Devonian athyridoid brachiopods with double spiralia

ANDRZEJ BALIŃSKI

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A double-spired athyridoid, morphologically transitional between Early Devonian *Helenathyris* and Late Devonian *Biernatella* has been identified in the Givetian of the Holy Cross Mts., Poland. It appears that in the course of evolution between these brachiopods dental plates and cardinal plate atrophied. The biernatellids may have developed a diplospiralium independently of Triassic diplospirellids. They originated either from the Siluro-Devonian lineage represented by *Coelospira*, *Anoplotheca*, *Bifida* and *Kayseria* or, more likely, they can be derived from their pre-Devonian common ancestors. Biernatellids were probably well adapted to environments with a poor supply of food. *Eobiernatella rackii* gen. et sp. n., *Biernatella ovalis* sp. n., and *B. lentiformis* sp. n. are proposed.

Key words: athyridoid brachiopods, diplospiralium, phylogenetic relationship, Devonian.

Andrzej Baliński, Instytut Paleobiologii PAN, Aleja Żwirki i Wigury 93, 02-089 Warszawa, Poland.

Introduction

Skeletal support for the lophophore in the form of delicate double spiral coils is very uncommon among Paleozoic and Mesozoic articulate brachiopods. During the course of evolution, however, several spire-bearing brachiopod lineages have developed this unusually elaborate type of brachidium (e.g.: Bittner 1890; Alekseeva 1969; Boucot *et al.* 1969: p. 807; Dagis 1972, 1974; Copper 1973: p. 128; Baliński 1977: p. 178; Campbell & Chatterton 1979). Among the athyridoids the double spiralia devoloped with the appearance of the Siluro-Devonian *Coelospira* or even earlier as suggested by Campbell & Chatterton (1979). This lineage (some authors include it in Dayiidina) was continued until the Middle Devonian when it was represented by double spired *Kayseria* and anoplothecid *Bifida* (Cop-

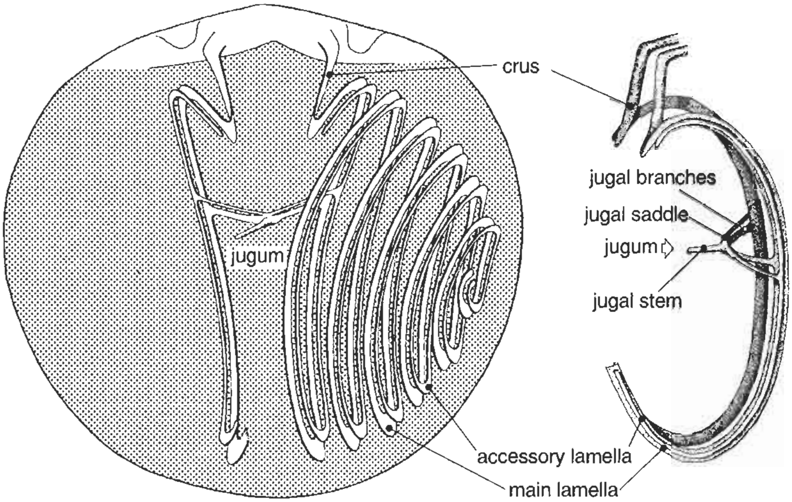


Fig. 1. Structure of diplospiralium and jugum in *Biernatella* Baliński; reconstruction based on serial sections. Not to scale.

per 1973). It is noteworthy that in *Kayseria* the diplospiralium consisted of two lamellae whereas in *Bifida* spiralium was single but with the volutions showing an U-shaped cross-section (Copper 1973: fig. 3, pl. 6: 2). This double-sided spiral lamellae of *Bifida* strongly suggest that their accessory lamellae were fused to the main lamellae (Copper 1973: p. 126), a condition observed occasionally also in *Coelospira* (Campbell & Chatterton 1979).

The second double spired athyridoid lineage developed with the appearance of the Early Devonian *Helenathyris*, then continued through the Middle and Late Devonian biernatellids. Finally, the diplospiralium appeared in the Triassic Diplospirellidae (Fig. 2) and Triassic retziid *Hungarispira* (Dagis 1972, 1974).

It should be mentioned that double spiralia developed also in the Triassic and Jurassic Koninckinidae whose systematic position, however, has been debated. Rudwick (1970) suggested that the koninckinid brachiopods should be included within Strophomenida. Brunton & McKinnon (1972: pp. 408–409) have proved that the shell structure of these brachiopods is typical of the Spiriferida.

Relationships of the Devonian double-spired athyridoids

During the late Silurian — early Devonian two athyridoid lineages developed a fused or divided diplospiralium. One of them is represented by *Coelospira, Bifida*, and *Kayseria* (in the new brachiopod *Treatise* the dayioids will be included as a family of Silurian Athyrida — Copper, written communication). The second lineage includes three genera. The oldest is

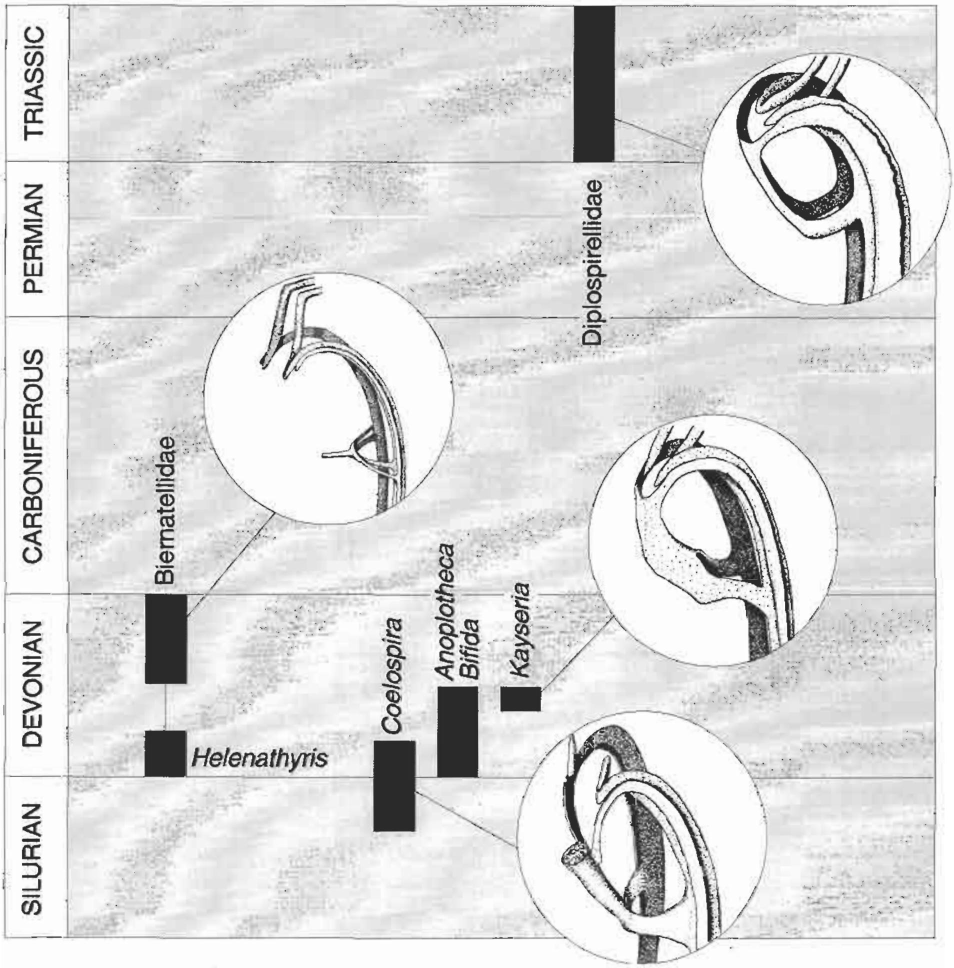


Fig. 2. Distribution of the main stocks of athyridoid brachiopods with diplospiralia. Structure of the jugum in *Coelospira*, *Kayseria*, and diplospirellids after data from Campbell & Chatterton (1979), Copper (1973), and Bittner (1890), respectively.

Helenathyris from the Early Devonian of the Kolyma-Mongolia region of NE Asia (Alekseeva 1969). The youngest Devonian double spired athyridoid, *Biernatella*, is known from the Frasnian of Poland (Baliński 1977). In the present study a third athyridoid genus with diplospiralium is recognized in the Givetian of the Holy Cross Mountains — it is a predecessor of the Frasnian genus *Biernatella* and the name *Eobiernatella* gen. n. is proposed herein. In all the mentioned brachiopods the spirally coiled support for the lophophore consists of two pairs of parallel lamellae. These are: the main lamellae, which project from the crura, and the accessory lamellae, which arise from the jugal saddle or jugal stem. In both cases the accessory lamellae are as long as the main lamellae and both run to the apices of spiralia (Fig. 1).

Although in athyridoid brachiopods with a diplospiralium the accessory spirals are connected with the jugum, their detailed development is different. In *Coelospira* and *Kayseria* the accessory lamellae start as two posteriorly directed outgrowths of a jugal stem. Then, the accessory lamellae approach the beginning of the main lamellae and from this point both run parallel to the ends of spiral coils (Copper 1973; Campbell & Chatterton 1979). In the Triassic Diplospirellidae the formation of accessory lamellae is basically the same, despite a time gap of 150 million years separating them from *Kayseria*. Not surprisingly, it was generally accepted that the diplospiralium evolved independently in these two stocks of athyridoids (Boucot *et al.* 1969: p. 807; Copper 1973: p. 128; Baliński 1977: p. 178). Recently, however, this opinion seems to be disputable (Copper, written communication).

The development of diplospiralia in both helenathyrids and biernatellids is strikingly similar, but different from that of kayseriids and diplospirellids. In the former the accessory lamellae rise from two delicate outgrowths of the jugal saddle which are directed dorsally, not umbonally. The outgrowths run more or less parallel to the branches of jugum (i.e. outgrowths of the main lamellae) and give origin to accessory lamellae in the vicinity of main lamellae (Figs 1–2).

There is a question whether this similarity in the formation of diplospiralium in helenathyrids and biernatellids is superficial or whether it is an expression of phylogenetic relationship. As was pointed out earlier (Baliński 1977) *Biernatella* differs from *Helenathyris* in many important aspects, i.e. in lacking a cardinal plate and distinct dental plates, and in having different shell micro-ornamentation. This morphological as well as stratigraphical gap prompted me (Baliński 1977: p. 179) to include *Biernatella* in the dayioids, as they were defined by Copper (1973). The recent discovery of a similar form in the Middle Devonian throws some new light on the relationship between the biernatellids and *Helenathyris*. The presence of dental plates and a short cardinal plate in the new species (*Eobiernatella rackii*) indicates that it represents an intermediate evolutionary stage between *Helenathyris* and *Biernatella*. The evolutionary process led to gradual atrophy of isolated dental plates by filling in of the dental cavities in the ventral valve and loss of cardinal plate in the dorsal valve, whereas the diplospiralium in this lineage does not show any important morphological change. The origin of this athyridoid lineage is either independent from *Coelospira* and *Kayseria* or, which seems more likely, can be derived from their pre-Devonian common ancestors.

The biernatellids are difficult to identify in the field. Because of their small shell size and simplified external morphology these brachiopods are usually neglected during faunistic investigations. It should be emphasized that the biernatellids can be recognized by the presence of the diplospiralium or by their characteristic shell micro-ornamentation. A thorough field investigation in the Holy Cross Mountains (Racki 1993) yielded several large samples of the biernatellids which are described in the present paper.

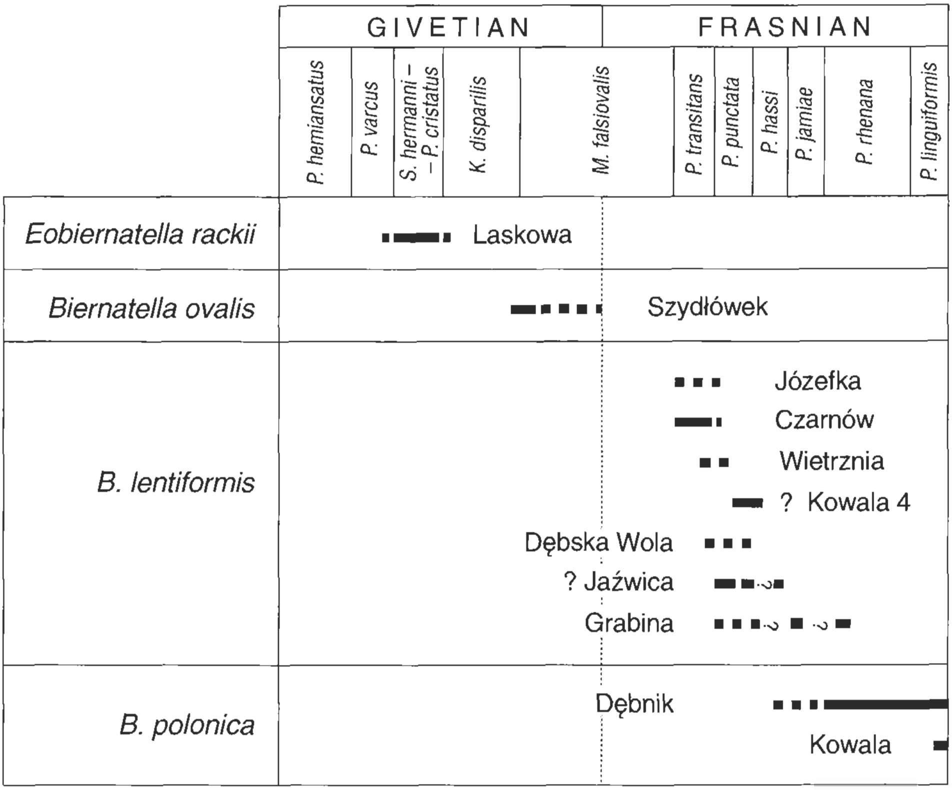


Fig. 3. Stratigraphical and geographical distributions of the biernatellid brachiopods in the Devonian of Poland.

Distribution of the biernatellids

The geologically oldest representative of the family is *Eobiernatella rackii* gen. et sp. n. occuring in the middle Givetian at Laskowa (for details on the localities referred to in the present paper see Racki 1993; here Fig. 3). Currently it is the only species of the genus. In the later part of the Givetian at Szydłówek (Holy Cross Mountains) *Biernatella ovalis* sp. n. occurs and that is the oldest representative of the genus. The related *B. lentiformis* sp. n. occurs at several localities representing the early and middle parts of the Frasnian (Fig. 3). The geologically youngest biernatellid is *B. polonica* (Baliński 1977) from the middle and late Frasnian at Dębnik (Cracow region) and Kowala (Holy Cross Mountains).

Outside Poland there are only two records of biernatellids. A questionable reference to *Biernatella*? sp. comes from the Frasnian of the Pyrenees (Joseph *et al.* 1980). An unnamed species of *Biernatella* was reported from the Frasnian of Timan (Russia) by Yudina (1994). However, there is no doubt, that biernatellid brachiopods may be much more common than can be inferred from the literature. They may be present in Frasnian samples of E. Maillieux's collection housed at the Institut royal des Sciences naturelles de Belgique (Bruxelles), examined by myself in 1985.

Evolution of the biernatellids

Internal shell structure of *Eobiernatella rackii* is basically typical for athyridoids in having dental plates in the ventral valve and a short cardinal plate in the dorsal valve (Fig. 5). The diplospiralium is fully developed and the jugum well preserved in one of the sectioned shells (Fig. 5C: distance 3.1); as in *Biernatella*, it originated at a distance of about 3 mm from the ventral valve umbo by convergent, ventrally directed outgrowths from the main lamellae. The outgrowths, forming the lateral branches of the jugum, arise medially at about the commissural plane of the shell. A long median rod-like jugal stem protrudes ventrally from the jugal saddle (Fig. 5: distance 3.1). Accessory lamellae are more delicate than the main lamellae and run parallel to the latter till the apices of the spiralia. There are up to six volutions of the spiralia in *E. rackii*.

In the later part of the Givetian the genus *Biernatella* appears, which continues until the latest Frasnian. It is represented by three species, i.e. *B. ovalis*, *B. lentiformis*, and *B. polonica*. All these species are characterized by filling of the dental cavities and loss of cardinal plate leading to a significant simplification of internal shell structure. In comparison to *Eobiernatella*, however, the diplospiralium of *Biernatella* does not show any important change. Its structure was studied in detail in several well-preserved, sectioned specimens of *B. lentiformis* (Figs 10–11). The crura start from long crural bases protruding perpendicular to the valve (Fig. 10A: distance 0.8 and 1.2). They extend anteriorly and attach to the primary lamellae of the spiralium. From these points, the primary lamellae deflect posteriorly and then curve gently dorsally, following the internal concavity of the dorsal valve. At about one-third of the shell length from the umbo two ventromedially directed outgrowths (jugal branches or processes) of the main lamellae appear. They are gently arched to coincide at the shell plane of symmetry to form the jugum (Figs 10A: distance 2.3–2.4, 10B, 10C: distance 2.7, 11A: distance 1.65–1.7). From the jugal saddle two delicate blades extend dorsally, subparallel to the jugal processes (e.g. Fig. 10A: distance 2.3–2.4). At their dorsal ends the blades form the accessory lamellae which extend in both directions, i.e. umbonally and anteriorly. The umbonal extensions of the accessory lamellae end near the tips of the crura, while anteriorly they parallel the main lamellae to their apices (Figs 10A: distance 2.9, 10C: distance 3.4). The accessory lamellae are narrower, and more delicate than the main lamellae and are angled from them at about 25–35°. A jugal stem is seen as a long, fairly massive and ventrally directed spine (e.g. Fig. 10A: distance 2.3).

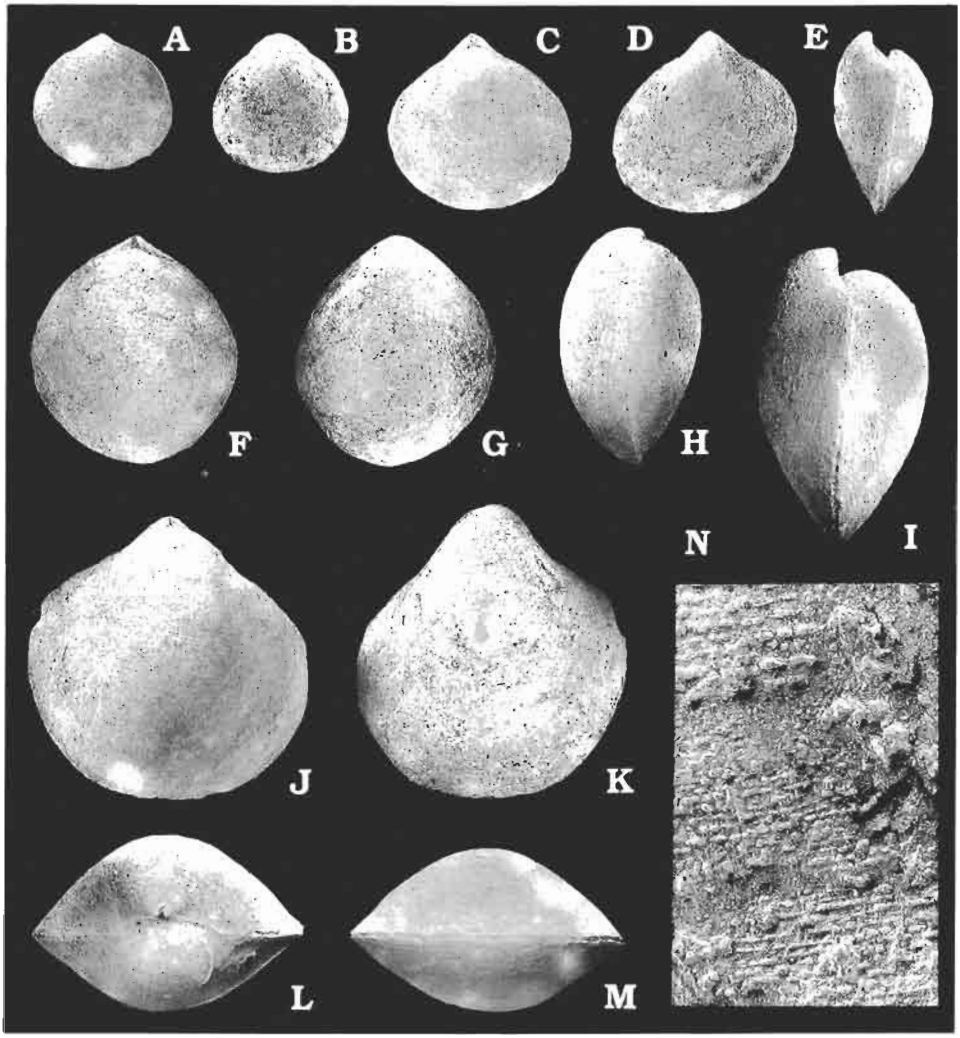


Fig. 4. A–N. *Eobiernatella rackii* gen. et sp. n., Givetian Laskowa Góra Beds of Laskowa in the Holy Cross Mts., Poland. ❑A–B. Juvenile specimen ZPAL Bp XXXVIII/2 in dorsal and ventral views. Dimensions (in mm): length (l) = 4.9, width (w) = 4.6, thickness (t) = 2.4. ❑C–E. Shell ZPAL Bp XXXVIII/9a in dorsal, ventral, and lateral views: l = 5.9, w = 5.9, t = 3.3. ❑F–H. Shell ZPAL Bp XXXVIII/5 in dorsal, ventral, and lateral views: l = 8.1, w = 6.7, t = 4.6. ❑I–M. Holotype ZPAL Bp XXXVIII/7 in lateral, dorsal, ventral, posterior, and anterior views: l = 9.6, w = 9.2, t = 5.9. ❑N. Shell ZPAL Bp XXXVIII/8, micro-ornamentation. All × 4; except for N that is × 35.

Biernatellids, as in other spire-bearing brachiopods, fed and breathed using a ciliated spirolophe-type of lophophore. The more complex skeletal support for the lophophore in biernatellids suggests a greater complexity in structure of the lophophore itself, and greater efficiency of this respiratory and feeding organ. Many biernatellids, however, can be found in sediments deposited in quite vigorous, well-aerated environments (Baliński 1977).

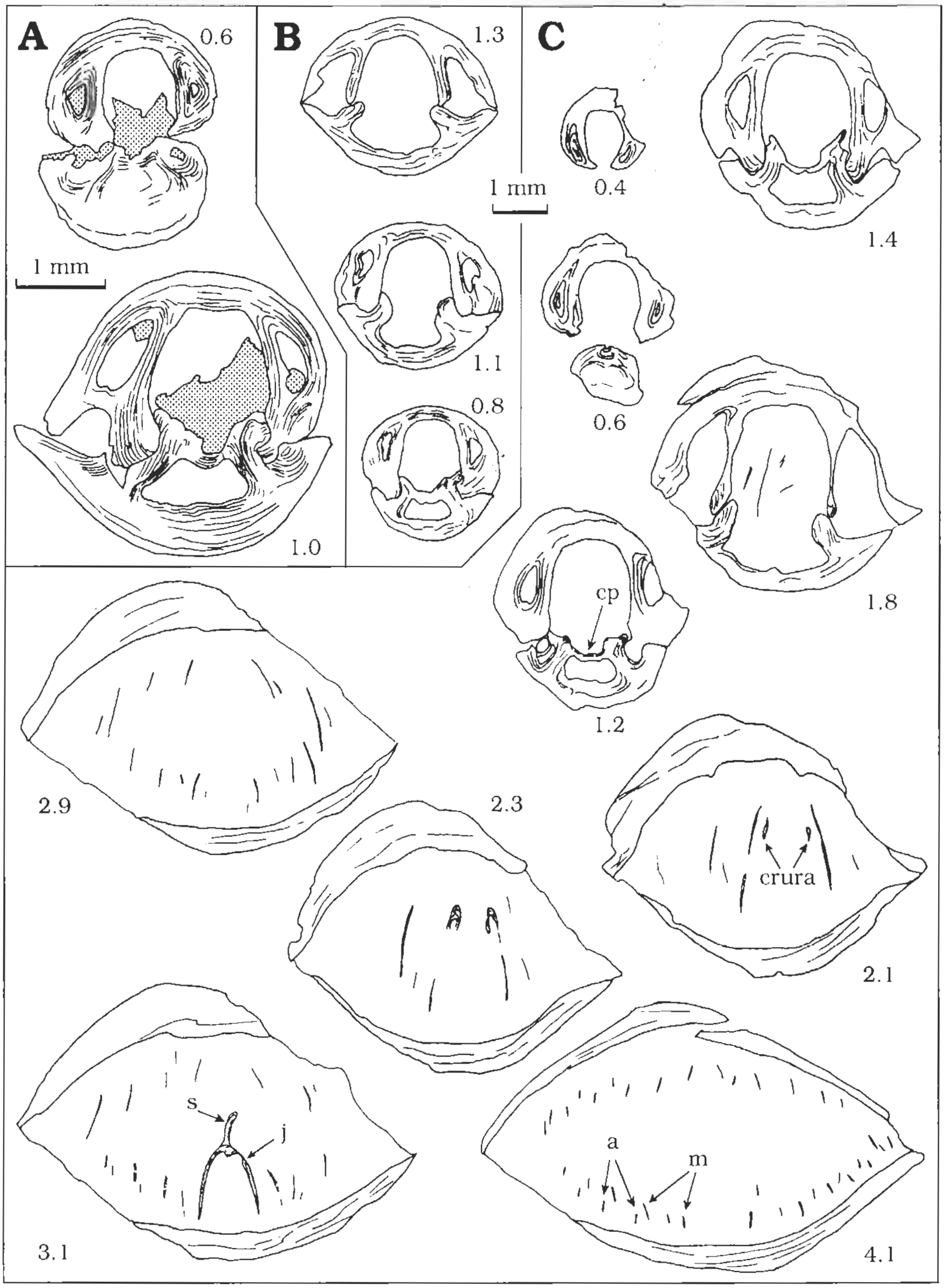


Fig. 5. Transverse serial sections of three specimens of *Eobiernatella rackii* gen. et sp. n. from Laskowa. Numbers refer to distances in mm from the ventral apex. Abbreviations: a — accessory lamellae, cp — cardinal plate, j — jugum, m — main lamellae, s — jugal stem.

Thus, the development of a diplospiralium in these brachiopods cannot simply be explained by adaptation to environments deficient in oxygen, as

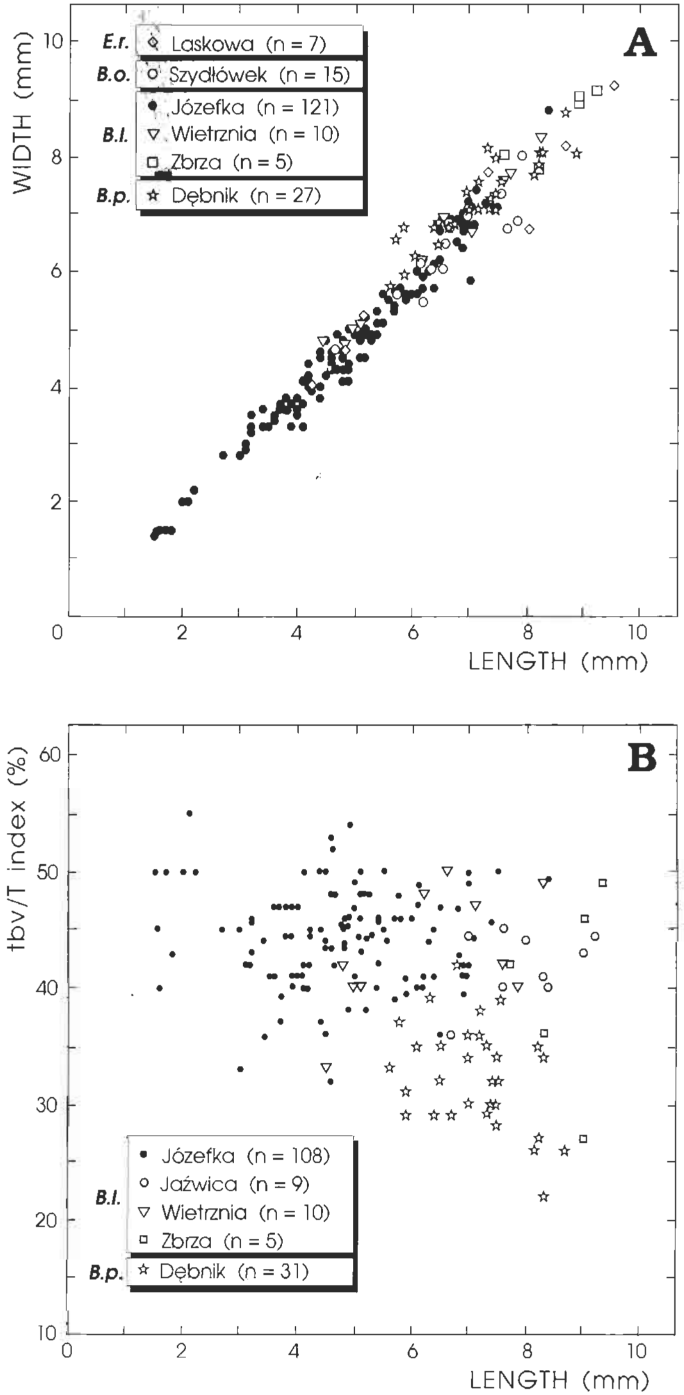


Fig. 6. A scatter diagram of length against width of shells (A) and of length against thickness index of dorsal valve (B) in species of biernatellids from major occurrences in Poland. *E.r. — Eobiernatella rackii*, B.l. — *Biernatella lentiformis*, *B.o. — B. ovalis*, *B.p. — B. polonica*.

those typified by Kellwasser-facies, which were wide-spread in the Late Devonian. It is possible that they were adapted to environments with a low supplies of food. In their very carefully done studies, Campbell & Chatterton (1979) discussed in details the possible function and structure of the lophophore in double spiral *Coelospira*. The authors claimed that this athyridoid possessed a double lophophore with two food grooves and with very short filaments. It is highly probable that biernatellid brachiopods were equipped with a similarly structured lophophore.

Systematic Palaeontology

Suborder Athyrididina Boucot, Johnson, & Staton 1964
Superfamily Athyridacea Davidson 1881
Family Biernatellidae Baliński 1977

Emended diagnosis. — Small smooth shelled, ventribiconvex athyridoids with very small ventral interarea; dental plates and cardinal plate in earlier taxa. Accessory lamellae extending from jugal saddle and continuing parallel to main lamellae to their apices. Micro-ornamentation of very dense concentric lamellae forming frilly projections.

Genera assigned. — *Biernatella* Baliński 1977 and *Eobiernatella* gen. n.

Occurrence. — Middle Devonian (Givetian) to Late Devonian (Frasnian) of Poland; Frasnian of Timan (Russia) (Yudina 1994); probably Late Devonian (Frasnian) of the Pyrenees (Joseph *et al.* 1980).

Eobiernatella gen. n.

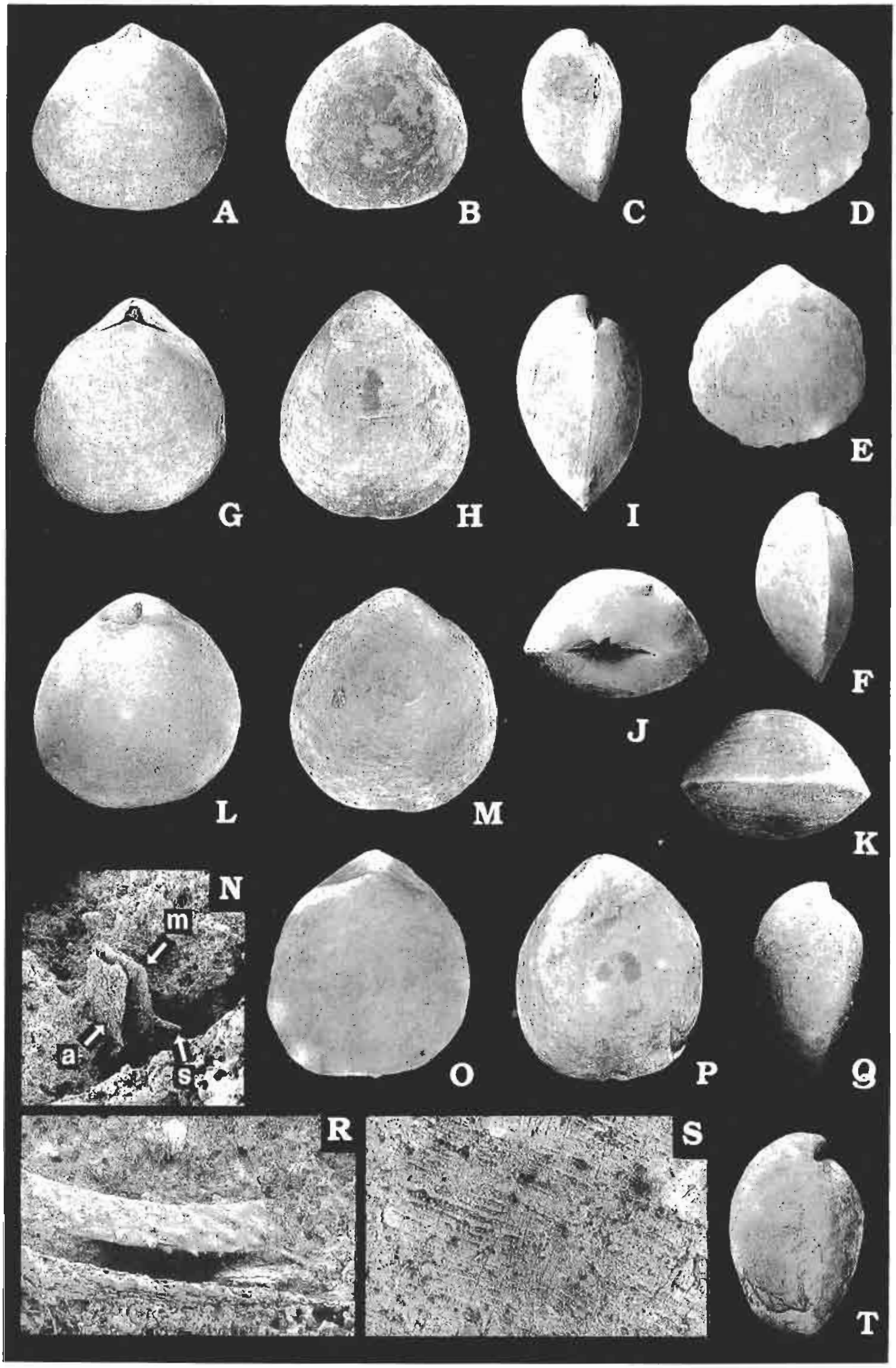
Type species: *Eobiernatella rackii* sp. n.

Derivation of the name: An early representative of the family and the predecessor of *Biernatella*.

Diagnosis. — A biernatellid with dental plates and cardinal plate.

Remarks. — The new genus differs from *Biernatella* mainly in internal morphology of the shell. In the new genus it has distinct dental plates, surrounding prominent dental cavities, and a short cardinal plate inside the dorsal valve. Both structures are missing in adult shells of *Biernatella*. Internally *Eobiernatella* displays great similarity to *Helenathyris* described

Fig. 7. ❑ A–C, G–M, O–Q, S–T. *Biernatella ovalis* sp. n. Givetian Szydłówek Beds of Szydłówek, Holy Cross Mts., Poland. A–C. Shell ZPAL BP XXXVIII/25-8 in dorsal, ventral, and lateral views: l = 6.7, w = 6.7, t = 3.8. G–K. Holotype ZPAL BP XXXVIII/25-10 in dorsal, ventral, lateral, posterior, and anterior views: l = 7.7, w = 6.7, t = 4.6. L–M, Q. Shell ZPAL BP XXXVIII/25-5 in dorsal, ventral, and lateral views: l = 7.6, w = 7.3, t = 4.2. O–P, T. Shell ZPAL BP XXXVIII/25-9 in dorsal, ventral, and lateral views: l = 7.9, w = 6.8, t = 4.3. S. Shell ZPAL BP XXXVIII/25-8, micro-ornamentation. All × 4, except for S that is × 50. ❑D–F, N, R. *Biernatella polonica* Baliński 1977. Frasnian of Dębnik in the Cracow region. D–G. Shell ZPAL BP XXIII/31d in dorsal, ventral and lateral views: l = 7.0, w = 6.8, t = 3.5. N. Weathered specimen ZPAL Bp XXIII/30g with partially exposed one pair of spiral lamellae with spines (s): a — accessory lamella, m — main lamella. R. Fragment of spiral lamella with preserved ornamentation in specimen ZPAL Bp XXIII/30f. D–F × 4, N × 35, R × 25.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from the Early Devonian of Siberia (Alekseeva 1969). Both genera share the presence of dental plates, dental cavities, a cardinal plate, and diplospiralium. The diplospiralium shows an almost identical mode of development. *Eobiernatella* differs from *Helenathyris* in its different shell micro-ornamentation with the latter possessing long hair-like spines, similar to those of *Nucleospira*.

Species assigned. — Type species only.

Eobiernatella rackii sp. n.

Figs 4–5.

Holotype: ZPAL BP XXXVIII/7.

Type locality: A hill N of the village Laskowa at latitude 50°55′45″N and longitude 20°33′05″E, Holy Cross Mts., Poland.

Type horizon: Lower part of the Laskowa Góra Beds, Givetian.

Derivation of the name: From Dr. Grzegorz Racki, the donor of the studied specimens.

Diagnosis. — Shell ventribiconvex, about 10 mm in length, subcircular to suboval in outline. Ventral valve with high, protruding umbo and high narrow interarea or palintrope. Dorsal valve with swollen umbonal part.

Material. — Eleven complete shells and sixteen specimens of incomplete and crushed shells.

Description. — Adult shell about 10 mm in length, ventribiconvex, subcircular to suboval in outline, width and length subequal. Hinge line angular especially in large specimens, lateral and anterior margins rounded, anterior commissure rectimarginate.

Ventral valve gently convex with high, protruding umbonal part; palintrope (or small, narrow interarea) is high, anacline. Delthyrium high and open except at lateral borders where narrow deltidial plates are developed. Dorsal valve subelliptic to subcircular in outline, gently convex with more swollen umbonal part, less convex than ventral valve.

Interior of the ventral valve with short but distinct dental plates and cavities (Fig. 5); the median septum is lacking; teeth are relatively strong. Dorsal valve interior with a very short cardinal plate (Fig. 5A–C; diplospiralium is described in the section on the evolution of biernatellids on page 134).

Micro-ornamentation consists of very densely arranged (about 30 per 1 mm) concentric frilly lamellae (Fig. 4N).

Remarks. — Besides the internal structure of the shell, *E. rackii* differs from species of *Biernatella* by its more protruding ventral umbo and higher ventral interarea. Generally the proportion of the main shell dimensions are the same as in species of *Biernatella* (Fig. 6).

Occurrence. — The species occurs in marly, fossiliferous (mostly biostromal) limestones with shaly intercalations representing the lower part of the Laskowa Góra Beds (Givetian) cropping out near Laskowa in the northern Kielce region of the Holy Cross Mountains. It was listed from there as a new species of *Biernatella* in Racki *et al.* (1985: p. 166).

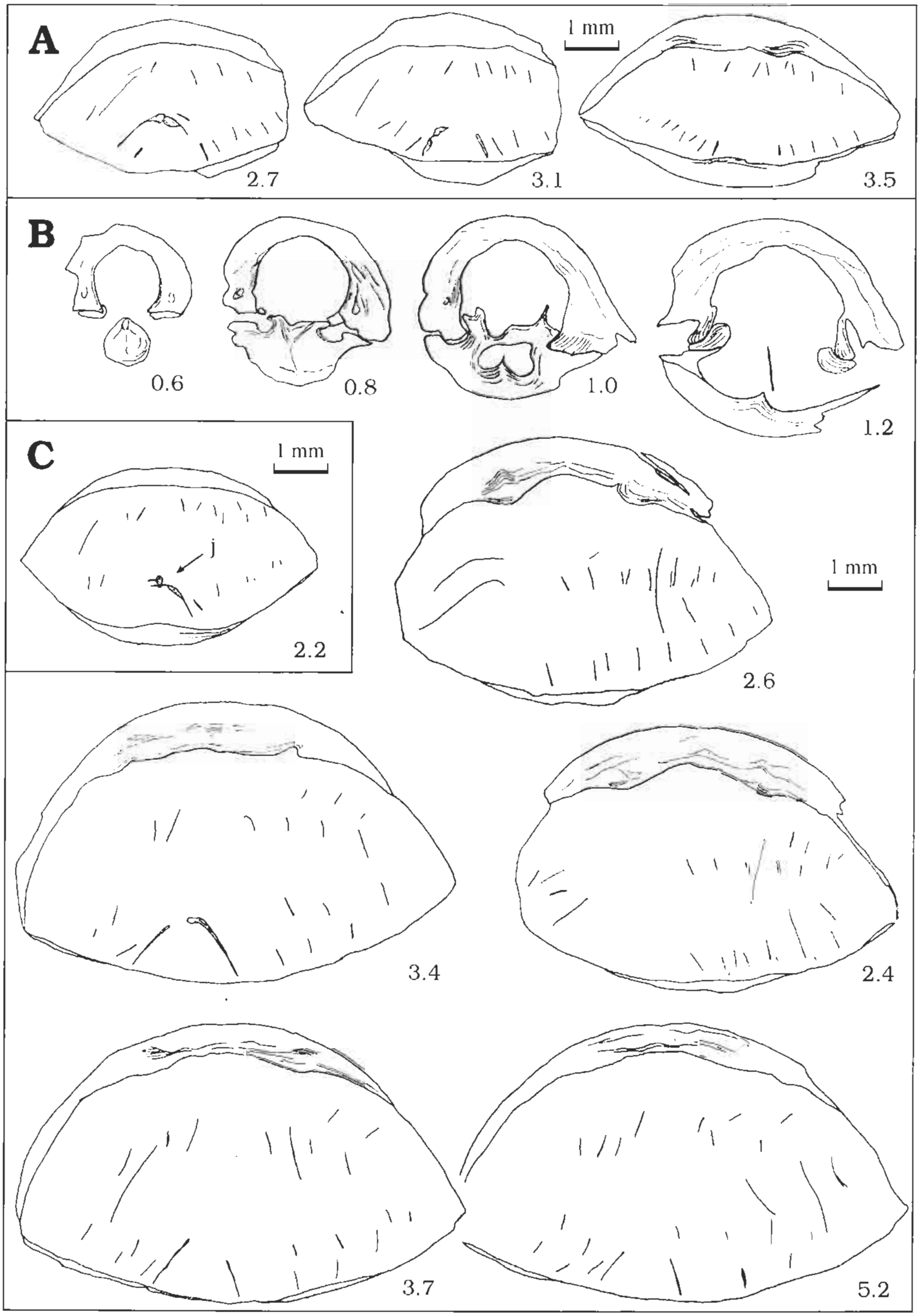


Fig. 8. Transverse serial sections of shells of *Biernatella ovalis* sp. n. from Szydłówek (A) and *Biernatella lentiformis* sp. n. from Dębska Wola (B) and Wietrznia (C). Numbers refer to distances in mm from the ventral apex. Abbreviation: j — jugum.

Genus *Biernatella* Baliński 1977

Biernatella ovalis sp. n.

Figs 7A–C, G–M, O–Q, S–T, 8A.

Holotype: ZPAL Bp XXXVIII/25-10.

Type locality: In a ditch, eastern Bocianek suburb of Kielce at latitude 50°53′10″N and longitude 20°39′50″E.

Type horizon: Szydłówek Beds, lower fossiliferous part (late Givetian).

Derivation of the name: *ovalis* – from the characteristic outline of the shell.

Diagnosis. – Suboval shell outline; shell length greater or subequal to the shell width, up to ca. 8 mm in length; maximum shell width situated anteriorly.

Material. – Sixteen complete shells, well preserved externally.

Description. – Shell up to 8.1 mm in length, ventribiconvex to subequal, suboval in outline, shell length greater or subequal to the shell width; maximum shell width is situated in the anterior half of the shell. Hinge line short, especially in wide specimens, slightly angular; lateral and anterior margins rounded in wide specimens to slightly arched or nearly straight in narrower forms.

Ventral valve regularly convex with massive umbonal part; small inter-area present; delthyrium open, beak erect to incurved. Dorsal valve subtrapezoidal in outline; valve thickness index (proportion of the dorsal valve thickness to the shell thickness) ranging from 33 to 53% (mean = 39%). Interior of ventral valve without dental plates; dorsal valve with diplospiralium (Fig. 8A).

Micro-ornamentation well preserved, consisting of very densely distributed concentric frilly lamellae (Fig. 7S).

Remarks. – The species is characterized by its subovate shell outline; it differs from *B. polonica* and *B. lentiformis* by its slightly narrower shell, less rounded antero-lateral margins, and by the maximum shell width being situated more anteriorly.

Occurrence. – *Biernatella ovalis* sp. n. occurs in the lower part of the Szydłówek Beds representig a late part of the Givetian (see Racki 1993). It was mentioned as a new species of *Biernatella* in Racki *et al.* (1985: p. 169).

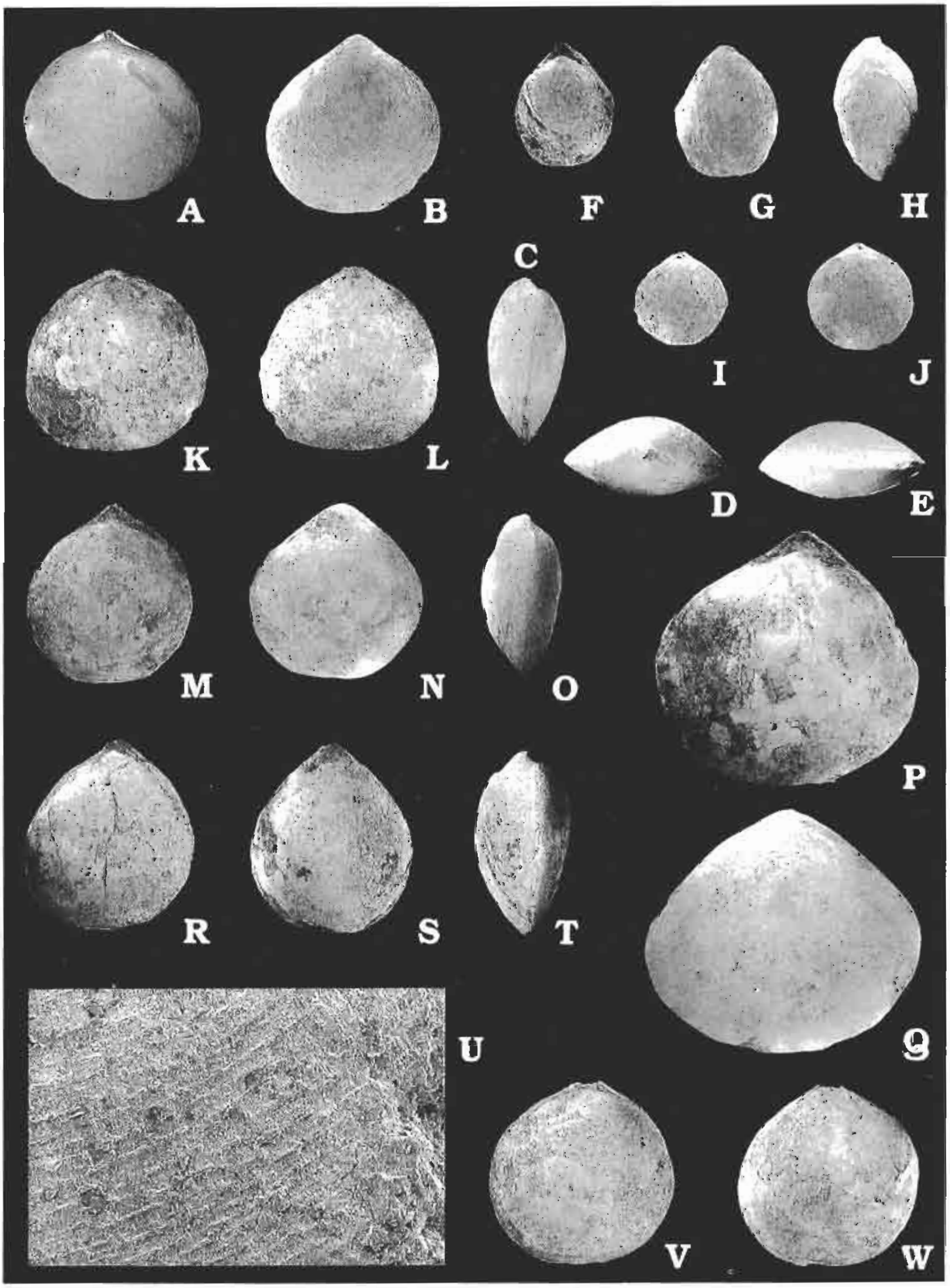
Biernatella lentiformis sp. n.

Figs 8B–C, 9–11.

Holotype: ZPAL Bp XXXVIII/32-76.

Type locality: An escarpment of the road leading from Górno to Daleszyce, S part of Józefka hill, 1.4 km S of the village Górno at latitude 50°50′30″N and longitude 20°48′25″E, northern Kielce region of the Holy Cross Mountains.

Fig. 9. ❑ A–W. *Biernatella lentiformis* sp. n. Frasnian Wietrznia Beds of Józefka in the Holy Cross Mts., Poland. ❑A–E. Holotype ZPAL BP XXXVIII/32-76 in dorsal, ventral, lateral, posterior, and anterior views: l = 5.8, w = 5.7, t = 2.8. ❑F–H. Juvenile shell ZPAL BP XXXVIII/32-22 in dorsal, ventral, and lateral views: l = 4.1, w = 3.3, t = 2.4. ❑I–J. Two juvenile shells ZPAL BP XXXVIII/35a, b in dorsal view. ❑K–L. Shell ZPAL BP XXXVIII/32-85



in dorsal and ventral view: l = 6.5, w = 6.2, t = 3.6. ❑M–O. Shell ZPAL BP XXXVIII/32-75 in dorsal, ventral, and lateral views: l = 5.9, w = 5.6, t = 3.0. ❑P–Q. Large shell ZPAL BP XXXVIII/32-97 in dorsal and ventral views: l = 8.4, w = 8.8, t = 4.7. ❑R–T. Shell ZPAL BP XXXVIII/83 in dorsal, ventral, and lateral views: l = 6.4, w = 5.7, t = 3.4. ❑U. Shell micro-ornamentation in specimen ZPAL BP XXXVIII/33. ❑V–W. Shell ZPAL BP XXXVIII/32-81 in dorsal and ventral views: l = 6.2, w = 6.2, t = 3.0. All × 4, except for I–J that are × 8, and U × 70.

Type horizon: Middle part of the Wietrznia Beds; early part of the Frasnian.
Derivation of the name: *lentiformis* — from the shape of the shell.

Diagnosis. — Subcircular shell outline, ventribiconvex to subequal, lenticular in shape, up to 9.4 mm in length.

Material. — Over 1600 specimens of shells from four localities.

Description. — Shell up to 9.4 mm in length, ventribiconvex to subequal, subcircular in outline, as long as wide; hinge line short, angular to arched, antero-lateral margins rounded.

Ventral valve with very small interarea; beak small, suberect; median sulcus lacking. Dorsal valve circular in outline, slightly less convex than the ventral valve.

Interior of the ventral valve without dental plates. Dorsal valve interior with diplospiralium basically the same as in *Biernatella polonica* (Figs 8B–C, 10–11; described in detail in the section on the evolution of biernatellids on page 134).

Shell micro-ornamentation as for the genus, but rarely preserved; density of concentric lamellae averages 32 in 1 mm (Fig. 9U).

Remarks. — *Biernatella lentiformis* is close to *B. polonica*. The main difference between them is the convexity of the valves: in *B. lentiformis* the ventral valve is not as deep, and its umbo is not as massive and swollen as in the latter species. The dorsal valve is evidently more convex in *B. lentiformis* and attains 46% of the total shell thickness, in comparison to 32% in *B. polonica* (Fig. 6). The shell wall posteriorly is much thinner in *B. lentiformis* than in *B. polonica*.

Occurrence. — This is a very common species in the detrital and marly limestones that crop out on the S part of Józefka hill near Górno (for details on locality see Małkowski 1981). The limestones are referred to the middle part of the Wietrznia Beds, which can be correlated with *P. transitans* to *P. punctata* Zones (early part of the Frasnian; Racki 1993). Two specimens were found in detrital limestones in the trench IIa at Czarnów (the early part of Frasnian). Six specimens come from brachiopod micritic limestones of Dębska Wola (*Phlogoiderhynchus* Level) and nineteen specimens come from set C of the Wietrznia Beds that crop out at Wietrznia I quarry (listed as *Biernatella*? in Racki *et al.* 1993: p. 85). Both localities represent the *Palmatolepis transitans* to *P. punctata* conodont Zones (Racki 1993). The species probably occurs also at the Kowala 4 quarry in the Detrital Beds, and at Jaźwica in the *Phlogoiderhynchus* Level and the Detrital Beds, but those specimens preserve neither any micro-ornamentation nor presence of a diplospiralium. Several shells embedded in rock which were found at Grabina quarry in loose block of detrital limestone (set B to C of the Detrital-Stromatoporoid Beds) probably represent *B. lentiformis* sp. n.

Biernatella polonica Baliński 1977

Fig. 7D–F, N, R.

Biernatella polonica gen. et sp. n.; Baliński 1977: pp. 179–183, Figs 2–4, Pls 9–10.
Biernatella polonica Baliński; Baliński 1979: p. 61, Pl. 10: 4.

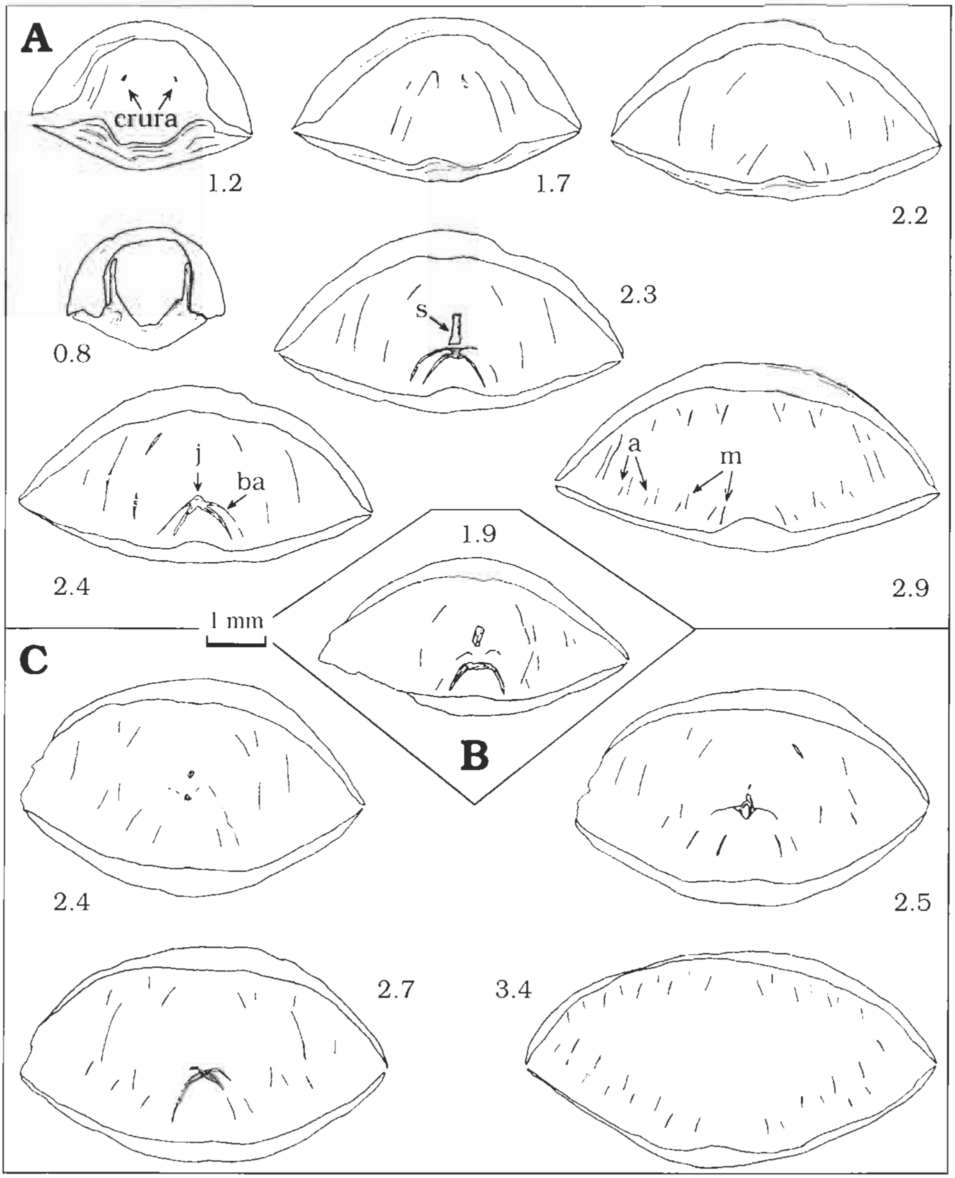


Fig. 10. Transverse serial sections of three specimens of *Biernatella lentiformis* sp. n. from Józefka. Numbers refer to distances in mm from the ventral apex. Abbreviation: ba — beginning of accesorry lamella; other as in Fig. 5.

Material. — Over 20 complete shells, 30 damaged shells and more than 80 fragments. Specimens frequently with exfoliated valves, some partially silicified.

Description. — See Baliński (1977).

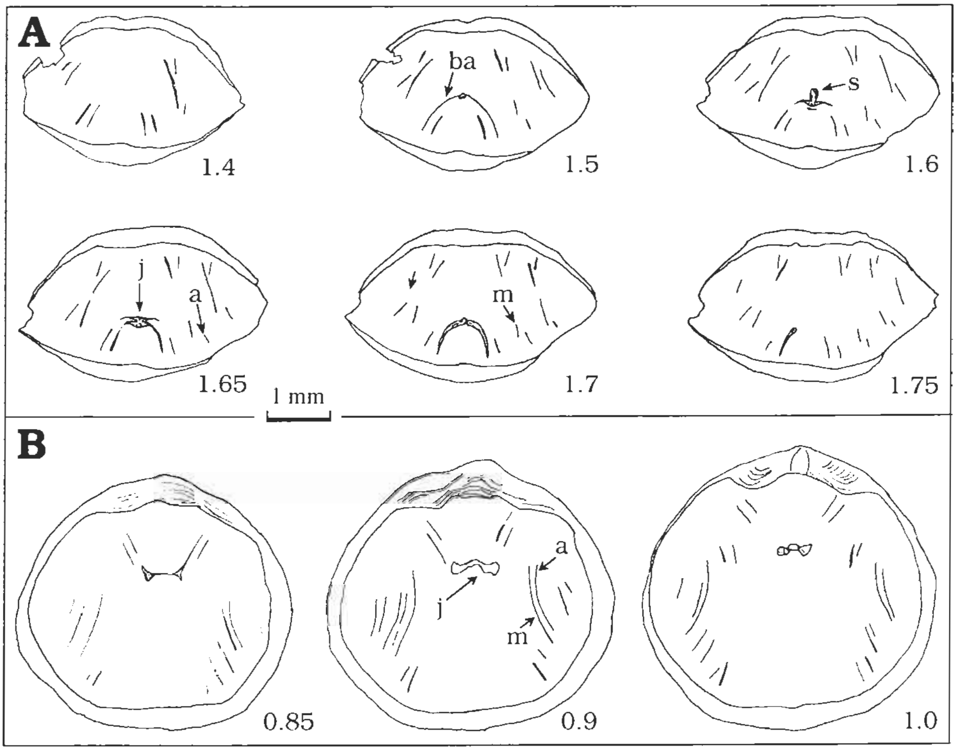


Fig. 11. Transverse serial sections of two specimens of *Biernatella lentiformis* sp. n. from Józefka. Numbers refer to distances in mm from the ventral apex (A) or from dorsal surface of the dorsal valve (specimens sectioned parallel to the commissural plane) (B). Abbreviations as in Fig. 5.

Remarks. — *B. polonica* is characterized by its very small ventral beak and interarea, very strongly swollen umbonal part of the ventral valve, and by a rather flattened dorsal valve (Figs 6, 7D–F). The difference between *B. polonica* and other species of the genus, i.e. *B. ovalis* and *B. lentiformis*, is discussed in the remarks on the latter forms.

It is noteworthy that the jugal stem was not identified in sectioned specimens of *B. polonica*. Sporadically, however, a brush of very short spines or spiny granules can be recognized on the anterior surface of the jugal saddle (Baliński 1977: fig. 3B: distance 2.4, 4). Some etched silicified specimens show that probably the surfaces of the spiralium were covered with a spinose ornament (Fig. 7N, R; Baliński 1977: pl. 10: 1–2).

Occurrence. — *B. polonica* occurs at Dębnik (southern Poland, Kraków region) in gray, thin-bedded biointrasparites and in black marly limestones representing the *Calvinaria albertensis* and *Caryorhynchus tumidus* brachiopod Zones. This interval can be correlated more or less precisely with the *Palmatolepis hassi* to *P. linguiformis* conodont Zones. A few specimens have been found in the latest Frasnian rocks at the railroad cut at Kowala (Holy Cross Mountains, Kielce region) in limestones representing the Detrital Beds (*P. linguiformis* conodont Zone).

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Streszczenie

Wśród paleozoicznych i mezozoicznych ramienionogów ze spiralnie skręconym aparatem ramieniowym trzykrotnie rowinął się skomplikowany szkielet ramion w postaci diplospiralium. Po raz pierwszy diplospiralium pojawiło się w górnym sylurze w szczepie reprezentowanym przez *Coelospira* i kontynuowanym do środkowego dewonu przez rodzaje *Anoplotheca*, *Bifida* i *Kayseria*. Po raz drugi diplospiralium rozwinęło się u dolnodewońskiej *Helenathyris* i jej środkowo- i górnodewońskich potomków z rodziny biernatellidów. W triasie pojawiły się diplospirellidy i hungarospirellidy stanowiące szczepy atyridów z diplospiralium. W tym samym czasie diplospiralium wykształciło się też u spiriferidów Koninckinellidae. W niniejszej pracy przedstawiono wyniki badań nad rozprzestrzenieniem rodziny Biernatellidae w dewonie Polski. Z żywetu Laskowej (Góry Świętokrzyskie) opisano *Eobiernatella rackii* gen. et sp. n., który jest najstarszym przedstawicielem tej rodziny stanowiącym jednocześnie ogniwo pośrednie między dolnodewońskim *Helenathyris* a głównie frańską *Biernatella* Baliński. W obrębie *Biernatella* opisano trzy gatunki: *B. ovalis* sp. n., *B. lentiformis* sp.n. i *B. polonica* Baliński, których występowanie stwierdzono w szeregu odsłonięciach w Górach Świętokrzyskich reprezentujących różne poziomy od górnego żywetu do najwyższego franu.