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A new species of *Lambdarina* (Rhynchonellida, Brachiopoda) from the Viséan of central Sudetes (Poland) and its phylogenetic position

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ABSTRACT:

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A new species of micromorphic articulate brachiopod (Rhynchonellida) *Lambdarina jugowiensis* sp. nov., from the upper Viséan (Sokolec Beds) of central Sudetes, SW Poland, is described. The studied specimens are calcified, what makes them unique in respect of their state of preservation. The material is represented by a full range of growth stages; from brephic to gerontic. Based on its morphological features and the palaeogeographical distribution of all its known species, two main evolutionary lines are proposed for the genus; the Australian and the European ones. *Lambdarina* was widely distributed in the equatorial-tropical waters of marginal seas of the Palaeotethys Ocean, mostly during Mississippian time.

Key words: Brachiopoda; Rhynchonellida; Lambdarinidae; Viséan; Sudetes; Palaeobiogeography.

INTRODUCTION

Brachiopods of the family Lambdarinidae (order Rhynchonellida) have rarely been documented in the palaeontological literature. The reasons are twofold. The first one is their microscopic size (3 mm maximum length) and the second is an infrequent use of micropalaeontological techniques aimed specifically in acquiring articulate brachiopods. All of the previously described material has been discovered accidentally, usually during recovery of microfossils in silicified residues.

There are several papers that discuss the systematic position of the Lambdarinidae and similar micromorphic brachiopods (Cardiarinidae) (Cooper 1956; Brunton and Champion 1974; Nazer 1983; Baliński 1982, 1999; Bassett and Bryant 1993; Morris 1994; Hoare and Mapes 1997; Martínez-Chacón 1997; Savage 2002; Baliński and Sun 2008). The first microscopic brachiopods were reported from the Pennsylvanian of New Mexico; referred to the genus *Cardiarina* and originally regarded as belonging to the Rhynchonellida (Cooper 1956). Subsequently, they were included in the Terebratulacea (Hoare and Mapes 1997) or left as taxonomically uncertain (Savage 2005). Currently, five genera are distinguished within the family Lambdarinidae (Savage 2002; Baliński and Sun 2008): *Lambdarina* Brunton and Champion 1974, *Loborina* Baliński 1982, *Minysphaenia* Grant 1988, *Hampsia* Morris 1994 and *Dacryrina* Baliński and Sun 2008. *Loborina* is the oldest (early Famennian) and most primitive genus of the family (Baliński 1982). For years it had been the only genus of the family reported from Poland (Cracow region); the other representatives were recently reported by Muszer and Ługowska (2007).

So far, seven species are recognized in the genus *Lambdarina*. The majority of them are known from the Missisippian (upper Tournaisian–upper Viséan) of Europe; England, Ireland, Spain and Belgium (Brunton and Champion 1974; Bassett and Bryant 1993; Morris 1994; Martínez-Chacón 1997). However, the genus is also known from the Viséan of Australia (Nazer 1983), the Tournaisian of China (Baliński 1999; Baliński and Sun 2005, 2008; Sun and Baliński 2011), and from the Upper Permian of Greece (*Lambdarina iota*, reported by Grant 1988; see Baliński and Sun 2008).

The present paper provides a description and discussion of the new species of *Lambdarina*, discovered in the upper Viséan limestones of the Góry Sowie Massif in central Sudetes, SW Poland. The specimens collected represent a full range of growth stages, from brephic to gerontic. In contrast to the other *Lambdarina* species described so far, which are silicified, the specimens described herein are calcified.

GEOLOGICAL SETTING

The Góry Sowie Massif is a fault-bounded tectonic unit situated in the central Sudetes, SW Poland, which represents part of the Lugicum (Żelaźniewicz 1995) (Text-fig. 1A). This unit is composed mostly of polymetamorphic gneisses and migmatites derived from Upper Proterozoic–lower Palaeozoic sedimentary and igneous protoliths (Aleksandrowski *et al*. 1997). The Góry Sowie Massif was metamorphosed under amphibolite facies conditions by the middle Devonian (van Breemen *et al.* 1988). The Sudetic Marginal Fault (SMF) divides the Massif into its western, elevated, and eastern, poorly exposed, parts (Text-figs 1A, 1B).

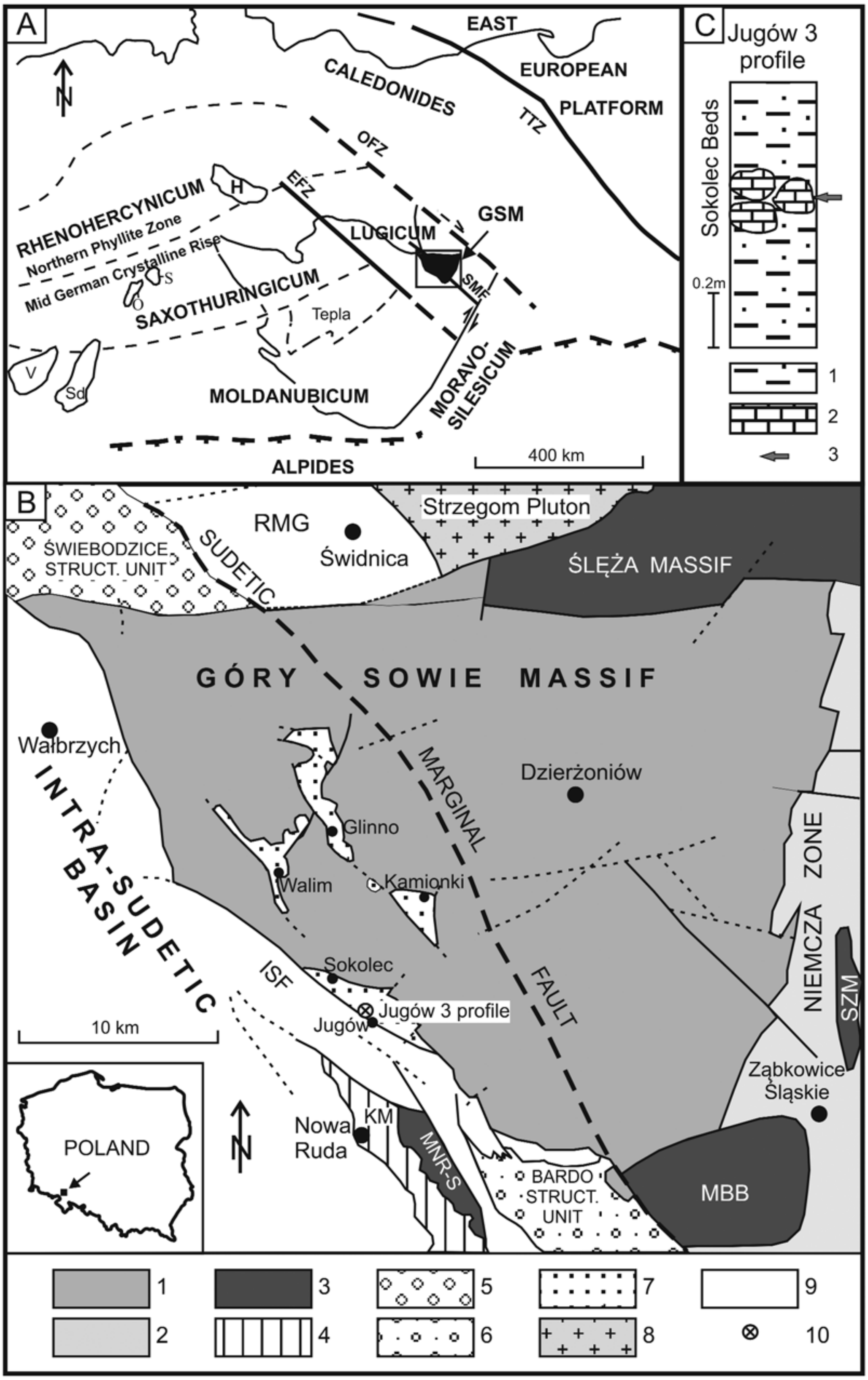
The Lower Carboniferous (Mississippian) of the Góry Sowie Massif occurs only in tectonic depressions in its western part (Text-fig. 1B). It is represented by sedimentary rocks of the so called Góry Sowie Culm (Żakowa 1966; Cwojdziński 1995). They are of middle and late Viséan age (Żakowa and Żak 1962; Żakowa 1966). The lithostratigraphic succession of these sediments is divided into three informal units (Łapot 1986; Cwojdziński 1995). The lowest unit, 10 to 30 m thick, is composed of gneiss or gabbro breccias, sandstones and conglomerates. The middle unit, 150 to 600 m thick (maximum thickness in the Jugów region), referred to as the Sokolec Beds (Żakowa 1963), consists of clayey-graywacke with interbeds of conglomerates, marls, limestones, arkoses, coaly shales, breccias and gneiss sandstones. The upper unit, 300 m thick, is represented by quartz conglomerates referred to as "the Kamionki conglomerates". The Carboniferous succession is the record of the late Viséan transgression into the central Sudetes (Żakowa and Żak 1962; Łapot 1986).

The source section of the material studied is located in the SW part of the Góry Sowie Massif, between the villages of Jugów and Sokolec, close to the Intra-Sudetic Fault (Text-fig. 1B). The Carboniferous succession is exposed in a 5 m long escarpment, in the western part of the village of Jugów, in the park of the Jugów Forest District. The 1 m-thick source succession represents the Sokolec Beds (Text-fig. 1C). They are represented by greenish-grey clayey-graywacke mudstones with 30 to 40 cm thick lenses of dark-grey limestone and grey marly limestone. The limestone lenses are commonly rounded and covered by a clayey film a few mm thick. The limestone lenses are richly fossiliferous, containing numerous brachiopods (including those described in this report), small gastropods, crinoids, foraminifers, ostracods, corals, ammonoids and bivalves. In contrast to the microfossils, some of the macrofossils are disarticulated. Żakowa (1966) assigned the Sokolec Beds to the late Viséan Goα ammonite ammonoid Zone.

MATERIAL AND METHODS

The microfossil assemblage was recovered from 2 kg limestone samples by thermal fragmentation using Glauber's salt (sodium sulphate Na_2SO_4). After washing and drying, the material was sieved into a series of fractions (<0.063; 0.063–0.125; 0.125–0.25; 0.25–0.35; >0.35 mm). Subsequently, the material was viewed under a Nikon SMZ-2T stereomicroscope. Measurements and photographs of microbrachiopods were taken using an Olympus SZX10 stereomicroscope and an Olympus DP71 camera with image analysis program Cell-D, in the Department of Palaeozoology of the

Text-fig. 1. A – Tectonic setting of the Mid-European Variscides (after Żelaźniewicz 1995, modified) and location of the Góry Sowie Massif (GSM). Abbreviations are as follows: TTZ (Teisseyre–Tornquist Zone), OFZ (Odra Fault Zone), SMF (Sudetic Marginal Fault), EFZ (Elbe Fault Zone), H (Harz), O (Odenwald), S (Spessart), Sd (Schwarzwald), V (Vosges). B – Generalized geological sketch of the Góry Sowie Massif (after Pieczka 2007, modified) and location of the Jugów 3 section. Tectonic units according to Żelaźniewicz and Aleksandrowski (2008). RMG – Roztoka-Mokrzeszów Graben, KM – Kłodzko Massif, MNR-S – Nowa Ruda-Słupiec Massif, MBB – Braszowice- Brzeźnica Massif, SZM – Szklary Massif, ISF – Intra-Sudetic Fault. 1 – metamorphic rocks of the Góry Sowie Massif, 2 – mylonites of the Niemcza Zone, 3 – fragments of the Sudetic ophiolite, 4 – metamorphic rocks of the Kłodzko Massif (metasediments and metavolcanics), 5 – sedimentary rocks of the Świebodzice Structural Unit, 6 – sedimentary rocks of the Bardo Structural Unit, 7 – Viséan sedimentary rocks of the Góry Sowie Massif, 8 – Variscan granitoids of the Strzegom Pluton, 9 – sedimentary rocks of the Intra-Sudetic Basin and Roztoka-Mokrzeszów Graben, 10 – location of the Jugów 3 section. C. Lithological log of the Jugów 3 section. 1 – greenish-grey clayey-graywacke mudstones. 2 - grey limestone lenses. 3 – place of sampling


A
EAST
EUROPEAN
PLATFORM
CALEDONIDES
TTZ
OFZ
EFZ
H
GSM
RHENOHERCYNICUM
Northern Phyllite Zone
Mid German Crystalline Rise
LUGICUM
SAXOTHURINGICUM
S
O
SMF
Tepla
V
Sd
MOLDANUBICUM
MORAVO-SILESICUM
ALPIDES
400 km
C
Jugów 3 profile
Sokolec Beds
0.2m
1
2
3
B
ŚWIEBODZICE STRUCT. UNIT
RMG
Świdnica
Strzegom Pluton
ŚLĘŻA MASSIF
SUDETIC
GÓRY SOWIE MASSIF
Wałbrzych
MARGINAL
Dzierżoniów
Glinno
Walim
Kamionki
INTRA-SUDETIC BASIN
ISF
Sokolec
Jugów 3 profile
Jugów
FAULT
NIEMCZA ZONE
SZM
10 km
POLAND
Nowa Ruda
KM
MNR-S
BARDO STRUCT. UNIT
Ząbkowice Śląskie
MBB
1
2
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Faculty of Biological Sciences of the University of Wrocław. Some of the photographs were taken under a JEOL JSM-5410 scanning electron microscope in the Laboratory of Scanning Electron Microscopy of the Institute of Zoology of the Jagiellonian University in Kraków.

In the samples studied, lambdarinid rhynchonelloids are very rare. The recovered microbrachiopods are calcified and well preserved, with conjoined valves. Unfortunately none of the specimens shows details of the internal shell structure.

All specimens described in the present paper are housed in the collections of the Institute of Geological Sciences of the Department of Stratigraphic Geology (catalogue numbers ING/J3-1 to ING/J3-71) of the University of Wrocław.

SYSTEMATIC PALAEONTOLOGY

The classification and terminology used herein follows Williams *et al*. (1997–2007).

Phylum Brachiopoda Duméril, 1806
Order Rhynchonellida Kuhn, 1949
Superfamily Lambdarinoidea Brunton and Champion, 1974
Family Lambdarinidae Brunton and Champion, 1974
Subfamily Lambdarininae Brunton and Champion, 1974
Genus *Lambdarina* Brunton and Champion, 1974

TYPE SPECIES: *Lambdarina manifoldensis* Brunton and Champion, 1974; lower Viséan, Manifold Valley, Carboniferous Limestone; Staffordshire, England.

Lambdarina jugowiensis sp. nov.
(Text-figs 2–4)

2007 *Lambdarina* sp.; Muszer and Ługowska, 89–90, fig. 1 a–c.

HOLOTYPE: Specimen ING/J3-10A (Text-fig. 2A1-A4); complete, conjoined shells.

PARATYPES: Forty-nine complete, to slightly damaged, conjoined shells; forty-eight fragments.

TYPE LOCALITY: The Jugów 3 section of the Sowie Góry Massif, central Sudetes, Poland.

TYPE HORIZON: The Sokolec Beds, Sowie Góry Massif, central Sudetes, Poland.

DERIVATION OF NAME: After the village of Jugów, where the species was found.

DIAGNOSIS: *Lambdarina* with strongly bilobate shell, up to 2.5 mm in length; anterolateral lobes rounded; beak elongate; dorsal valve with deep sulcus; ventral sulcus shallow, median ridge separating lobes absent.

DESCRIPTION: The shell is minute (see Table 1), strongly bilobate, with maximum length 2.47 mm. The outline is equilaterally triangular. The adult shells are biconvex (Text-fig. 2A3). The lobes are rounded, flattened, attaining from 10% (juvenile forms) to 30% (adult forms) of the total shell length. Some specimens show asymmetry in the development of the shape and length of the lobes (e.g. Text-figs 3D, G). The ventral umbo is narrow and elongated; its height varies from 0.1 mm (juvenile forms) to 0.64 mm (adult forms). The delthyrium is covered by a flat symphytium. The pedicle opening is small, rounded, and situated at the apex of the ventral umbo (Text-figs 2H1, 3C1). Its diameter ranges from 0.04 mm (juvenile forms) to 0.1 mm (adult forms). The shell is impunctate and its surface is smooth, albeit with growth-lines visible near the anterior edges of the lobes (e.g. Text-fig. 2H). The details of the internal structure are unknown.

ONTOGENY: There are forty-one juvenile specimens in the collection. Text-figs 2 and 5 show a representative growth series illustrating the main ontogenetic changes in morphology. Juvenile shells differ from adult shells in having a more slender, elongate outline. They also have a shallower sulcus, shorter lobes and a shorter ventral umbo. The smallest shell is 0.57 mm long and 0.4 mm wide (Table 1, Text-fig. 2). It is a non-lobate, triangular shell with rounded corners. The shell bilobations and the sulcation of the dorsal valve appear in specimens about 1 mm long (Text-fig. 2D). Similar ontogenetic changes were observed in *Lambdarina glaphyra* by Bassett and Bryant (1993). In shells up to 1 mm long, dorsal valves are convex, whereas the ventral ones are concave (Text-figs 2B, C, D), similarly as observed in *Lambdarina sinensis* of Baliński and Sun (2008).

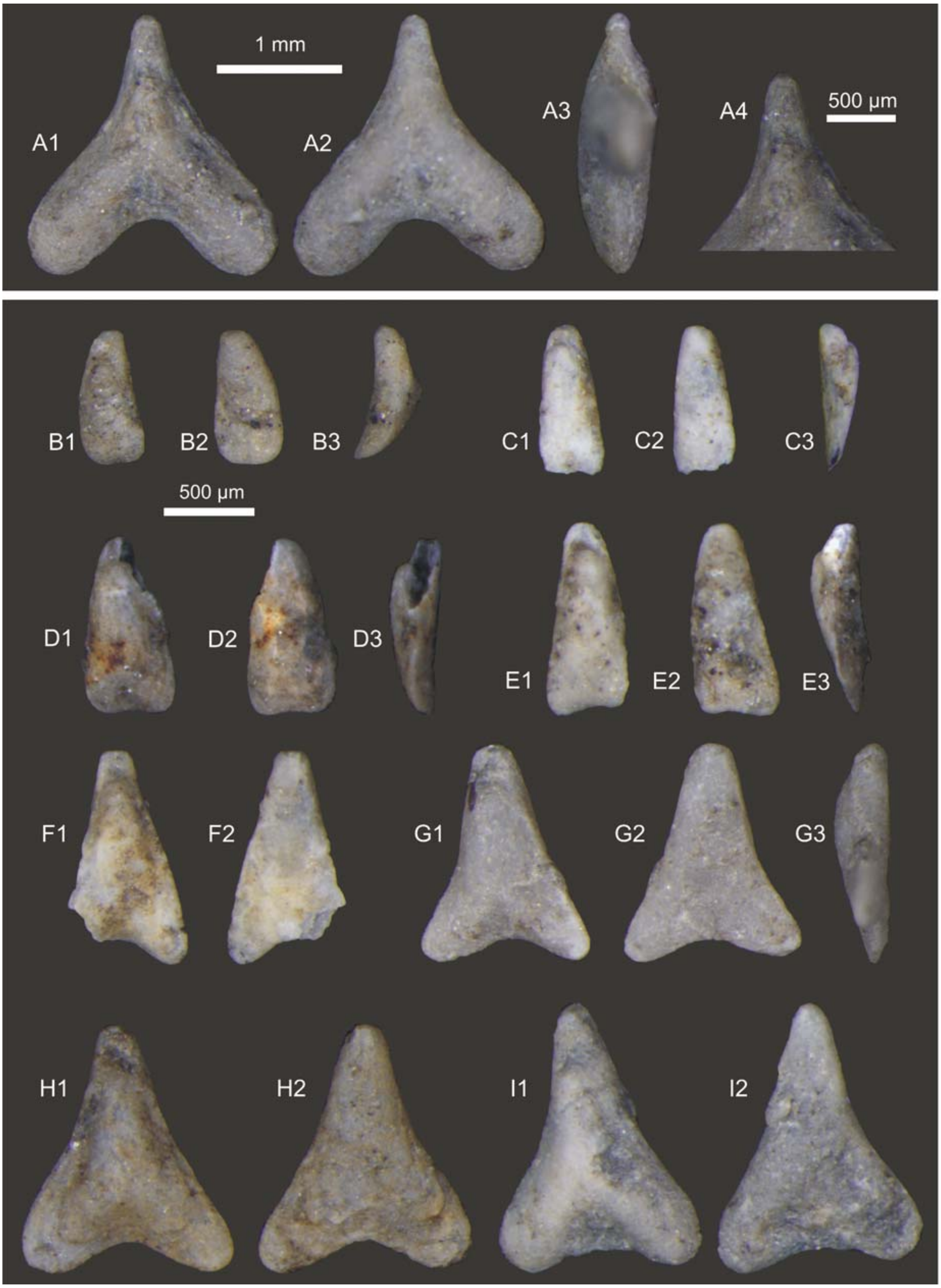
REMARKS: The measurements of the ventral length/width ratio of the holotypes of all known *Lambdarina* species are shown in Text-fig. 6. In this respect, *L. jugowiensis* sp. nov. shows the greatest similarity to *Lambdarina manifoldensis* Brunton and Champion, 1974, but differs from it in lacking the ventral median ridge in the sulcus (Text-figs 6, 7). The lobes in *L. jugowiensis* are commonly asymmetrical, as in *Lambdarina glaphyra* Bassett and Bryant, 1993, from Belgium;

the Polish species, however, is slightly narrower. *L. jugowiensis* sp. nov. has a slightly deeper sulcus and narrower lobes than other species of *Lambdarina*, with the exception of *L. brownendensis* Morris, 1994 and *L. iota* Grant, 1988. The Australian species, *Lambdarina granti* Nazer, 1983, has distinctly broader and shorter lobes and commonly possesses a median fold. *Lambdarina iota* Grant, 1988 from Greece lacks a ventral median ridge, has a shorter ventral umbo, and deeply invaginated lobes.

Text-fig. 7 shows a suggested phylogeny of the genus *Lambdarina,* with the inferred position of *Lambdarina jugowiensis* sp. nov. The first phylogenetic interpretation of the superfamily Lambdarinoidea was

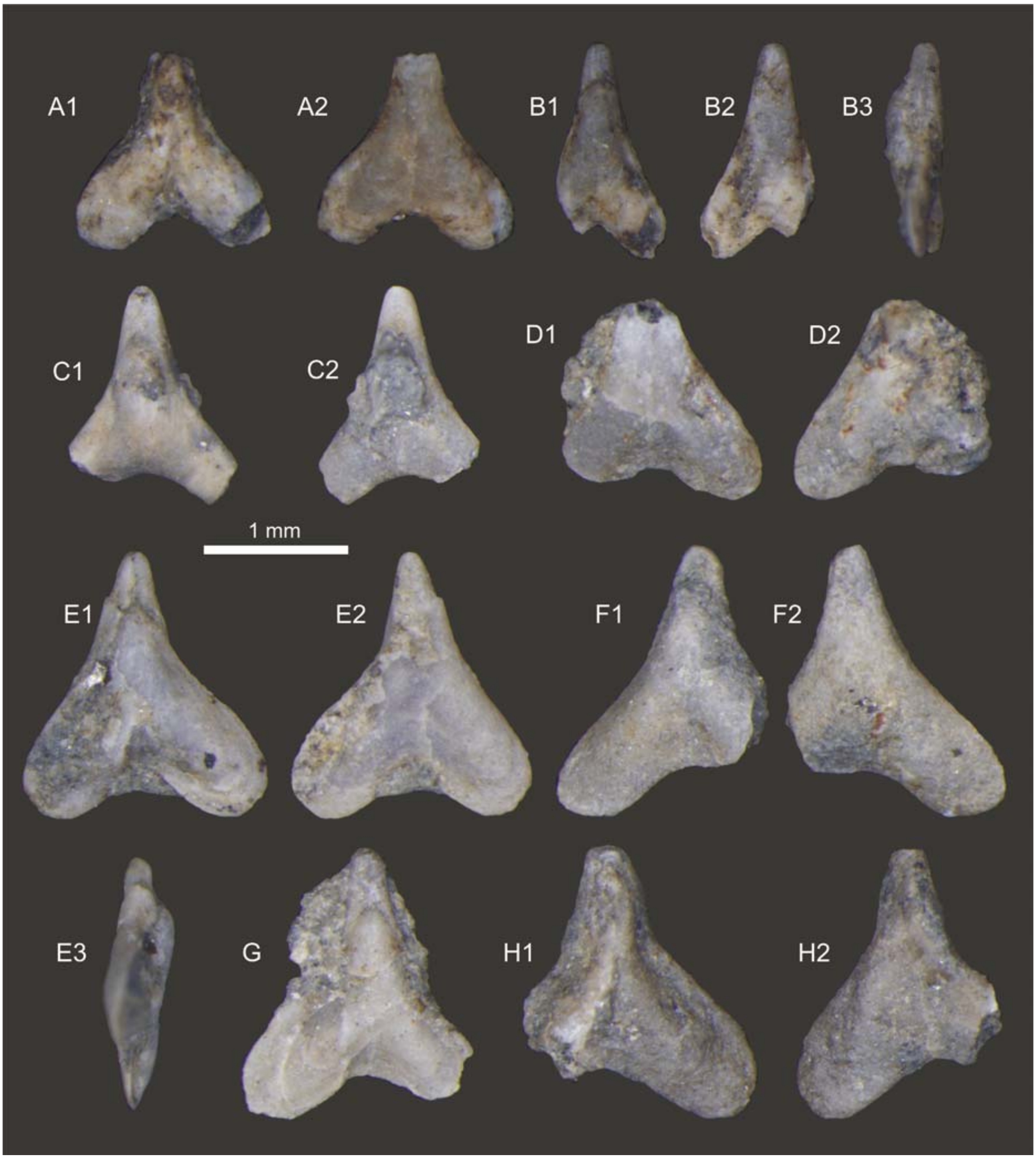
Cat. no. ING/J3-	Ventral length (lv)	Width (w)	Umbo height (uh)	Thickness (th)	Ventral angle (α)
66	0.57	0.41	–	0.24	60
69	0.65	0.51	0.1	0.27	67
65	0.68	0.4	–	0.23	55
70	0.75	0.53	0.13	0.36	76
43	0.78	0.37	0.2	0.3	–
48	0.84	0.35	0.1	0.23	30
57	0.9	0.42	0.12	0.28	45
56	0.94	0.52	–	–	45
60	0.94	0.62	–	–	–
44	0.98	0.54	0.12	0.27	36
54	1.0	0.51	0.14	0.29	36
53	1.03	0.44	–	–	32
55	1.06	0.51	0.14	0.29	34
52	1.21	0.7	0.16	0.31	36
47	1.24	0.96	0.17	0.33	48
49	1.29	0.78	0.23	0.33	38
9	1.39	0.81	0.36	–	39
31	1.41	1.37	–	–	55
11	1.42	1.18	0.22	0.4	53
6	1.43	1.43	–	–	68
14	1.44	1.34	0.44	0.5	61
13	1.51	1.15	0.31	0.43	48
23	1.54	0.96	0.28	0.37	42
18	1.67	1.47	0.34	–	56
17	1.7	1.44	0.38	0.6	56
40	1.72	1.37	0.34	–	60
38	1.8	1.82	0.39	–	66
12	1.82	1.66	0.37	0.49	61
25	1.86	1.42	0.46	0.45	50
16	1.88	1.79	0.39	–	58
20	1.9	2.0	0.1	–	–
15	1.92	1.88	0.26	0.6	60
7	2.13	1.59	0.64	–	51
10	2.15	2.04	0.47	0.67	62
8	2.17	1.74	0.45	–	54
21	2.21	2.38	0.48	0.81	71
5	2.47	2.35	0.54	–	61

Table 1. Dimensions (in mm) of selected specimens of *Lambdarina jugowiensis* sp. nov.

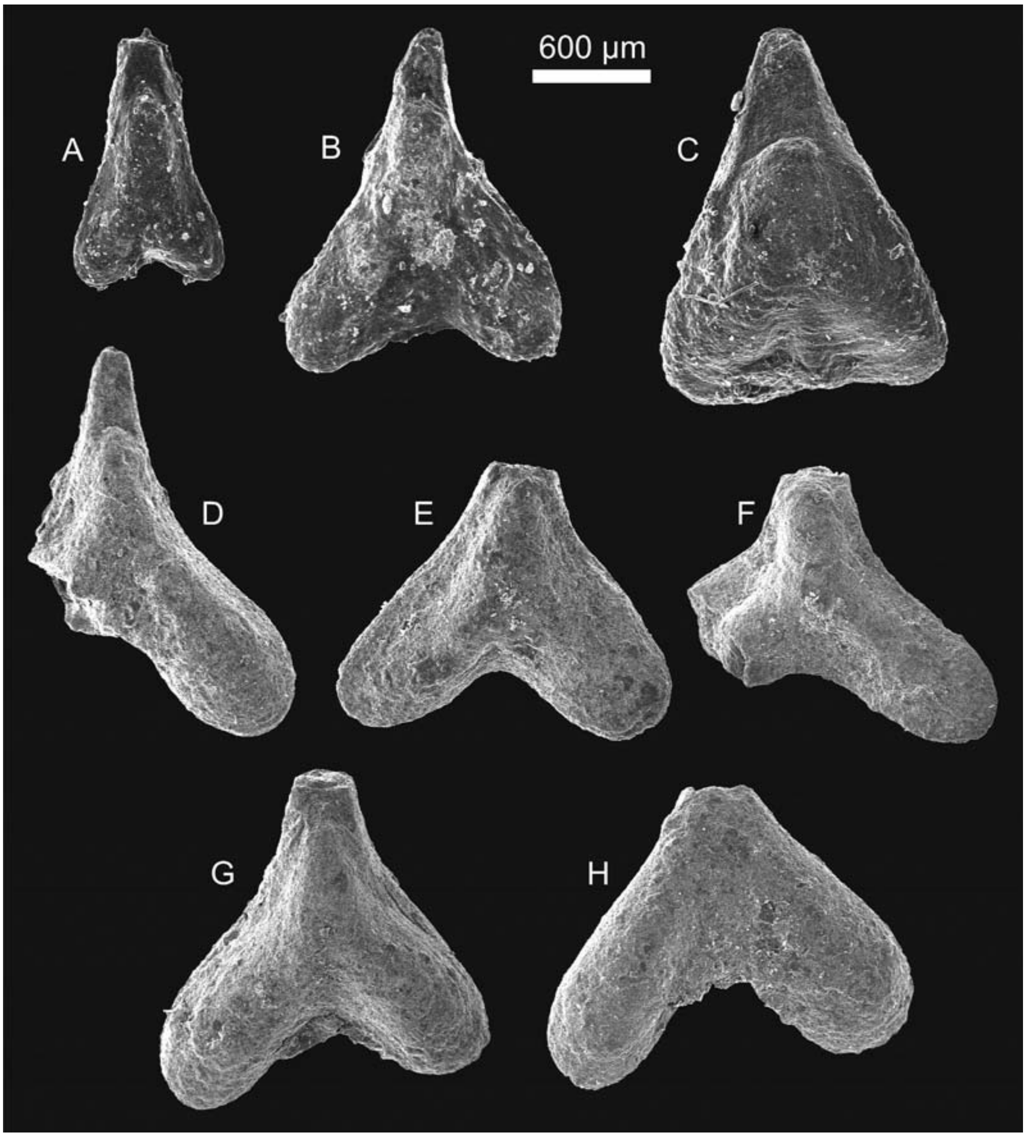


Text-fig. 2. *Lambdarina jugowiensis* sp. nov. A – holotype ING/J3-10, shell in dorsal (A1), ventral (A2), lateral (A3) views. A4 – enlarged detail with symphytium. B–I – paratypes as representative growth series of juvenile shells. B – ING/J3-43. C – ING/J3-48. D – ING/J3-54. E. cat. nr ING/J3-55. F – ING/J3-52. G – ING/J3-47. H – ING/J3-11. I – ING/J3-13. 1 – dorsal, 2– ventral, 3 – lateral views of conjoined shells presented by Baliński and Sun (2008). According to these authors, the shorter and wider shell lobes seem to be a rather primitive feature. They also noted that *L. sinensis* Baliński and Sun, 2008, from the middle Tournaisian, is most similar externally to *L. granti* Nazer, 1983 from the Viséan of Australia. Baliński and Sun (2008) pointed out some differences between the two species. *L. sinensis* is also the smallest species of the genus (Text-fig. 7). It seems that *L. granti* Nazer represents a distinct phylogenetic lineage (Australian) with dominant primitive features, which originated from the Chinese *L. sinensis* Baliński and Sun.

The European species of *Lambdarina* probably formed a separate phylogenetic lineage, which also originated from the Chinese *L. sinensis* Baliński and Sun (Text-fig. 7). The oldest representative of the lineage is



Text-fig. 3. *Lambdarina jugowiensis* sp. nov. A–H. paratypes of various state of preservation, mostly juvenile shells. A – ING/J3-22. B – ING/J3-23. C – ING/J3-29. D – ING/J3-33. E – ING/J3-12. F – ING/J3-15. G – ING/J3-16. H – ING/J3-20. 1 – dorsal, 2 – ventral, 3 – lateral views of conjoined shells. C1. with visible foramen

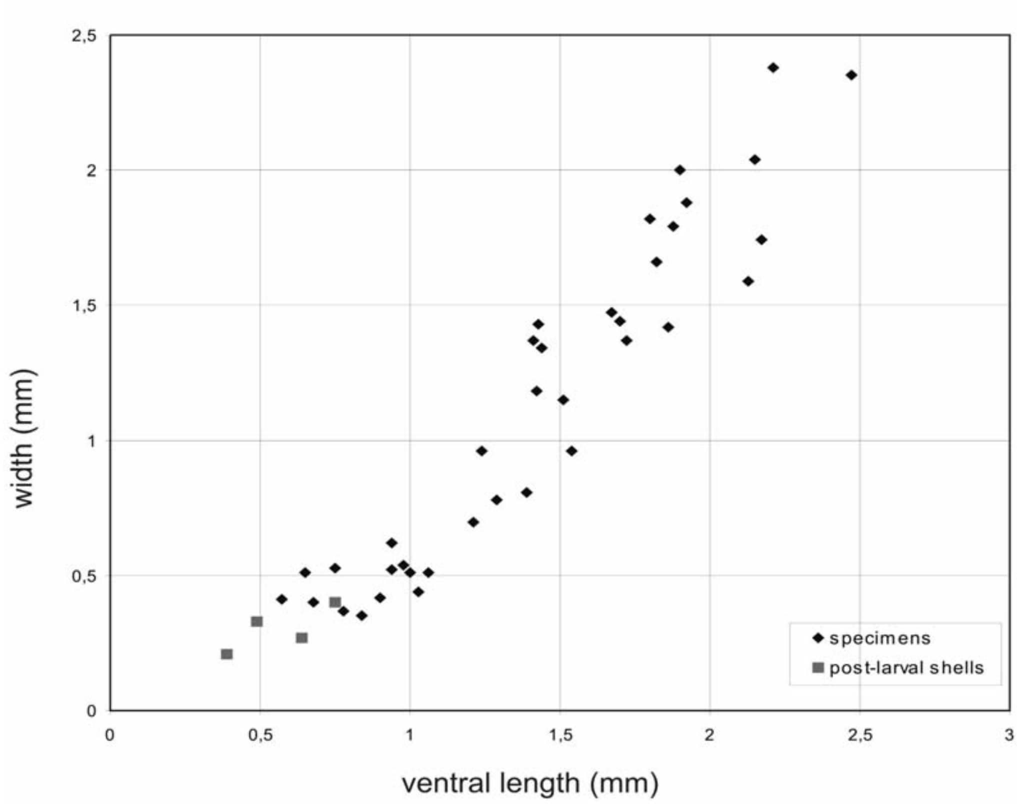


Text-fig. 4. SEM photographs of *Lambdarina jugowiensis* sp. nov. A – ING/J3-9, juvenile shell, dorsal view. B – ING/J3-8, juvenile shell, dorsal view. C – ING/J3-7, juvenile shell, dorsal view. D – ING/J3-5, adult shell, dorsal view. E – ING/J3-2, adult shell, dorsal view. F – ING/J3-3, adult shell, dorsal view. G – ING/J3-1, adult shell dorsal view. H. – ING/J3-4, adult shell, ventral view

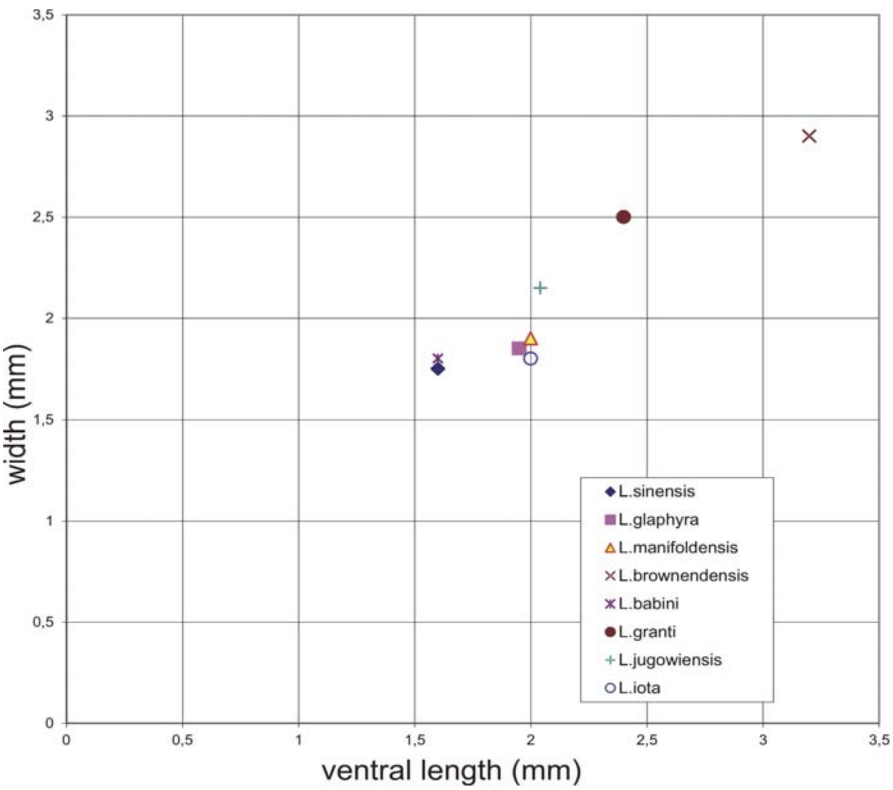
the late Tournaisian *L. glaphyra* Bassett and Bryant, 1993. *L. brownendensis* Morris, 1994 from the lower Viséan of England, represents the largest form with the narrowest and longest lobes. *L. babini* Martínez-Chacón, 1997 has short lobes as a primitive feature, but they are distinctly narrower than in Chinese and Australian species. It differs also in having a wider ventral umbo. The morphological similarity suggests that *L. manifoldensis* Brunton and Champion, 1974 may be the ancestor of both the late Viséan *L. babini* Martínez-Chacón, 1997, described from Spain, and of *L. jugowiensis* sp. nov. described herein from Poland. Unclear remains the ancestor of *L. iota* Grant, 1988, known exclusively from the Upper Permian of Greece. This species is separated from the rest of lambdarinids by a long time-gap, of about 56 myr (Baliński and Sun 2008).

The characteristic feature of the lambdarinids and cardiarinids found in other localities is frequent drilling of their shells by unknown predators, probably gastropods (Cooper 1956; Brunton and Champion 1974; Martínez Chacón, 1997; Hoffmeister *et al*. 2003). No clear drilling traces have been observed on the studied specimens of *L. jugowiensis* sp. nov.

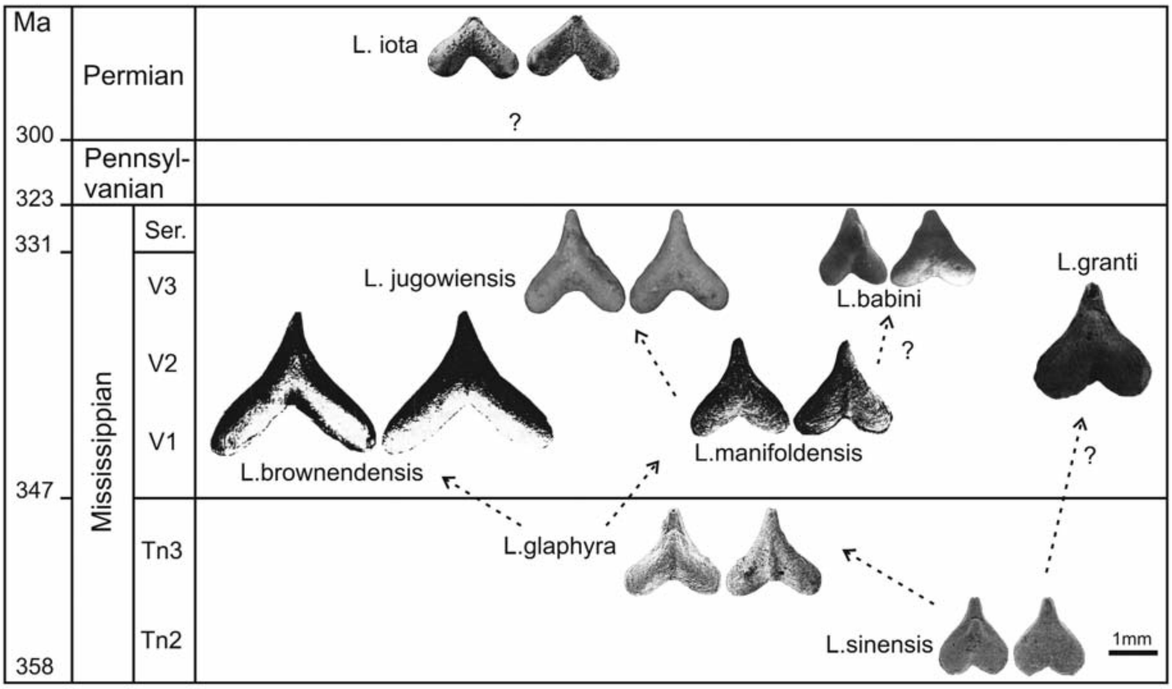
OCCURRENCE: Limestone lenses of the Sokolec Beds of the Jugów 3 section.



Text-fig. 5. Dimensions (in mm) of specimens of *Lambdarina jugowiensis* sp. nov. representing the growth series



Text-fig. 6. Dimensions (in mm) of the holotypes of all known *Lambdarina* species



Text-fig. 7. Presumed phylogenetic relationship among species of the genus *Lambdarina* against stratigraphic time scale. Left form – dorsal view, right form – ventral view

PALAEOECOLOGY AND PALAEOGEOGRAPHY OF LAMBDARINIDS

The life habitat and palaeoecology of lambdarinid and cardiarinid brachiopods is poorly known, mostly because of their scanty records. The existing reports, however, suggest that they are limited to bedded limestones (micrites, biomicrites, biomicrorudites and pelletal levels) and silicified limestones, and are not known in bioherms or reef settings (Brunton and Champion 1974; Grant 1988; Bassett and Bryant 1993; Baliński 1999).

Nazer (1983) suggested that the species lived in clusters, attached by a functional pedicle throughout life, in a relatively quiet-water, carbonate environment. Grant (1988) reviewed the various ecological aspects of all known taxa within the family Cardiarinidae and suggested that low-energy environments were probably their optimum. According to Bassett and Bryant (1993), *Lambdarina glaphyra* colonized low-energy proximal peri-reefal facies (the Leffe facies) adjacent to Waulsortian carbonate mud mounds.

The small size and form of the umbo meant that they probably occurred in clusters occupying small crevices on a rocky sea bottom or they were epiplanktonic, attached to floating plants or other animals (Brunton and Champion 1974; Morris 1994). While such speculative life habits remain equivocal, Bassett and Bryant (1993) noted that many other equally small brachiopods (e.g., the Recent genus *Gwynia*) live benthically, both interstitially in gravels and epifaunally on rocks and pebbles.

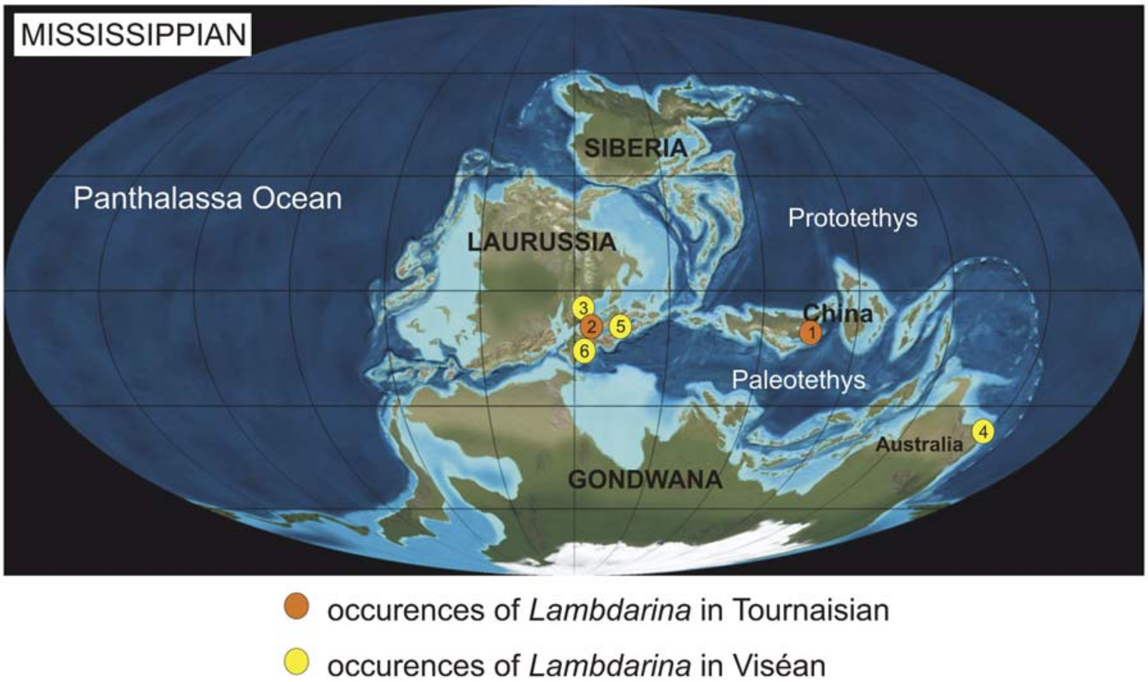
The lambdarinids from Jugów are accompanied by a rich benthic fauna: brachiopods, corals (mainly solitary Rugosa), gastropods, bivalves, crinoids, ostracods and foraminifers with less numerous nektonic cephalopods. The lithological features and composition of the fossil record suggest a shallow marine environment.

So far, *Lambdarina* is known mostly from low latitude equatorial-tropical waters (Text-fig. 8). Only the Australian *L. granti* seemed to occur in higher latitudes, and possibly in slightly colder waters. All European species of *Lambdarina* are limited to the Variscan marginal seas of Laurussia, connected to the Palaeotethys Ocean, to the south.

CONCLUSIONS

As demonstrated by the material studied herein, micromorphic brachiopods also occur as calcified specimens. The acid-etching of limestones is thus not a prerequisite to obtain these tiny brachiopods, as claimed sometimes (Grant 1988).

Lambdarina jugowiensis sp. nov. comes from the upper Viséan limestones of the Góry Sowie Massif, in SW Poland. It differs from all other species of the genus



Text-fig. 8. Palaeogeographic reconstruction for the Mississippian (after Blakey R., unpublished map from http://cpgeosystems.com; last updated July 2011; modified) and distribution of *Lambdarina* species according to stratigraphical order: 1 – China, 2 – Belgium, 3 – England, 4 – Australia, 5 – Poland (Sudetes), 6 – Spain

by sulcus depth, width of lobes and the lack of a median ridge in the sulcus. The Polish specimens reveal a full range of growth stages, from brephic to gerontic. The observed ontogenetic changes are similar to those described by Bassett and Bryant (1993) and Baliński and Sun (2008). Juvenile shells differ from adult shells in having a more slender outline, a shallower sulcus, shorter lobes and a shorter ventral umbo. In shells above 1 mm long both valves (especially ventral valve) become gradually more convex.

So far, *Lambdarina* is known from Europe, China, and Australia, with most of its species limited to the Mississippian. The highest taxonomic richness the genus attained was in the Viséan, with five out of eight known species of this group known from this time (Text-fig. 7). Two main evolutionary lineages of *Lambdarina* are proposed; the Australian and the European ones. The Australian lineage has primitive features including wide and short lobes. The European lineage is characterized mostly by forms with narrower, longer lobes and a deeper sulcus. It seems that both lineages originated from the Chinese species *L. sinensis*. The majority of *Lambdarina* species lived in shallow, low-energy environments of equatorial-tropical waters of the marginal seas of the Palaeotethys Ocean.

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