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## Eocene brachiopods from Wola Łużańska and Skalnik in the Central Carpathians

**ABSTRACT:** An assemblage of articulated brachiopods from the Upper Eocene Menilitic Series of the vicinity of Wola Łużańska and Skalnik (Central Carpathians, Poland), consists of small forms of the genera *Terebratulina* d'ORBIGNY, *Argyrotheca* DALL, and *Lacazella* MUNIER-CHALMAS.

### INTRODUCTION

The articulated brachiopods of the bryozoan-lithothamnian sandstones of the Upper Eocene Menilitic Series from Wola Łużańska (Gorlice — Żmigród area, Central Carpathians in Poland; see Text-fig. 1), were first described by UHLIG (1886), who reported 8 species. UHLIG had only a scanty material, often poorly preserved, and hardly identifiable to the species level. During the next hundred years, these brachiopods were only rarely mentioned (KRAJEWSKI & URBANIAK 1964). A rich collection of brachiopods associated with the bryozoan fauna studied by MAŁECKI (1963) was taken from the strata investigated by UHLIG (1886), PERGENS (1889), and PAZDRO (1929); in 1980, it was donated by Professor J. MAŁECKI to the Museum of the Earth, Polish Academy of Sciences, Warsaw, where it is presently housed (Paleozoology Division, Catalogue Number MZ VIII Bra-1437-1449).

### MATERIAL

The collection includes over a thousand specimens of articulate brachiopods, derived primarily from coarse sandstones with abundant fauna of foraminifers, bryozoans, ostracodes, echinoids, and bivalves (cf. MAŁECKI 1963, p. 8).

The brachiopod assemblage is dominated by whole shells and dorsal valves of *Lacazella mediterranea* (RISSO) and, to a lesser degree, *Argyrotheca altavillensis* (MORGAN). Representatives of the genera *Argyrotheca* DALL and *Terebratulina* d'ORBIGNY occur in minor amounts. Except for *Terebratulina* sp. (see Pl. 1, Fig. 6b), all the specimens are small-sized, with shell length ranging from 1 to 4 mm, often with features characteristic of the neanic stage (cf. ELLIOTT 1938).

#### SYSTEMATIC ACCOUNT

##### Family Cancellothyrididae THOMSON, 1926

###### Genus *Terebratulina* d'ORBIGNY, 1847

###### *Terebratulina rufis* KOENEN, 1894

(Text-figs 2—3 and Pl. 1, Figs 1—3)

1894. *Terebratulina rufis* v. KOENEN; A. von KOENEN, p. 1349, Pl. 1C, Figs 10—13; Pl. 2C, Fig. 5.

1895. *Terebratulina rufis* KOENEN, 1894; V. A. ZELINSKAYA, p. 119, Pl. 12, Figs 4—7.

MATERIAL: 2 specimens from Wola Łużańska (No. 1438/2-3) and 9 specimens from Skalnik (No. 1437/1-9). Shell length 1.6—3.8 mm; shell width 1.1—3.2 mm; shell thickness 0.5—1.2 mm.

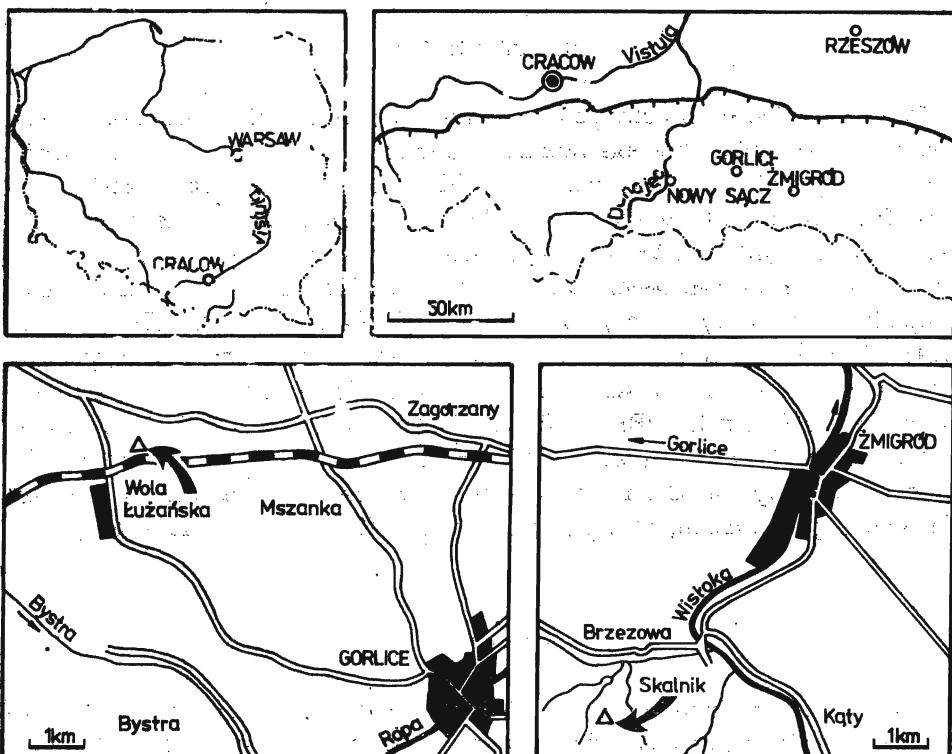


Fig. 1. Location of the exposures yielding the investigated brachiopods at Wola Łużańska (see UHLIG 1886) and Skalnik, Central Carpathians, Poland

**REMARKS:** The investigated specimens show distinctively juvenile features: nodulose costae, small auricles at the hinge line of brachial valve, and a large, circular foramen with small, triangular deltoidal plates. The number of primary costae ranges from 10 in the smallest to 16 in the largest specimens. Secondary costae, intercalated or dichotomous, are confined to the anterior margin of both valves. They occur in specimens approaching 3 mm in length, thus resembling the Lower Eocene *T. wardenensis* ELLIOTT at the 3-mm stage of growth (ELLIOTT 1938, Fig. 23/5-7). The investigated specimens, however, acquire at this stage deltoidal plates, which appear in the latter species only at 4 mm in length. The presence of dichotomous costae on the anterior margin of brachial valve makes the specimens from Wola Łużańska and Skalnik similar to *T. nysti* BOSQUET from the Lower Oligocene of Unseburg near Bünde, West Germany (KOENEN 1894, p. 1352, Pl. 1C, Figs 2b and 3b).

Serial transverse sections (Text-figs 2-3) indicate the presence of a well developed cardinal process and a typical, but open, loop. The shape of the loop may be due either to the juvenile age of the specimens, or to destruction of a part of the crural processes during preparation, or it may actually be characteristic of these forms. Such a loop occurs indeed in some specimens of the Eocene species *T. delheidi* VINCENT from Hrubý Regiel in the Tatra Mts (BARCZYK 1973, p. 494

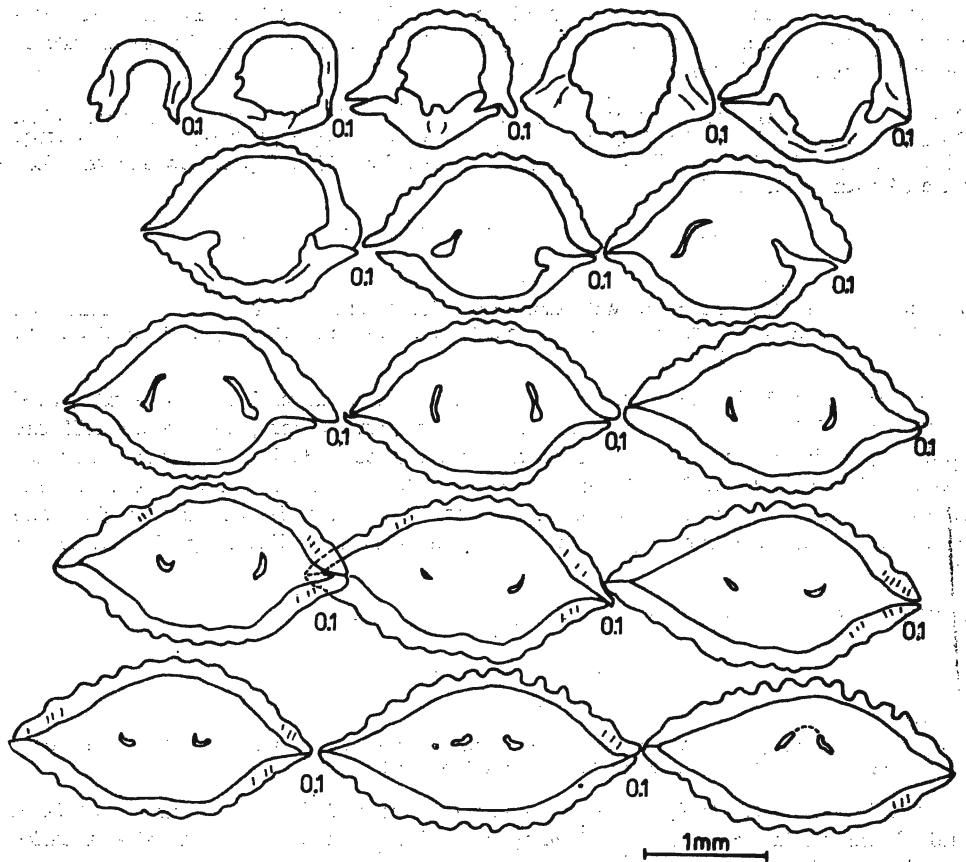


Fig. 2. Serial transverse sections of *Terebratulina rudis* KOENEN from Skalnik.

and Figs 3—4), in some congeneric forms from the Tertiary of Cuba (COOPER 1973, p. 373), and in the extant species *T. crossei* DAVIDSON from Japan (COOPER 1973, Pl. 43, Fig. 7) and *T. septentrionalis* (COUTHOUY) from the Bay of Fundy, Canada (LOGAN 1979, p. 38, Pl. 3, Fig. 19).

The investigated specimens of *T. rufis* are closer in their shell dimensions to those described by KOENEN (1894) from Germany than to their conspecific forms from the Ukraine (ZELINSKAYA 1962, 1975). The criterion of shell dimensions is here regarded as crucial, while comparing the Carpathian material to their Paleogene congeners from Europe (ELLIOTT 1938, 1954) and America (TOULMIN 1940). The nodulose costae are in common for many Eocene species of *Terebratula* in various geographic regions (TOULMIN 1940, Pl. 28, Figs 17—21) and cannot facilitate their differentiation.

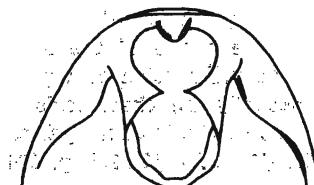


Fig. 3

Loop reconstruction of *Terebratulina rufis* KOENEN, a specimen from Skalnik, the same as used for serial transverse sections given in Text-fig. 2

The shell ornamentation clearly differs the investigated specimens from the almost smooth specimen described by UHLIG (1886, p. 210, Pl. 2, Fig. 4) as "*Terebratulina* sp. ind. aff. *parva* MATYASZ".

OCCURRENCE: Lower Oligocene of Lattorf and Unseburg near Bünde, West Germany (KOENEN 1894); Upper Eocene of the Crimea and South Ukraine (ZELINSKAYA 1962, 1975; ZELINSKAYA & SOKOLOV 1971); Upper Eocene of Wola Lużańska and Skalnik.

*Terebratulina* aff. *rufis* KOENEN, 1894  
(Pl. 1, Figs 4—5)

MATERIAL: 2 shells, one from Wola Lużańska (No. 1438/1), the other from Skalnik (No. 1437/7). Shell length 3.4 and 3.7 mm; shell width 2.4 and 3.2 mm; shell thickness 1.6 and 1.7 mm, respectively.

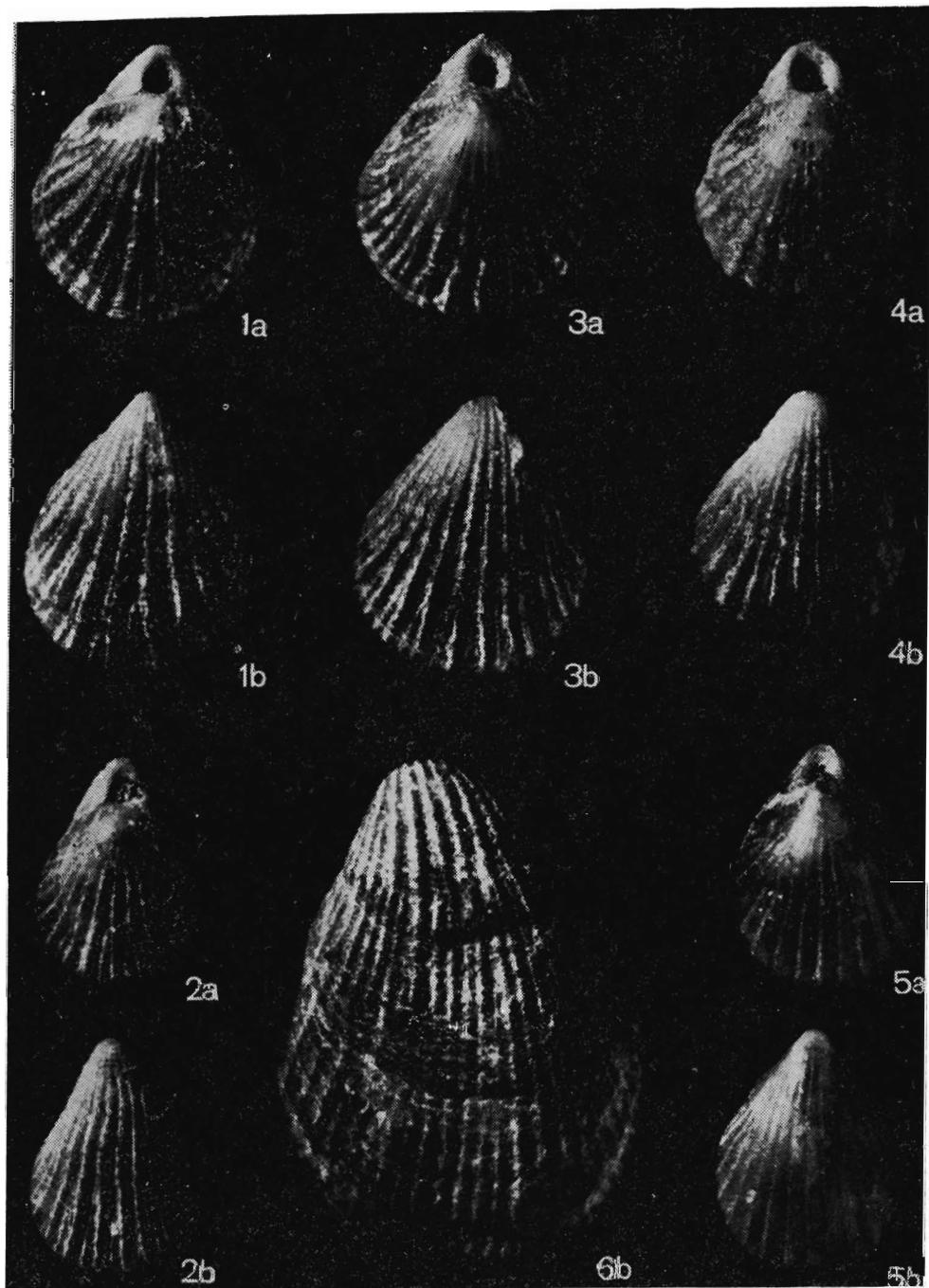
REMARKS: Both the specimens differ in ornamentation from those attributed to *T. rufis* KOENEN. At the shell length exceeding 3 mm, the costae still are nodulose, without any intercalated or dichotomous secondaries. The specimen from Wola Lużańska (Pl. 1, Fig. 5a—5b) has furthermore much smaller foramen and shorter beak in the pedicle valve, as compared to *T. rufis* at similar size. The costae of these two specimens are also lower and less distinctly than those of *T. rufis*.

OCCURRENCE: Upper Eocene of Wola Lużańska and Skalnik.

*Terebratulina* sp.  
(Pl. 1, Fig. 6)

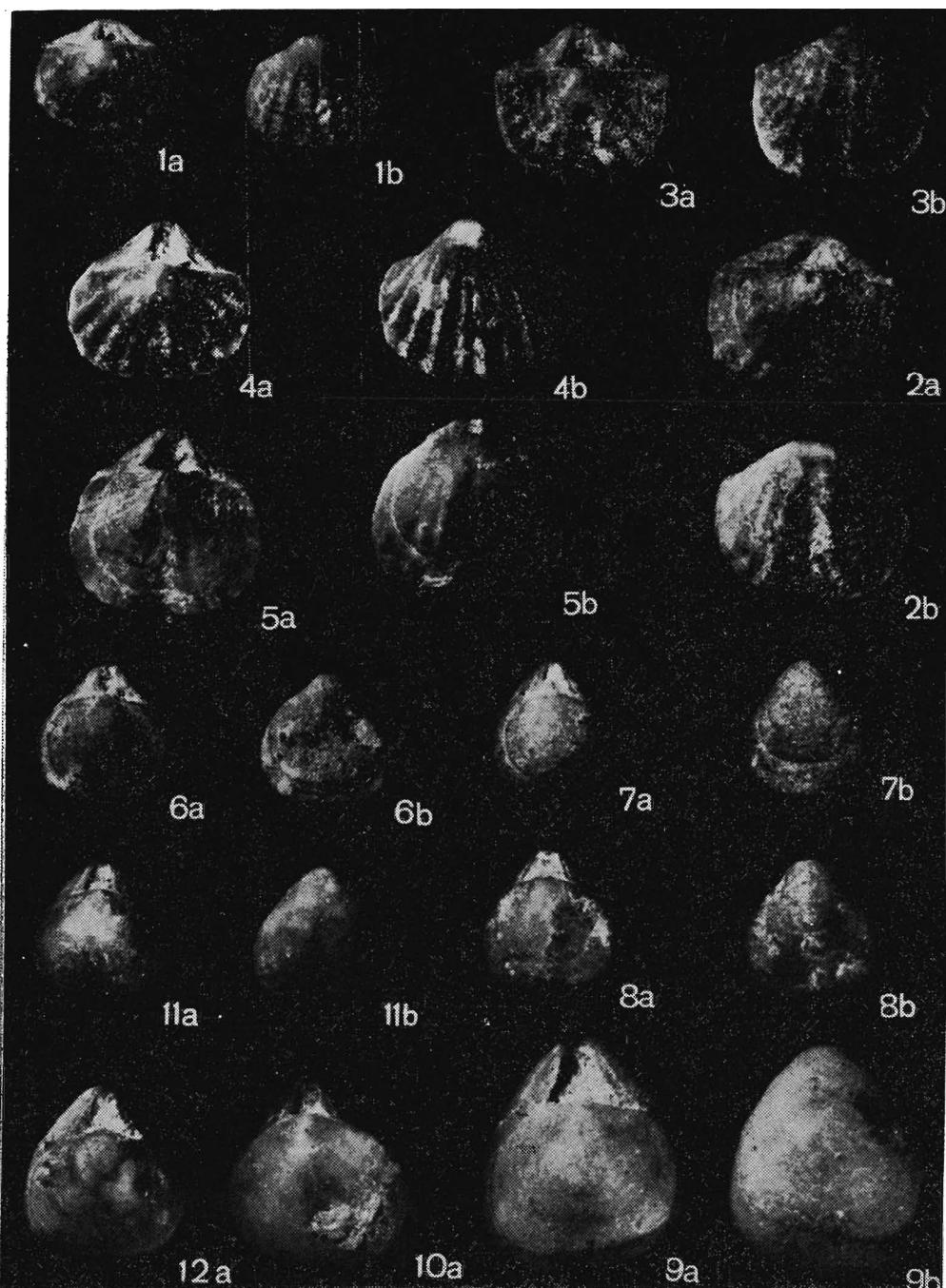
MATERIAL: A fragment of pedicle valve from Skalnik and 1 pedicle valve from Wola Lużańska (No. 1439). Valve length 7 mm; valve width 5 mm.

REMARKS: Relatively large, strongly convex pedicle valve with long beak and dense radial costae. Well-developed median ventral sinus at the anterior margin. Nodulose costae increase in number with valve size, due to the appearance of intercalated secondaries; there are 13 costae at the first growth line, 23 at the



1-3 — *Terebratulina rudis* KOENEN; 1-2 from Skałnik, 3 from Wola Łużańska  
4-5 — *Terebratulina* aff. *rudis* KOENEN; 4 from Skałnik, 5 from Wola Łużańska  
6 — *Terebratulina* sp.; pedicle valve from Wola Łużańska

a — brachial, b — pedicle valve views; all  $\times 10$



1-3 — *Argyrotheca lunula* (KOENEN); 1-2 from Skalnik, 3 from Wola Łużańska  
 4-5 — *Argyrotheca piperipyxis* ELLIOTT; 4 from Wola Łużańska, 5 from Skalnik  
 6-12 — *Argyrotheca altavillensis* (MORGAN); 6-10 from Skalnik, 11-12 from Wola Łużańska

a — brachial, b — pedicle valve views; all  $\times 10$

second, 29 at the third, and 32 at the anterior margin. These costae show less nodosity than in the congeneric forms described above. A wide pedicle collar occurs inside the valve, as well as traces of internal ornamentation near the front margin.

The presence of median ventral sinus and internal ornamentation and the nature of costae make this specimen resembling *T. asperula* KOENEN from the Lower Oligocene of Lattorf, West Germany (KOENEN 1894, Pl. 3C, Figs 2–3). The same features resemble also the Recent species *T. retusa* (LINNAEUS, 1758) from the Mediterranean Sea (LOGAN 1979, Pl. 3, Figs 1–18), which is now regarded as the type species of the genus (BRUNTON & al. 1967, LOGAN 1979).

OCCURRENCE: Upper Eocene of Wola Łużańska and Skalnik.

### Family Megathyrididae DALL, 1870

#### Genus *Argyrotheca* DALL, 1900

##### *Argyrotheca altavillensis* (MORGAN, 1883)

(Text-fig. 4; Pl. 2, Figs 6–12; Pl. 3, Figs 1–2)

1883. *Cistella altavillensis* de MORGAN\*; J. de MORGAN, p. 389, Pl. 12, Figs 9–13.

1903. *Cistella altavillensis*, de MORGAN; M. COSSMANN & G. PISSARRO, p. 65, Pl. 12, Figs 38–40.

MATERIAL: 38 specimens from Wola Łużańska (No. 1445/1–38) and 32 specimens from Skalnik (No. 1444/1–32). Shell length 1.2–2.7 mm; shell width 1.1–2.4 mm.

REMARKS: The investigated specimens are small, smooth, and triangular in outline, exactly like those from the Eocene of France, which are referred to in the synonymy. They are only a bit smaller in size, partly due to their juvenile age indicated by the large foramen and narrow deltidial plates. Some specimens show large pores (Pl. 3, Fig. 2), growth lines closely spaced at the anterior margin, and a large and massive dorsal median septum, clearly visible through the thin valve, even through the pedicle one (Pl. 2, Fig. 11b). Median sinuses present but poorly developed; they are more distinct on the dorsal valve (Pl. 2, Figs 8a and 11a).

Serial transverse sections indicate the presence of one dorsal median septum. Its composite structure (Text-fig. 4) may be due either to a possible presence of rudimentary ascending branches of the loop, as recorded in some fossil (POPIEL-BARCZYK & SMIRNOVA 1978, SMIRNOVA & al. 1983) and Recent megathyrids (LOGAN 1979), or to serrations at the top of the septum, observed in some other megathyrids (MORGAN 1883, 1915; COSSMANN & PISSARRO 1903; LOGAN 1979).

The investigated specimens of *A. altavillensis* include some asymmetric forms (Pl. 2, Figs 9–10 and 12). As demonstrated by serial sections through the fully regular internal shell elements, this asymmetry concerns exclusively the shell outline, which suggests that it was caused by extrinsic ecological factors, for example, crowding or unsuitable attachment sites (see ASGAARD 1968).

The species *A. altavillensis* (MORGAN) is entirely smooth and differs from *A. puncticulata* (DESHAYES) from the Eocene of France (DESHAYES 1863, COSSMANN 1891) and Belgium (VINCENT 1893), as well as from its close relative and possible synonymous *A. parisiensis* (MORGAN), only in its smaller size and weaker

\* The original description of the species has a typographic error in the species name; the name employed on the preceding and succeeding pages of the same work (MORGAN 1883, pp. 382, 388, 390) is correctly spelled *Cistella altavillensis*, and it has thus been spelled by successive authors (COSSMANN & PISSARRO 1903, ELLIOTT 1955, PAJAUD & TAMBAREAU 1970).

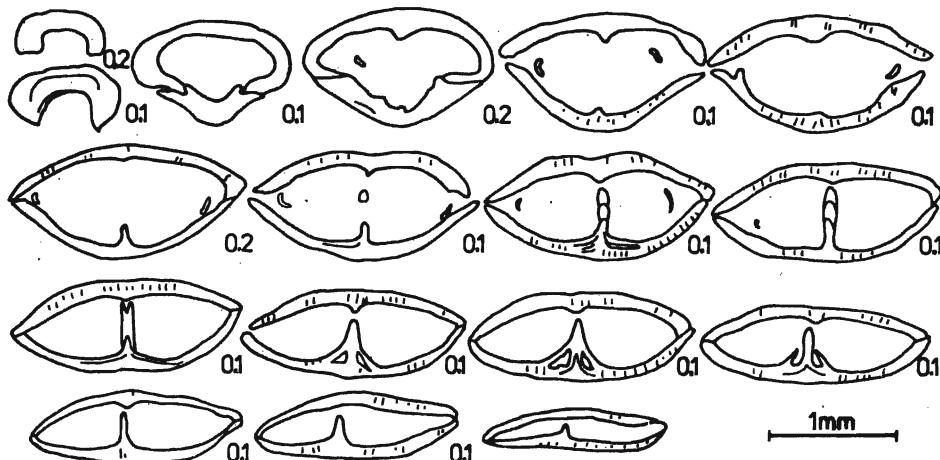


Fig. 4. Serial transverse sections of *Argyrotheca altavillensis* (MORGAN) from Skalnik, to show high brachial median septum, and branches of the loop

median sinus. Both *A. altavillensis* and *A. parisiensis* were in fact described by MORGAN (1883) as resembling the Recent species *A. cuneata* (RISSO).

OCCURRENCE: Eocene of Cotentin Peninsula and Freville, France (MORGAN 1883, COSSMANN & PISSARRO 1903); Upper Eocene of England (ELLIOTT 1955); Upper Eocene of Wola Łużańska and Skalnik.

*Argyrotheca lunula* (KOENEN, 1894)  
(Text-fig. 5 and Pl. 2, Figs 1–3)

1894. *Argiope lunula* v. KOENEN; A. von KOENEN, p. 1360, Pl. 2C, Figs 8–10.

MATERIAL: 2 specimens from Wola Łużańska (No. 1441/1-2) and 5 specimens from Skalnik (No. 1440/1-5). Shell length 1.8–2.6 mm; shell width 2.0–3.2 mm; shell thickness 1.0–1.5 mm.

REMARKS: The investigated specimens resemble in shell outline those described by KOENEN (1894) from the Lower Oligocene of West Germany; their weaker ribbing (10–12 ribs per valve), without intercalated secondaries, may be due to the juvenile age. Median sinus, in turn, is more distinct than in KOENEN's specimens. The maximum shell width is at the hinge margin but it extends also toward the anterior margin, thus making the shell outline a bit semicircular. Shell surface bears large and distinct pores.

Serial transverse sections (Text-fig. 5) clearly show one median septum and traces of the loop in the brachial valve, and a pedicle collar and a septum running anteriorly from the collar in the pedicle valve.

The investigated specimens of *A. lunula* resemble also in shell outline the Upper Eocene forms described from the Ukraine by ZELINSKAYA (1962, 1975) as "*Megathyris lunula percostata* (KOENEN)". They differ, however, from the latter in their smaller size, median sinuses on both valves, and the absence of intercalated secondary ribs. As demonstrated by serial sections (ZELINSKAYA 1962, p. 110, Fig. 2B; 1975, Pl. 14, Figs 9 and 19), the Ukrainian specimens have one septum in the brachial valve and two or even more lateral septa, in addition to the median one, in the pedicle valve (ZELINSKAYA 1962, Fig. 2A/I-III; 1975, p. 125); the occurrence of these lateral septa rules out identification of those specimens with the species *A. lunula* (KOENEN).

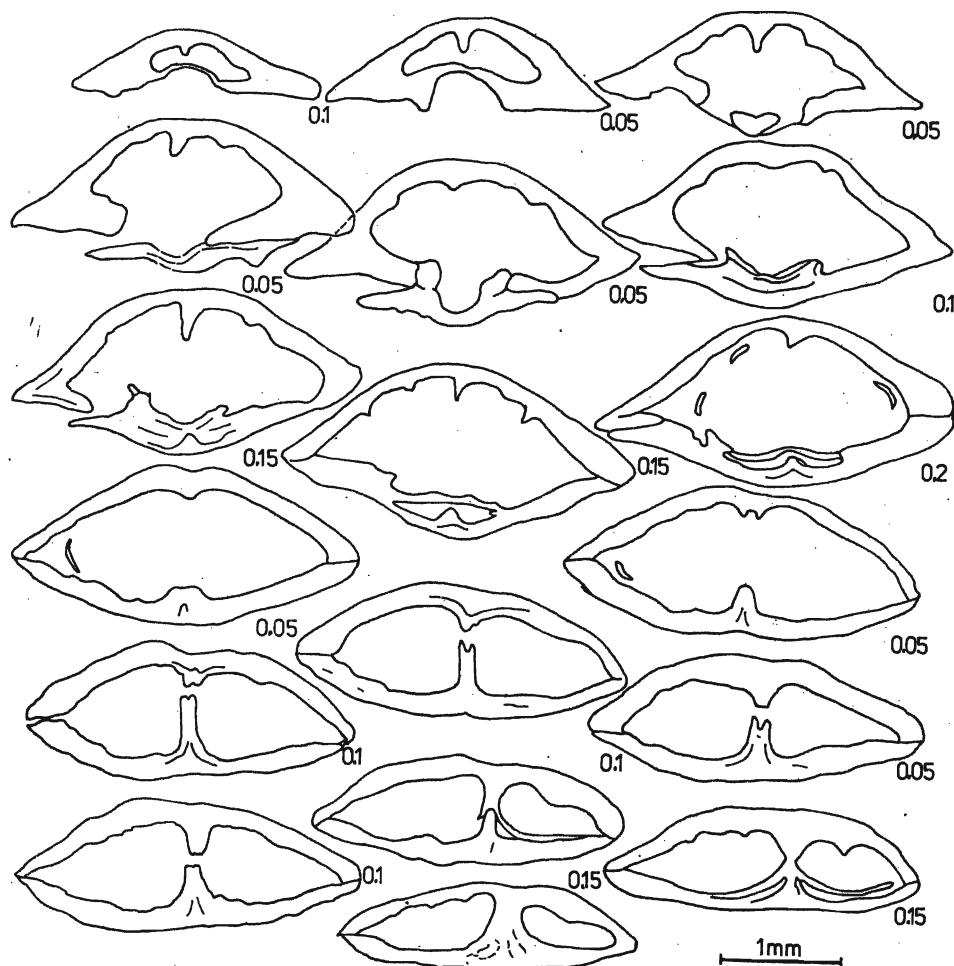


Fig. 5. Serial transverse sections of *Argyrotheca lunula* (KOENEN) from Skalnik (see Pl. 2, Fig. 2a-b)

The specimens from Wola Łużańska and Skalnik resemble in shell outline and ornamentation the Lower Eocene *A. sabaratensis* from Ariège, southern France (PAJAUD & TAMBARÉAU 1970, PAJAUD & PLAZIAT 1972), the difference consisting in the internal morphology of the brachial valve.

Several Eocene species of *Argyrotheca* are known from South America and the Caribbean (TOULMIN 1940, COOPER 1979). The presence of median sinuses on both the valves makes the investigated specimens similar to the Lower Eocene *A. saltmountainensis* TOULMIN from Alabama (TOULMIN 1940, Pl. 28, Figs 22–28), but the latter species has a weaker ribbing.

OCCURRENCE: Lower Oligocene of West Germany (KOENEN 1894); Upper Eocene of Wola Łużańska and Skalnik.

*Argyrotheca piperipyxis* ELLIOTT, 1954  
(Text-fig. 6 and Pl. 2, Figs 4–5)

1954. *Argyrotheca piperipyxis*, sp. nov.; G. F. ELLIOTT, p. 725, Pl. 15, Fig. 1.

MATERIAL: 1 specimen from Wola Łużańska (No. 1442) and 2 specimens from Skalnik (No. 1443/1-2). Shell length 2.1–2.5 mm; shell width 2.3–2.6 mm; shell thickness 1.2–1.3 mm.

REMARKS: Shell dimensions, shape, and ornamentation (8–10 ribs per valve) are entirely consistent with the type material from the Upper Eocene of Hampshire (ELLIOTT 1954).

Serial transverse sections (Text-fig. 6) show a pedicle collar and one septum in the pedicle valve. The brachial valve, in turn, bears a massive median septum, prominent inner socket ridges on both sides of bifurcated cardinal process, and traces of the loop. The inner socket ridges are also visible on the external side of the hinge margin in the brachial valve.

The species *A. piperipyxis* ELLIOTT differs from *A. lunula* (KOENEN) in its more elongated shell, especially the beak of the pedicle valve, as well as in its narrower hinge margin, more medially located maximum shell width, and less numerous ribs. The specimen from Wola Łużańska (Pl. 2, Fig. 4) has stronger ribs than the specimen from Skalnik, which makes it more similar to *A. douvillei* (MORGAN) from the Paris Basin (MORGAN 1883, Pl. 12, Fig. 37) and from the

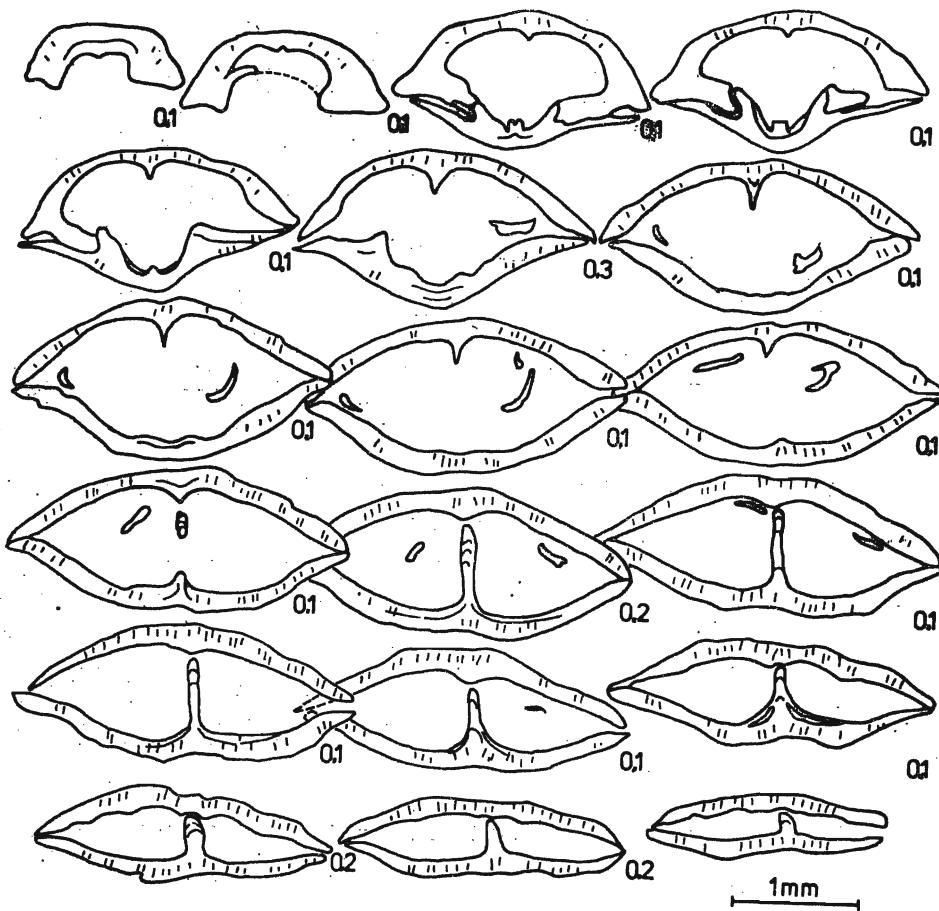
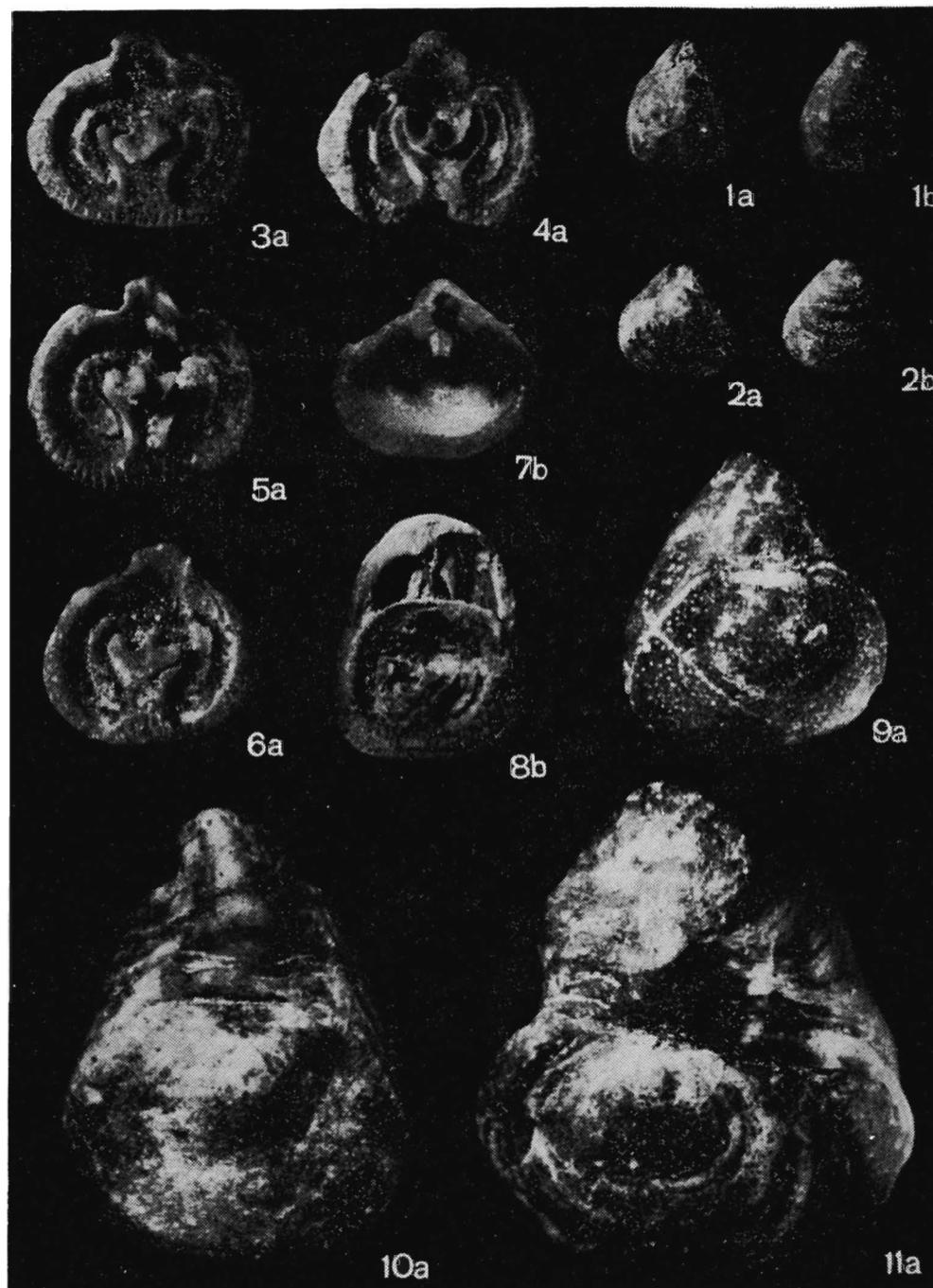


Fig. 6. Serial transverse sections of *Argyrotheca piperipyxis* ELLIOTT from Skalnik (see Pl. 2, Fig. 5a-b), to show well preserved internal features (cardinal process, brachial median septum, and fragments of the loop)



1-2 — *Argyrotheeca altavillensis* (MORGAN); specimens from Skalnik,  $\times 10$   
 3-11 — *Lacazella mediterranea* (RISSO) from Skalnik: 3-6 — interior of brachial  
 valves ( $\times 10$ ), 7-8 — interior of pedicle valves ( $\times 10$ ), 9-11 — complete  
 specimens ( $\times 15$ )

a — brachial, b — pedicle valve views

Ukraine (ZELINSKAYA 1975, Pl. 15, Fig. 4). The French forms, however, have more numerous ribs (15-20 per valve), while the Ukrainian ones have intercalated secondaries. A specimen from Skalnik resembles in shell outline the Upper Eocene *A. megapora* ZELINSKAYA from the Ukraine (ZELINSKAYA 1975, Pl. 16, Fig. 1), but it has less numerous ribs than the latter.

OCCURRENCE: Upper Eocene of England (ELLIOTT 1954, 1955); Upper Eocene of Wola Łużańska and Skalnik.

Family *Thecididae* GRAY, 1840

Genus *Lacazella* MUNIER-CHALMAS, 1881

*Lacazella mediterranea* (RISSO, 1826)

(Pl. 3, Figs 3—11)

1886. *Thecidium mediterraneum* RISSO; V. UHLIG, p. 213, Pl. 2, Figs 5—6.

1970. *Lacazella mediterranea* (RISSO, 1826); D. PAJAUD, pp. 128—138, Text-figs 50—52; Pl. 1, Fig. 4; Pl. 5, Fig. 4; Pl. 7, Fig. 3; Pl. 10, Figs 1—6; Pl. 11, Fig. 3; Pl. 12, Fig. 2; Pl. 16 (*cum syn.*).

1979. *Lacazella mediterranea* (RISSO); A. LOGAN, p. 73, Pl. 10, Figs 1—8.

MATERIAL: 35 shells and 7 brachial valves from Wola Łużańska (No. 1446) and 570 shells and 423 brachial valves from Skalnik (No. 1447). Shell length 1.8—5.3 mm; shell width 2.9—4.2 mm; shell thickness 1.6—3.1 mm.

REMARKS: When analyzing UHLIG'S illustrations (1886, Pl. 2, Figs 5—6), PAJAUD (1970) concluded that the Carpathian assemblage is conspecific, while its differentiation is phenotypic, due to environmental conditions and the mode of attachment. The investigated specimens from Wola Łużańska and Skalnik closely resemble the forms described by DAVIDSON (*vide* PAJAUD 1970) as "*Thecidium Mediterraneum* var. *Latdorfense*", which is distinctive in its relatively small size, peculiar hemispondylium (no tubercles or spines on the branches and the ramus median), and weakly developed median ridge. Similar specimens were also described by COOPER (1979) from the Caribbean as the species *L. caribbeensis* COOPER, though they are even smaller-sized and with smoother brachidium. As discussed by PAJAUD (1970), however, all these morphological differences fall within the range of intraspecific variation of *L. mediterranea* (RISSO).

OCCURRENCE: Upper Eocene of southern Italy (PAJAUD 1979); Eocene of the Gulf Coast of the USA (COOPER 1979); Lower Oligocene of West Germany (PAJAUD 1970); Miocene and Pliocene of northern Italy (THOMSON 1927, PAJAUD 1970); Recent Mediterranean Sea (THOMSON 1927, PAJAUD 1970, LOGAN 1979, COOPER 1979); Upper Eocene of Wola Łużańska and Skalnik.

#### ECOLOGICAL REMARKS

Associations of various species of *Lacazella* and *Argyrotheca* were observed in a wide range of modern and ancient habitats (JACKSON & al. 1971, PAJAUD & PLAZIAT 1972, PAJAUD 1974). These brachiopods prefer hard substrates for attachment, although *Argyrotheca* is also capable of inhabiting weakly lithified substrates (PAJAUD & PLAZIAT 1972). The modern species clearly prefer sheltered undersurfaces of submarine rocks (PAJAUD & PLAZIAT 1972), crevices and fissures (JACKSON & al. 1971, LOGAN 1979, NEKVASILOVA 1983), and small submarine caves (LOGAN 1979); they abound in the neighborhood of

powerful sessile filter-feeders capable of causing considerable water circulation. After death, their shells are rapidly displaced deeper into the basin, and hence their *in situ* accumulations are virtually unknown (PAJAUD & PLAZIAT 1972). Consequently, similar ecological requirements are suggested for the investigated Eocene brachiopods from Wola Łużańska and Skalnik.

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**EOCEŃSKIE RAMIENIONOGI Z WOLI ŁUŻAŃSKIEJ I SKALNIKA  
W KARPATACH**

**(Streszczenie)**

Praca niniejsza przedstawia charakterystykę zespołu ramienionogów występujących w piaskowcach mszywielowo-litotamniowych serii magurskiej odsłaniającej się w okolicach Woli Łużańskiej i Skalnika koło Gorlic (patrz fig. 1). W zespole tym, analogicznym do opisanego przez V. UHLIGA (1886), rozpoznamo 7 gatunków należących do rodzajów: *Terebratulina* d'ORBIGNY, *Argyrotheca* DALL i *Lacazella* MUNIER-CHALMAS. Zwrócono uwagę, iż w badanym zespole (patrz fig. 2–6 oraz pl. 1–3) występują okazy na ogół mniejsze niż analogiczne formy znane z innych obszarów. W obrębie dominującego rodzaju *Lacazella* zwraca z kolei uwagę duża ilość osobników (ponad 1000 sztuk) reprezentowanych w znacznym stopniu przez pojedyncze skorupki grzbietowej. Badany zespół, złożony głównie z przedstawicieli rodzaju *Lacazella* i *Argyrotheca*, wykazuje duże analogie do zespołów współcześnie występujących w płytowych strefach Morza Śródziemnego (patrz PAJAUD & PLAZIAT 1972, LOGAN 1979).

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