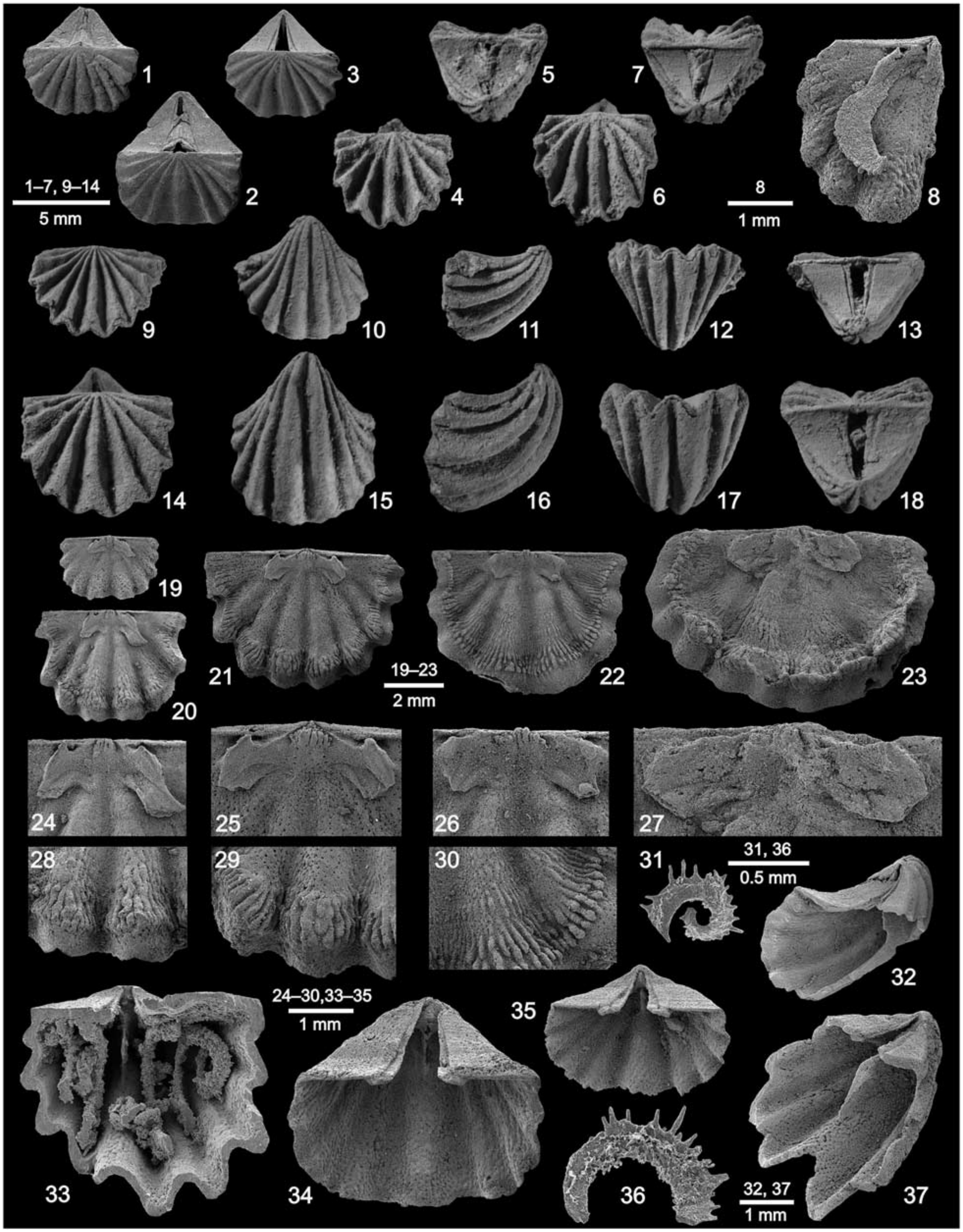


Figure 6. *Flabellocyrtia flabellulum* Chorowicz and Termier, 1975: external and internal morphology of shells. (**1–3**) articulated shells BJ 3105, 3070, and 3072 showing different preservation of the deltidium (preserved in **1**, **2**; not preserved in **3**). (**4–7**) Articulated shells ZPAL Bp 72/1/3 and 72/1/4 in dorsal and posterior views. (**8**) Fragmentary dorsal valve ZPAL Bp 72/1/5 with an almost entire crus. (**9–18**) Articulated shells ZPAL Bp 72/1/1 and 72/1/2 in dorsal, ventral, lateral, anterior, and posterior views. (**19–30**) Dorsal interiors BJ 3062 (**19**), 3061 (**20, 24, 28**), 3060 (**21, 25, 29**), 3059 (**22, 26, 30**), and 3058 (**23, 27**), general views (**19–23**), enlargements of cardinalia (**24–27**), and of marginal regions (**28–30**). (**31, 36**) Fragments of spiralium BJ 3068 and 3069 showing spines. (**32, 37**) Fragmentary ventral valves BJ 3063 and 3064 (apical regions preserved) in antero-lateral view showing different shapes of the median septum. (**33**) Ventral valve BJ 3065 showing spiralium. (**34–35**) Ventral valves BJ 3066 and 3067 in postero-dorsal views. (**1–3, 8, 19–37**) SEM micrographs; (**4–7, 9–18**) images taken in visible light.

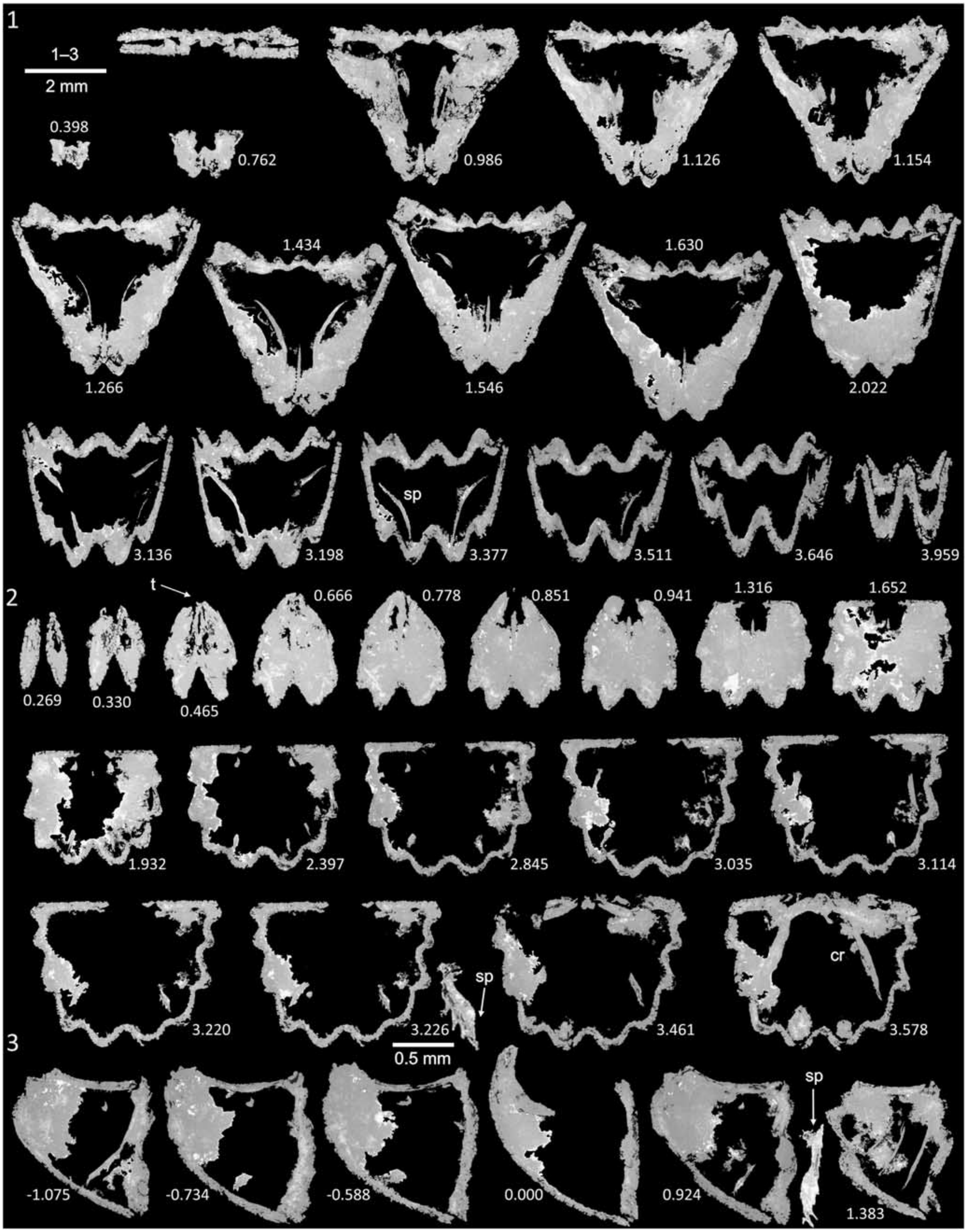


Figure 7. *Flabellocyrtia flabellulum* Chorowicz and Termier, 1975: X-ray microtomograph sections of the articulated shell BJ 3106. (**1**) Sections parallel to the delthyrium, distances (in mm) measured from the tip of the ventral umbo; (**2**) sections parallel to the commissural plane, distances as above; (**3**) sections parallel to the symmetry plane, distances (in mm) measured either side from the latter. S = septum, sp = spiralium, t = tichorhinum.

Table 2. Comparison of Permian to Recent representatives of Gwyniidina new suborder

Taxon			Character		
Family	Genus	Stratigraphic Distribution	Submarginal Ridges	Ventral Septum	Dorsal Septum
Gwyniidae	*Simpliciforma*	Recent	absent	none or simple	none
	Gwynia	Pleistocene to Recent	present	none	none
Dispheniidae	*Zellania*	Jurassic	present	simple	with an intra-septal cavity
	Albasphe	Triassic	present	none	with an intra-septal cavity
	Disphenia	Permian	absent	with an intra-septal cavity	simple, massive

five genera belonging to the superfamily Gwynioidea is given in Table 2. A new formal classification of the superfamily Gwynioidea is given in the Appendix.

Grant (1988) suggested (without giving any reason) that Dispheniidae might be related to the superfamily Zeillerioidea Schuchert *in* Schuchert & LeVene, 1929. Such a classification was probably inspired by shape similarity (indented anterior margin) between *Disphenia* and well-known Liassic representatives of *Zeilleria* like *Z. cor* (Delance, 1974). However, zeillerioids are quite different, having a well-developed loop and a mesothyrid or permesothyrid foramen (Baker, 2006). Generally speaking, shape alone is a poor taxonomic character in brachiopods. For example, Halamski and Segit (2006) disproved an evolutionary scheme among Paleozoic terebratulides based on external shapes on account of micro-ornamentation. Such a criterion is unfortunately not utilisable in the lineage studied: *Disphenia* and *Albasphe* are known solely from silicified specimens, so the information is missing; *Zellania*, *Gwynia*, and *Simpliciforma* are entirely devoid of micro-ornamentation. Weakly developed cardinal process in *Disphenia myiodes* may also have been an argument for a relationship with the Zeillerioidea in which a cardinal process is most often absent (Baker, 2006). However, among the Terebratulida cardinal process presence or absence does not seem to be such an important taxonomic criterion as, for example, in Rhynchonellida. Among nine species of the genus *Xenobrochus* (Dyscolioidea, Terebratulidina) most possess a cardinal process but three species have lost it secondarily (Bitner, 2011). Grant's (1988) suggestion is therefore rejected herein and the family Dispheniidae is accommodated within the Gwynioidea (see diagnosis above).

In a preliminary communication Savage (2005) suggested that *Disphenia* and *Cardiarina* Cooper, 1956 (the latter originally described as a possible rhynchonellide) may be related and both included into the Terebratulida; however, in the definitive treatment of the same matter (Savage, 2006) *Cardiarina* has been considered as *incertae sedis* and *Disphenia* was omitted. *Cardiarina* seems unrelated to *Disphenia* given lack of septa in both valves and different microstructure (impunctate in the former, punctate in the latter); it has been interpreted as a possible representative of the Lambdarinidae by Baliński and Sun (2008).

The Recent species *Simplicithyris kurilensis* Zezina, 1976, lacking both crura and loop, has strong dental plates (Zezina, 1976); this character distinguishes it from all representatives of the Gwynioidea (cf. supra, diagnosis). The systematic position of another Recent terebratulide species lacking a loop, *Oceanothyris juveniformis* Bitner and Zezina *in* Bitner et al., 2013, requires further investigation. Despite the similarity of name reflecting external homeomorphy, the Paleocene genus *Gwyniella* Johansen, 1987 is unrelated to *Gwynia*; it possesses a poorly developed brachidium and was tentatively assigned to the family Megathyrididae by Johansen (1987, p. 26; superfamily and family uncertain in Lee et al., 2007).

Family Dispheniidae Grant, 1988

Diagnosis.—Gwynioidea possessing either a dorsal or a ventral septum with an intra-septal cavity.

Subfamily Albasphinae Halamski and Bitner, new

Diagnosis.—Dispheniidae with submarginal ridges and the dorsal septum with a cavity.

Genera included.—*Albasphe* n. gen., Ladinian (Middle Triassic); *Zellania* Moore, 1855, Early to Middle Jurassic (discussion on stratigraphic range of this genus is reported to the Appendix).

Genus *Albasphe* new genus

Type species.—*Albasphe albertimagni* n. gen. n. sp., as below.

Other species.—Type species only.

Diagnosis.—Shell minute, rounded to bilobate in outline. Ventral valve: accessory ridges absent; median septum absent, sometimes a low myophragm present. Dorsal valve: delthyrium open; median septum high, with an intra-septal cavity; submarginal ridges present.

Etymology.—An arbitrary combination of letters consisting of *alb*, for Albertus and of *a*, without and *sphe* from Greek *sphen*, wedge; the first part from the specific epithet, the second and the third to recall that the new genus has not the wedge-shaped outline unlike its probable evolutionary predecessor *Disphenia*. The genus name is feminine.

Remarks.—*Albasphe* n. gen. differs from the Jurassic *Zellania* in the anatomy of the ventral valve, namely in lack of accessory ridges (present in the latter) and weak development of the septum (only a short and low ridge vs. a high and long blade-like ventral septum in *Zellania*), as well as in larger size.

Albasphe albertimagni new species
Figures 4.2, 8, 9, 10

Type material.—Holotype, BJ 3073; illustrated paratypes, BJ 3073–3080, ZPAL Bp 72/2/1–7; type locality, Svilaja,

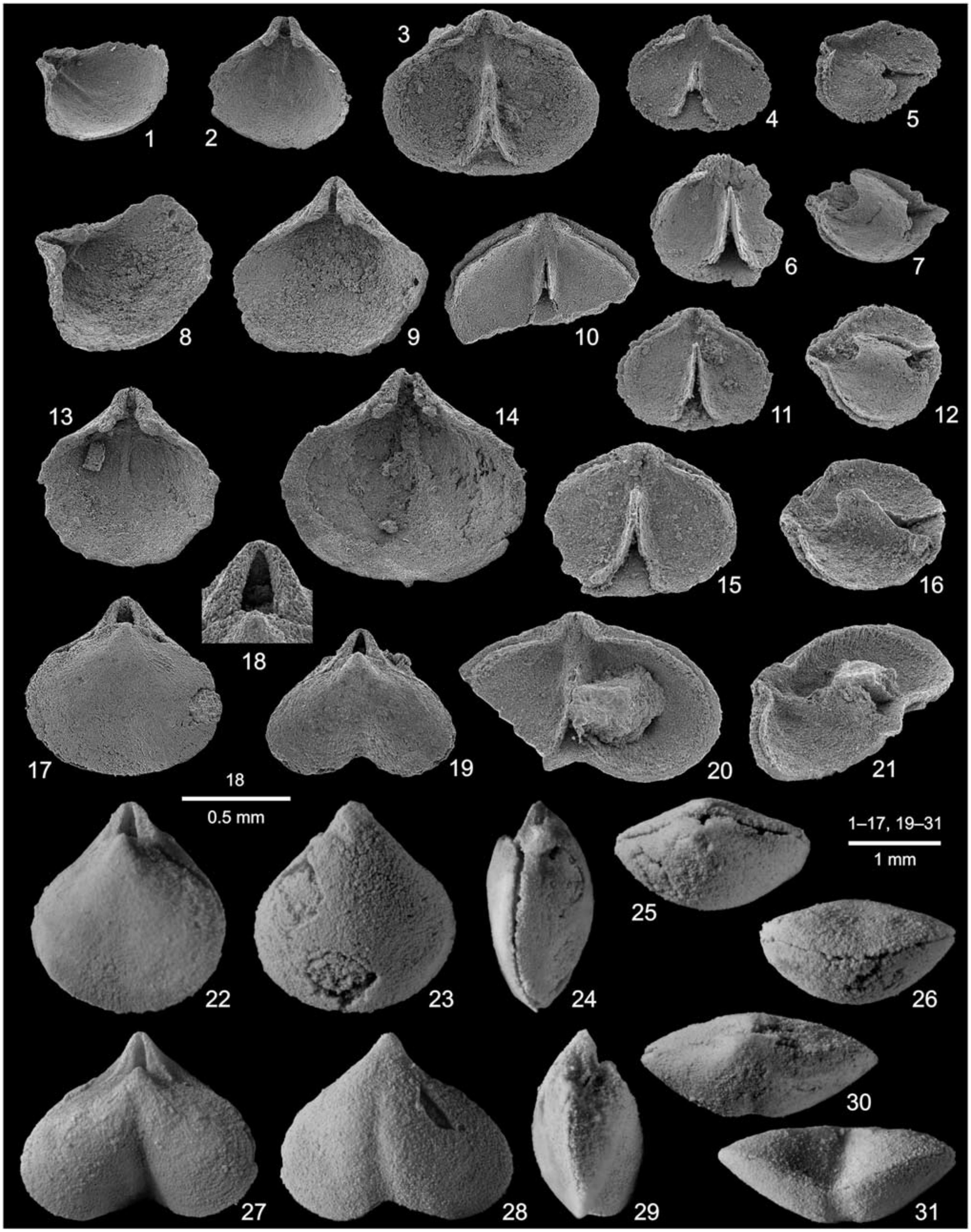


Figure 8. *Albasphe albertimagni* Halamski, Bitner, Kaim, Kolar-Jurkovšek, and Jurkovšek n. gen. n. sp. (**1–2, 8–9, 13, 14**) Ventral valves ZPAL Bp 72/2/6, 72/2/5, BJ 3079, and 3080 in oblique (**1, 8**) and dorsal (**2, 9, 13, 14**) views. (**3–7, 10, 11–12, 15–16, 20–21**) Dorsal valves ZPAL Bp 72/2/7, BJ 3078, 3076, 3077, 3075, ZPAL Bp 72/2/4, and 72/2/1 in ventral (**3, 4, 6, 10, 11, 15, 20**) and oblique (**5, 7, 12, 16, 21**) views. (**17–19**) Articulated shells ZPAL Bp 72/2/2 and 72/2/3 in dorsal views (**17, 19**) and enlargement of the delthyrium (**18**). (**22–31**) Articulated shells BP 3074 and 3073 (holotype) in dorsal, ventral, lateral, posterior, and anterior views. (**1–21**) SEM micrographs. (**22–31**) images taken in visible light.

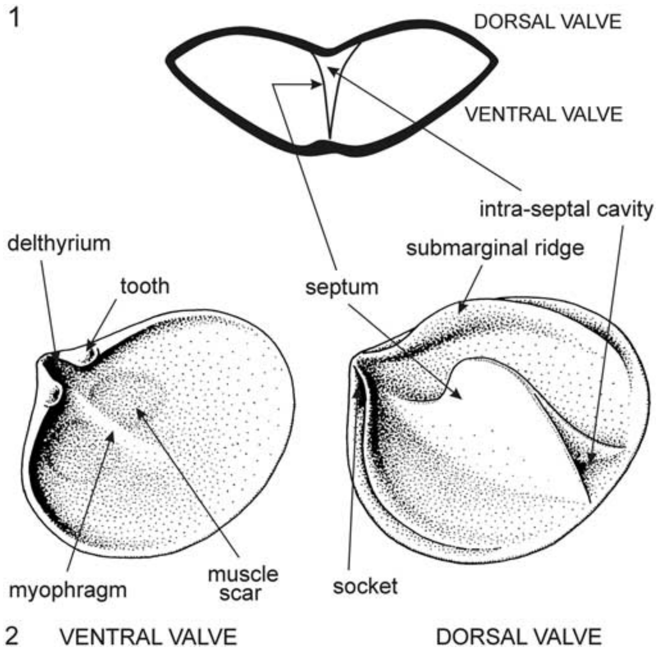


Figure 9. *Albasphe albertimagni* Halamski, Bitner, Kaim, Kolar-Jurkovšek, and Jurkovšek n. gen. n. sp. (**1**) Transverse section through the shell (based on the section at 1.422 mm in Fig. 10.1). (**2**) Reconstructions of internal structures showing both valves in oblique views (not to scale).

Dinarides; cherty limestones and dolomites, Ladinian, Middle Triassic.

Diagnosis.—As for the genus.

Description.—Shell teardrop-shaped and rounded (Fig. 8.17, 8.22) to transversely subtriangular in outline (Fig. 8.19, 8.27), width to length ratio 0.90–1.33 (mean 1.08; N = 20); in the latter case bilobed through a median indentation of the anterior commissure, the length of the indentation not exceeding one sixth of that of the dorsal valve; weakly to moderately ventribiconvex. Maximal width of the shell at about ⅔ of its length. Anterior commissure gently unisulcate. Dorsal valve moderately convex, in transverse individuals with a V-shaped sulcus; beak acute. Ventral valve convex either with a weak sublinear median sulcus (Fig. 8.28, 8.31) or regularly convex (Fig. 8.23, 8.26); beak nearly straight; delthyrium open (Fig. 8.18), symphytium absent. Shell smooth; shell substance punctate (Fig. 4.2); micro-ornamentation, if any, not preserved.

Dorsal interior: median septum beginning about the posterior fourth of the valve length, rising abruptly and arching backwards, its posterior extremity thus consisting in lateral profile of a rounded sinus in the lower part and of an overhanging upper part (Fig. 8.7, 8.12, 8.16), nearly reaching the ventral valve floor (Fig. 9.1), then bifurcating about the midlength of the valve, thus forming an internal cavity, open anteriorly in form of an isosceles concave-sided triangle (Fig. 8.6, 8.11, 8.15). Submarginal ridges situated in the immediate proximity of the margin, the angular length of each ridge ca. 90° (Fig. 8.10). Inner socket ridges either of the same thickness as the submarginal ridges of which they form a mere continuation (Figs 8.12, 9.2) or much thicker (Fig. 8.3).

Ventral interior: a short and low myophragm is present in some specimens (Fig. 8.1, 8.13); faint muscle scars on its either scars are visible in a single shell (Fig. 8.13); accessory ridges absent; teeth rounded, stout but rather small (Fig. 8.14).

Etymology.—In honor of Albertus Magnus (ca. 1200–15.11.1280), naturalist.

Material.—One hundred and sixty-one articulated shells, 17 ventral valves, and 25 dorsal valves.

Dimensions.—Holotype BJ 3073: length 2.1 mm; width 2.6 mm; thickness 1.0 mm. Paratype BJ 3074: length 2.3 mm; width 2.1 mm; thickness 1.2 mm.

Remarks.—*Albasphe albertimagni* n. gen. n. sp. shows important shape variability. In a single sample both rounded and bilobate individuals are found, the former resembling the inferred evolutionary predecessor *Disphenia*, the latter similar to the inferred descendant *Zellania*. This variability cannot be explained by ontogenetic differences alone, as rounded individuals ("morphological juveniles") attain a size comparable to that of bilobed individuals (compare Fig. 8.22 and 8.27 representing shells 2.3 and 2.1 mm long, respectively).

A. albertimagni is externally homoeomorphic with representatives of the family Lambdarinidae (Rhynchonellida, Late Devonian to Permian) from which it is distinguished by shell microstructure and internal features. In the Lambdarinidae such a shape difference as seen in the studied sample is indicative of a distinction at genus level (bilobed: *Lambdarina*; rounded: *Dacryrina*; Baliński and Sun, 2008).

Suborder Terebratulidina Waagen, 1883
Superfamily and family unknown
Terebratulidina? gen. et sp. indet.
Figure 3.17–3.21

Material.—A single fragmentary adult specimen and two complete articulated shells of juvenile specimens.

Remarks.—The material is very limited and poorly preserved, precluding any precise determination. Nevertheless, a smooth, biconvex shell with astrophic hinge line, a large, labiate permesothyrid foramen, and a partly visible symphytium strongly suggest the suborder Terebratulidina; similar morphologies, however, do occur among representatives of the order Athyridida, so in absence of diagnostic interior characters such an assignment cannot be excluded either (even if judged much less probable by the authors).

Functional interpretation of intra-septal cavities in Gwyniidae

The intra-septal cavities in septa of *Disphenia*, *Albasphe*, and *Zellania* are an unusual feature as they have no analogue in any of over 4,000 described brachiopod genera. Neither Baker (1970) describing *Zellania* nor Grant (1988) dealing with *Disphenia* proposed a functional interpretation thereof.

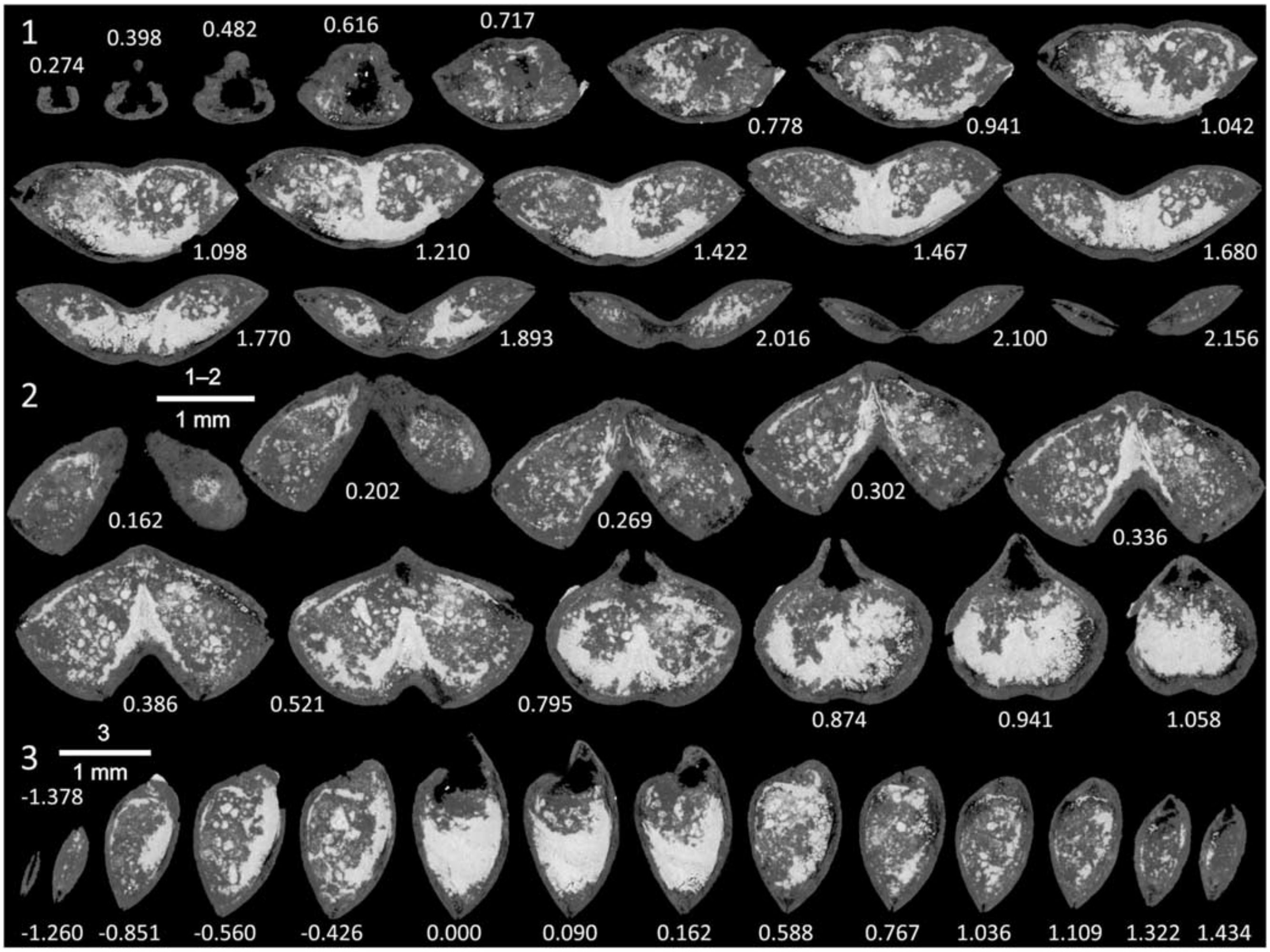


Figure 10. *Albasphe albertimagni* Halamski, Bitner, Kaim, Kolar-Jurkovšek, and Jurkovšek n. gen. n. sp.: X-ray microtomograph sections of the holotype BJ 3073. (**1**) Transversal sections, distances (in mm) measured from the tip of the ventral umbo; (**2**) sections parallel to the commissural plane, distances (in mm) measured from the highest point of the dorsal valve; (**3**) Sections parallel to the symmetry plane, distances (in mm) measured either side from the latter.

The most elementary explanation would be that such a cavity might have contained a peculiar anatomic structure. This, however, seems quite implausible. In effect, the opening of those cavities is located at the anterior margin of the valve, so they could have been filled only by the edge of the mantle. It is improbable that any special organ be situated in such a position. It might be hypothesized that this opening served as a brood pouch, a specialised excrescence of the mantle (Lüter, 2007). This, however, seems unlikely as well, as brood pouches are usually situated in the posterior region of the shell (Rudwick, 1964, 1966; Hoffmann and Lüter, 2009; Seidel et al., 2012; Kaulfuss et al., 2013) and, even if in rare cases they may be situated anteriorly (Michalík, 1996), they are paired structures unlikely to be located in a median position.

It is more promising to try explaining function of this structure in terms of constructional morphology. The role of an anterior widening of the septum is evidently a support of the lophophore; quite different structures having the same role and position may be observed in the Devonian orthide *Phragmophora* (Cooper, 1955; Biernat, 1959; Halamski, 2009). A solid structure of the same width as the septum with an internal cavity would be very heavy. A large open delthyrium suggests that a functional pedicle was present in *Albasphe*; a burden at the anterior end of the shell would therefore cause an unstable situation. A hollow septum works as well as the lophophore support without having the above-mentioned inconvenience.

It follows that the function of the intra-septal cavities may be interpreted as a simple way of reducing the weight of a broad-base septum.

Evolution of the Gwynioidea

A sparsely recorded evolutionary line represented by five monospecific genera, formally described herein as the suborder Gwyniidina, is postulated to have existed since the Permian. The oldest two representatives, Permian *Disphenia* and Triassic *Albasphe*, are related to similar shallow water biotopes and quite similar in external morphology.

The phylogenetic relation between *Disphenia* to *Albasphe* is intriguing as the bifurcated septum, present in the ventral valve of *Disphenia*, is found in the dorsal valve of *Albasphe*.

The morphological difference between *Albasphe* and *Zellania* is accompanied by some size diminution (*Albasphe* is up to ca. 2.5 mm long, while *Zellania* is ca. 1.5 mm long; maximal recorded length of *Disphenia* is 3.3 mm). This might be related to different habitats of these taxa: *Albasphe* is interpreted to have dwelt in submarine meadows, whereas *Zellania* lived in cryptic habitats (Baker, 1970). Nonetheless, internal structures of *Zellania* are not simplified in respect of those of *Albasphe*; in fact, quite the opposite. The evolutionary line is presented (Fig. 11) as if stratigraphic succession reflected directly the phylogenetic order.

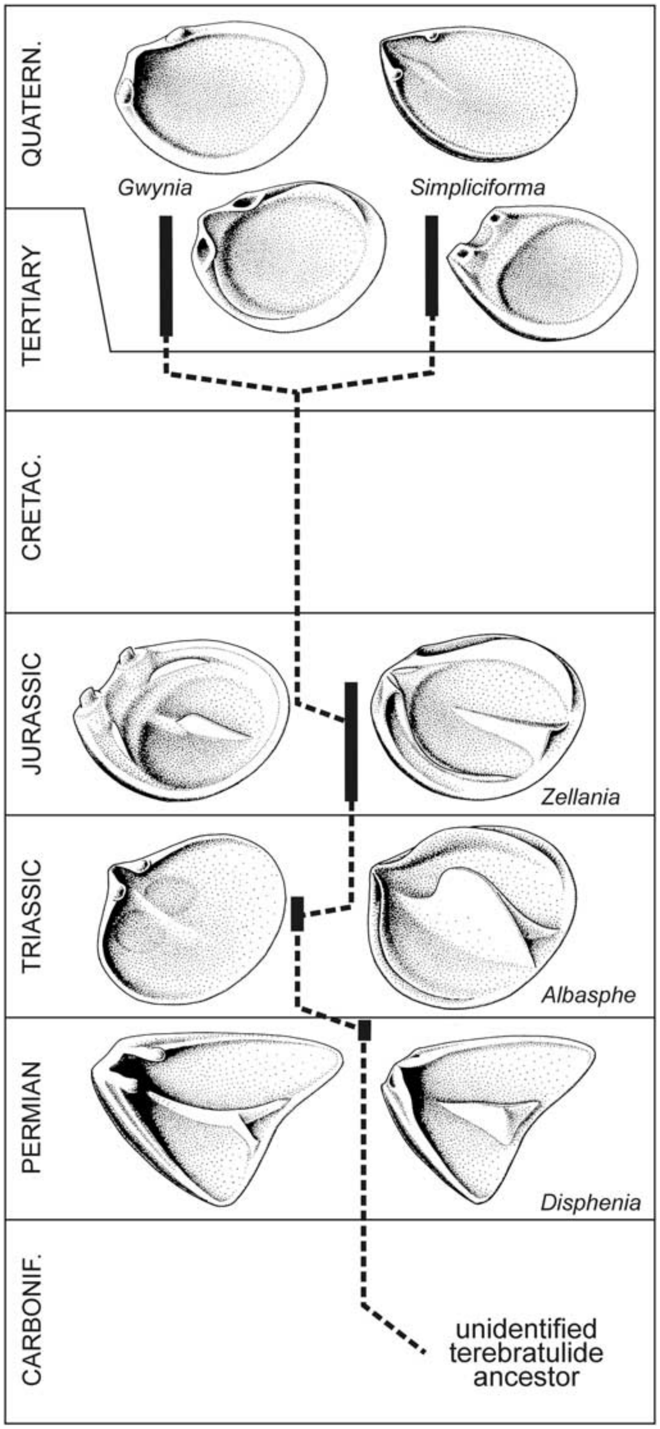


Figure 11. Stratophenetic intepretation of the terebratulide suborder Gwyniidina. Ventral valves on the left, dorsal ones on the right. *Disphenia* redrawn after Grant (1988), *Zellania* after Baker (1970), *Gwynia* after Simon and Willems (1999), the dorsal valve of *Simpliciforma profunda* after Bitner et al. (2013), the ventral valve of *S. macrodentata* after Lüter (2008). Drawings by B. Waksmundzki.

The Recent representatives of Gwyniidina are pedomorphic and simplified, a fact probably related to their abyssal habitat (Bitner et al., 2013). *Simpliciforma macrodentata* (Lüter, 2008) has still a low ventral median septum, *Gwynia capsula* has none, and *S. profunda* Bitner and Zezina *in* Bitner et al., 2013 has lost even the ridges supporting the lophophore. It may be added that representatives of *Zellania* were interpreted by Rollier (1917, p. 183) as probably juvenile shells.

The lophophore of *Zellania* is interpreted as schizolophe (Baker, 1970) and similarity of internal structures allows to extend this interpretation to *Albasphe*. In contemporary *Gwynia* the lophophore is simpler, trocholophe, as described by Emig (1992) who subsequently argued that this condition is plesiomorphic for all Brachiopoda. In this case, however, it is merely a simplification of a more advanced lophophore (see also Carlson *in* Williams and Carlson, 2007, p. 2870, who argued that the ancestral condition of the adult lophophore in brachiopods is spirolophe).

The origin of the order Terebratulida is interpreted as pedomorphic (Jin and Chatterton, 1996) and pedomorphosis played an important role in the evolution of the terebratulides (e.g., MacKinnon, 2001; Pérez-Huerta, 2004). The representatives of the suborder Gwyniidina characterized by small size and lack of the loop (simplification of previously existing structures) may be interpreted in their turn as pedomorphic descendants of the Stringocephaloidea (as suggested for *Zellania* already by Baker, 1970, on account of the shell microstructure and the ontogeny of dorsal cardinalia). The evolutionary trends in the Gwyniidina include size diminution and simplification of internal structures, once again features of pedomorphosis.

Paleoecology

The fauna at Svilaja is extremely rich by means of the abundance but in some groups also in terms of diversity. Characteristic are abundant occurrences of algae, corals and sponges, which seemingly constitute the framework of the community. Apparently the most diversified is motile epibenthos represented mainly by gastropods and echinoderms. Infaunal animals are rare and represented mostly by bivalves. Sessile animals are not much diversified but may reach large numbers as it is in the case of the brachiopods studied herein. The brachiopods in Svilaja occur abundantly but are of low diversity. All five species identified in the brachiopod assemblage are small-sized and were probably tiering above the sea bottom. Most likely they lived attached to the dasycladalean algae which served as the only suitable substrate in this environment. Such an interpretation is supported by a specimen of *Thecocyrtella dagysii* found *in situ* on an algal thallus (Fig. 4.1). All in all, the environment at Svilaja might be interpreted as a submarine “meadow” composed of representatives of at least five species of Dasycladales (Chorowicz and Termier, 1975; Grgasović et al., 2007). This kind of biocoenosis was common in the Anisian (Termier and Termier, 1968, p. 153–156; Kotański, 2013) but much rarer in the Ladinian (Flügel, 1991; Bassi and Fugagnoli, 2005).

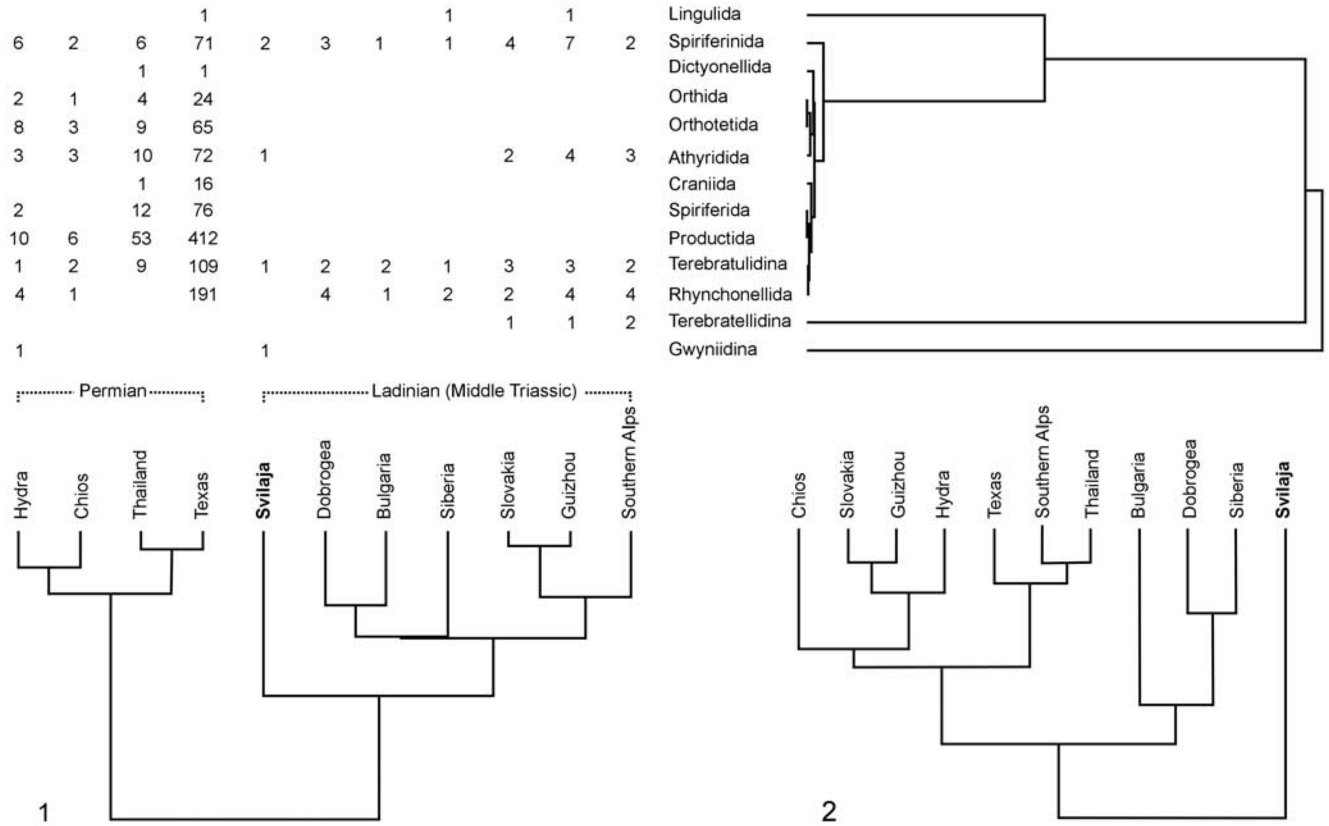
Comparison

The brachiopod fauna at Svilaja displays high degree of endemicity. Out of four named taxa described in the present paper, only one species is known from elsewhere. The athyridide *Cassianospira humboldtii* has been originally described from southern Alps (von Klipstein, 1843–45). Although the full taxonomic treatment of bivalves from Svilaja is not yet assessed, Chorowicz and Termier (1975) suggested similar level of endemicity also in this group. The three named species of ammonites reported from Svilaja by Balini et al. (2006) are also unknown outside the study area. On the contrary, anthozoans from Svilaja are similar to those from Carnian deposits of the Dolomites, at least at genus level (J. Stolarski, unpublished data).

As it would be difficult to compare the brachiopod fauna from Svilaja with the other faunas on the specific, generic, or even familial level (because of the low number of species in particular faunas), a preliminary comparison on the ordinal level has been attempted. The following Ladinian brachiopod faunas have been taken into account (in order of decreasing number of species; species grouped by orders except for the Terebratulida, in which suborders are distinguished; see Fig. 12 for taxonomic composition): the fauna from Guizhou Province (southern China: c. 24 taxa, possibly less due to uncertain taxonomy; Yang and Xu, 1966; supplemented after data in Enos et al., 2006 and references therein; Fig. 1.3: a); the fauna from southern Alps (17 species; Torti and Angiolini, 1997; Fig. 1.3: b); the fauna from Ostrý vrch (Carpathians, southern Slovakia: 12 species; Kochanová and Pevný, 1982; Fig. 1.3: c); the fauna from the Tulcea Zone in Dobrogea (Romania: 10 species; Iordan, 1993; Fig. 1.3: d), consisting of 10 species; the fauna from Siberia (8 species; Dagys, 1965; Fig. 1.3: e); the fauna from western Bulgaria (4 species; Benatov, 2001; Fig. 1.3: f).

Single Ladinian brachiopod taxa were also reported from Iran (Siblík 1991; Fig. 1.3: g), Israel (Feldman, 2002, 2013; Fig. 1.4: h), Spain (Márquez-Aliaga et al., 1999, 2007; Fig. 1.4: k), and British Columbia (Sandy and Blodgett, 2011; Fig. 1.3: i). A richer late Ladinian fauna from Nevada remains undescribed (Balini, 2008; Bonuso and Hernandez, 2013; Fig. 1.3: j). These data are enumerated here for sake of completeness but disregarded in further comparison.

The presence of Gwyniidina at Svilaja, which are otherwise known only from the Permian, gave an impression that the fauna might be more similar to Permian brachiopod faunas than to the Triassic ones. Therefore, we decided to include additionally four Permian brachiopod faunas to our analysis, and namely: the fauna from the Glass Mountains in Texas (1026 species after Cooper and Grant, 1977); the Artinskian fauna from southern



Hydra	Chios	Thailand	Texas	Svilaja	Dobrogea	Bulgaria	Siberia	Slovakia	Guizhou	Southern Alps	
			1				1		1		Lingulida
6	2	6	71	2	3	1	1	4	7	2	Spiriferinida
		1	1								Dictyonellida
2	1	4	24								Orthida
8	3	9	65								Orthotetida
3	3	10	72	1				2	4	3	Athyridida
		1	16								Craniida
2		12	76								Spiriferida
10	6	53	412								Productida
1	2	9	109	1	2	2	1	3	3	2	Terebratulidina
4	1		191		4	1	2	2	4	4	Rhynchonellida
								1	1	2	Terebratellidina
1				1							Gwyniidina

Figure 12. Results of cluster analysis; Morisita similarity measure with paired group algorithm: (**1**) two-way cluster analysis of seven Ladinian (Middle Triassic) brachiopod faunas and four Permian faunas; (**2**) cluster of the same faunas after excluding Dictyonellida, Productida, Orthotetida, Orthida, and Spiriferida (orders that became extinct before the Ladinian) and Terebratellina (appeared after the Permian). Analyzes performed with PAST v.2.17b software (Hammer et al., 2001).

Thailand (109 species after Grant, 1976); the Kungurian to Wordian fauna of the Chios (Khios) island in Greece (18 species after Grant, 1993b; Angiolini et al., 2005); and the Lopingian fauna of the Hydra island also in Greece (37 species after Grant, 1972, 1988, 1993a, 1995; Shen and Clapham, 2009).

The cluster analysis (Fig. 12.1) shows that fauna at Svilaja stands out of all the other Ladinian faunas worldwide, still however, is separate in respect to any of the Permian faunas. The latter might be, however, biased by the absence of Dictyonellida, Productida, Orthotetida, Orthida, and Spiriferida in the Ladinian faunas (became extinct before the Ladinian) and the Terebratellidina in the Permian faunas (appeared after the Permian). After removal of these groups from the data matrix we re-ran the analysis and it appears that the fauna from Svilaja again stands out of all Ladinian and Permian faunas (Fig. 12.2). This is probably related to presence of spiriferinides and athyridides in the Svilaja assemblage and absence of rhynchonellides and terebratellidines that became increasingly important in the Mesozoic faunas. Most likely this composition reflects the unusual environment of algal meadows where the brachiopods are small pendent animals living attached at some distance above the sea floor while rhynchonellides and terebratellidines are usually living directly on the sea floor. The environment recorded in the silicified assemblage from Svilaja is rarely so well preserved in the fossil record and perhaps that is the reason why it does not fit into the scheme of Mesozoic brachiopod biofacies established by Ager (1965, 1993).

Conclusions

Ladinian deposits at Mt. Svilaja in Dalmatia (Outer Dinarides, Croatia) yielded an abundant brachiopod fauna of low diversity. It consists of five species and the most common is *Flabellocyrtia flabellulum* Chorowicz and Termier, 1975 making over 70% of the material. The remaining species are *Cassianospira humboldtii* (von Klipstein, 1845) (the only one known elsewhere, i.e. from the Anisian of Southern Alps), *Thecocyrtella dagysii* n. sp., *Albasphe albertimagni* n. gen. n. sp., and poorly preserved Terebratulidina? gen. et sp. indet. The assemblage is interpreted as parautochthonous and representing the ecosystem of a dasycladacean submarine meadow.

Thecocyrtella dagysii n. sp. differs from the other representatives of the genus in possessing a ventral sulcus. Dorsal cardinalia of *Flabellocyrtia flabellulum* Chorowicz and Termier, 1975 are reinterpreted in comparison with the original description and shown to consist of a small cardinal process situated on a large platform.

Albasphe albertimagni n. gen. n. sp. possesses a dorsal septum with an intra-septal cavity and dorsal submarginal ridges, both features in common with Aalenian *Zellania davidsonii* Moore, 1855 from which it differs in lack of the ventral septum and of ventral submarginal ridges.

Permian *Disphenia*, Triassic *Albasphe*, and Jurassic *Zellania* are interpreted as members of a sparsely recorded pedomorphic evolutionary line of terebratulides with secondarily lost loop, described formally as Gwyniidina n. subordo, consisting of the single superfamily Gwynioidea MacKinnon, 2006, and subdivided into newly emended Dispheniidae Grant, 1988 (Dispheniinae Grant, 1988 with the single genus *Disphenia* and Albasphinae n. subfam. with *Albasphe* and *Zellania*) and Gwyniidae Grant, 1988 (*nomen translatum* herein; including Recent *Gwynia* and *Simpliciforma*).

We consider the trocholophe lophophore of *Gwynia* as secondarily simplified, not a plesiomorphic condition as interpreted by Emig (1992).

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Appendix. Classification of the suborder Gwyniidina

The terebratulidine superfamily Gwynioidea was introduced (MacKinnon, 2006) for two genera without a formal description of a family. As emended by the present authors, the superfamily contains as many as five genera, wherefore a few nomenclatural acts are necessary. Given that the concerned material is not dealt with in the systematic part, the newly characterized family group taxa Gwyniidae and Dispheniinae are diagnosed in the present Appendix.

Suborder Gwyniidina Halamski and Bitner, new

Diagnosis.—See above.

Superfamily Gwynioidea MacKinnon, 2006

Diagnosis.—See above.

Remarks.—The newly redefined superfamily Gwynioidea MacKinnon, 2006 includes the family Dispheniidae Grant, 1988. If priority and coordination principles (Art. 36.1 of the ICZN) were to be strictly applied, the name of the superfamily would have to be derived from the older family name (therefore, "Disphenioidea Grant, 1988"). However, on virtue of the Art. 35.5 of the ICZN ("If after 1999 a name in use for a family-group taxon is found to be older than a name in prevailing usage for a taxon at higher rank in the same family-group taxon, the older name is not to displace the younger name"), the name in current usage is maintained.

Family Dispheniidae Grant, 1988

Diagnosis.—See above.

Subfamily Dispheniinae Grant, 1988

Diagnosis.—Dispheniidae without submarginal ridges and having a ventral septum with a cavity.

Remarks.—Given the introduction of Albasphinae subfam. nov., it is necessary to erect another subfamily of the Dispheniidae containing the type genus. The name Dispheniinae is a *nomen translatum ex* Dispheniidae Grant, 1988.

Genera included.—*Disphenia* Grant, 1988.

Range.—Permian.

Subfamily Albasphinae Halamski and Bitner, new

Diagnosis, genera included, range.—See above.

Genus Albasphe, new

Diagnosis, species included, range.—See above.

Genus *Zellania* Moore, 1855

Remarks.—Our interpretation of *Zellania* is based on the detailed redescription of the type species *Z. davidsonii* from the Upper Aalenian of the Cotswolds, South England (Baker, 1970). Concerning that taxon, it may be observed that the original spelling of the epithet was *davidsonii* (Moore, 1855, p. 111, 112), so the variant *davidsoni* used by Moore himself (1860, p. 444), Davidson (1876, p. 112) and Baker (1970) must be treated as an incorrect subsequent spelling (Art. 33.4 of the ICZN). More interestingly, it should also be noted that several other species have been reported under that generic name, namely:

Zellania laboucherei Moore, 1855; Dundry, England; inferior oolite, Aalenian. Said by Moore (1855, p. 113) to differ from *Z. davidsonii* by "shape, the absence of radiating striae, and by the constant presence of lines of growth". However, as Baker (1970) failed to find any striae in *Z. davidsonii*, the two co-occurring species may be hypothesised to be synonymous.

Zellania liasiana Moore, 1855; Ilminster, England; Upper Lias (= Toarcian?). The interior shows clear submarginal ridges (Moore, 1855, pl. 1, fig. 8), so the generic identification seems secure.

Zellania globata Moore, 1860. Hampton, oolite (= Aalenian?). Reported also from the Fuller's Earth (= Bajocian) at Bath and the Coral Rag (= Oxfordian) at Lyneham, Wiltshire (Davidson, 1876, p. 112). "The interior of the dorsal valve possesses a well defined circular ridge, entirely encircling the inner portion of the shell. In this species I have been unable to observe any trace of a central septum, which in those previously figured is well defined." (Moore, 1860, p. 444). Requires restudy. Davidson's material is lost (Muir-Wood, 1936, p. 105).

Zellania oolitica Moore, 1860. Same locality and stratum as *Z. davidsonii* and *Z. laboucherei*. The characters reported by Moore (1860, p. 444) do not seem to warrant a specific distinction. However, Davidson (1872, p. 113) notes: "I have not seen any good interior, or indication of the presence of a septum in either valve." Requires restudy.

Zellania obesa Moore, 1867; Stout's Hill, lower Lias (= Hettangian to Sinemurian). Known from a single specimen (Moore, 1867, p. 540, pl. 16, fig. 28; Davidson, 1876, p. 303, pl. 11, fig. 22). Interior unknown.

Zellania pictolithica (Manceñido and Damborenea, 1991); Piedra Pintada, Neuquén Province, Argentina; Pliensbachian, Lower Jurassic (= *Scumulus*? *pictolithicus* Manceñido and Damborenea, 1991; see Manceñido and Damborenea, 1991 for description and Manceñido, 2010 for reinterpretation). Interior not figured.

Family Gwyniidae MacKinnon, 2006

Diagnosis.—Gwynioidea not having any septum with an intraseptal cavity.

Remarks.—The superfamily Gwynioidea MacKinnon, 2006 was introduced (MacKinnon 2006) without any subordinate family-group taxon. Given that Dispheniidae Grant, 1988 are now included, it is necessary to erect a family. The name Gwyniidae is a *nomen translatum ex* Gwynioidea MacKinnon, 2006.

Genera included.—*Gwynia* King, 1859, Pleistocene to Recent; *Simpliciforma* Bitner and Zezina in Bitner et al., 2013, Recent.

Range.—Pleistocene to Recent.

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