Acta Geologica Polonica, Vol. 58 (2008), No. 4, pp. 395-406

The Upper Oxfordian (Jurassic) thecideide brachiopods from the Kujawy area, Poland

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ABSTRACT:

KRAWCZYŃSKI, C. 2008. The Upper Oxfordian (Jurassic) thecideide brachiopods from the Kujawy area, Poland. *Acta Geologica Polonica*, **58** (4), 395-406. Warszawa.

Thecideide brachiopods from the slope facies of a sponge-cyanobacterial bioherm exposed in the Wapienno and Bielawy quarries (Kujawy, Poland) are described. Numerous specimens were found in the upper part of the section, in the Hauffianum-Planula Subzones of the Oxfordian, and constitute the first record of these brachiopods from the Jurassic deposits in the area. Two species: *Rioultina wapiennensis* sp.nov. and *Neothecidella ulmensis* QUENSTEDT, 1858, are described, the first being the only representative of the genus *Rioultina* found in Poland. Excellent preservation of some specimens enabled recognition of details of their internal morphology usually inaccessible in fossil material, including features associated with reproduction and the development of the brachidium. Study of relatively large numbers of thecideides still cemented to the substrate, together with analysis of the associated fauna, allowed the reconstruction of aspects of their ecology.

Key words: Brachiopods, Thecideides, *Rioultina*, *Neothecidella*, Upper Jurassic, Poland.

INTRODUCTION

Thecideides are small, articulated brachiopods which cement their shells to the substrate and are widely distributed in Recent tropical or subtropical seas. They live mostly in shallow waters at depths ranging from a few metres down to about 150 m, in cryptic habitats such as crevices, submarine caves, coral undersurfaces, etc. (PAJAUD 1970, 1974; LOGAN 1979, 2005; LEE & ROBINSON 2003; LÜTER 2005). The species reported in this paper, *Rioultina wapiennensis* sp. nov. and *Neothecidella ulmensis* (QUENSTEDT, 1858), belong to two subfamilies represented also in the modern fauna; Thecidellininae ELLIOTT, 1953 and Lacazellinae BACKHAUS, 1959. This fact has important interpretational value for their ecological interpretation.

The material studied herein comes from fossil-rich slope deposits of a sponge-microbialitic bioherm, exposed in the Wapienno and Bielawy quarries in the southeast part of the Zalesie Anticline, Central Poland (Text-fig. 1). The deposition of organogenic carbonates in the Zalesie structure occurred in the Middle and Late Oxfordian (MATYJA & *al.* 1985; MATYJA & WIERZBOWSKI 1985, 2002). The fossil thecideides come from the upper part of the section, spanning the Hauffianum Subzone of the Bimammatum Zone (WIERZBOWSKI, pers. comm.) to the Planula Subzone (close to the base of the Galar Subzone) of the Planula Zone (MATYJA & WIERZBOWSKI 2002). The absence of these brachiopods in the lower part of the succession most probably results from the fact that the bioherm developed initially at a relatively great depth, as postulated by MATYJA & WIERZBOWSKI (1985).

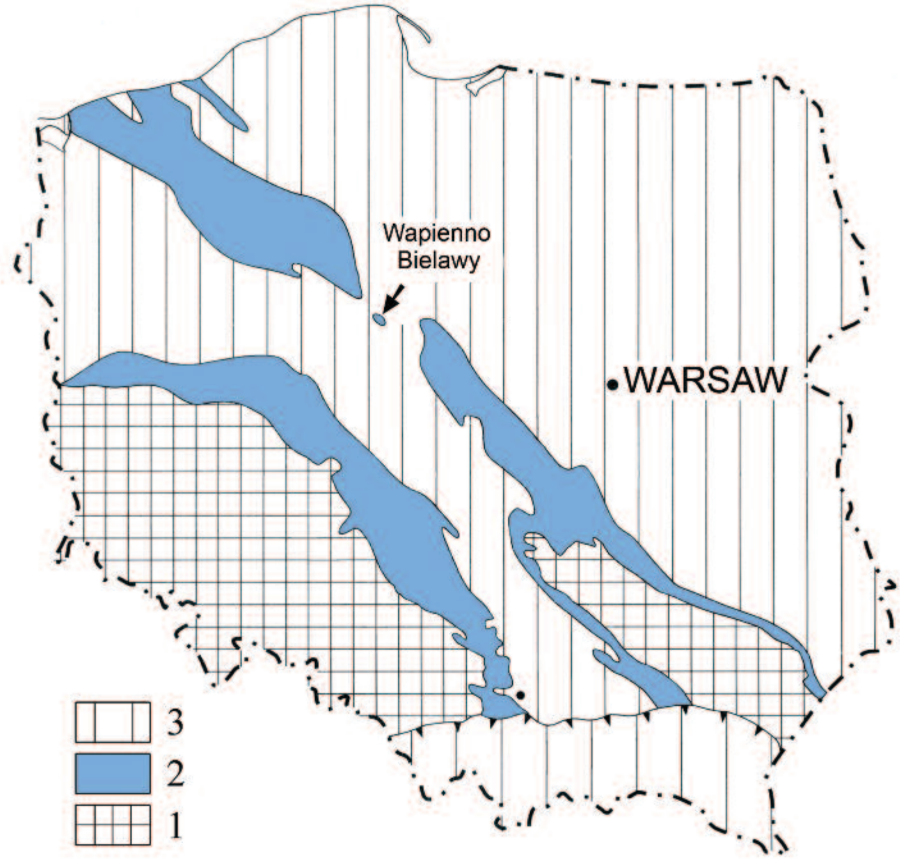

Fig. 1. Geological Map of Poland without Caenozoic deposits showing location of the Wapienno and Bielawy quarries (adopted from Matyja & Wierzbowski 2002, fig. 1); 1 – pre-Jurassic, 2 – Jurassic, 3 – Cretaceous and Mesozoic of the Carpathians

Repository of specimens

The material is housed in the Department of Palaeontology, Faculty of Geology, University of Warsaw under catalogue numbers (starting from): RW1-..., RW6-..., RW11-..., RB2-..., NW1-..., NW6-..., NW11-..., NB2-..., LNW1-..., LNW6-..., LNW11-..., LNB2-.

SYSTEMATIC DESCRIPTION

The classification used follows the fifth volume of the revised *Treatise on Invertebrate Paleontology, part H Brachiopoda* (Baker 2006).

Order Thecideida Elliott, 1958
Superfamily Thecideoidea Gray, 1840
Family Thecidellinidae Elliott, 1958
Subfamily Thecidellininae Elliott, 1953

Genus *Rioultina* Pajaud, 1966

TYPE SPECIES: *Rioultina triangularis* (d'Orbigny, 1850)

Rioultina wapiennensis sp.nov.
(Pl. 1, Figs 1-3; Pl. 2, Figs 1-7; Pl. 3, Figs 1-4; Pl. 8, Figs 2, 4, 6, 8)

HOLOTYPE: The specimen RW6-P2-B5, illustrated in Pl. 1, Fig. 3.

PARATYPES: Five specimens: three dorsal valves – RW6-P2-B4 (Pl. 1, Fig. 1), RW6-P2-B6 (Pl. 1, Fig. 2), RB2-P1-D5 (Pl. 2, Fig. 1); one ventral valve – RB2-P1-D1 (Pl. 3, Fig. 3) and one complete shell – RB2-P1-A5 (Pl. 3, Fig. 4).

TYPE LOCALITY: Wapienno and Bielawy quarries in the Zalesie Anticline, Kujawy region, north-central Poland.

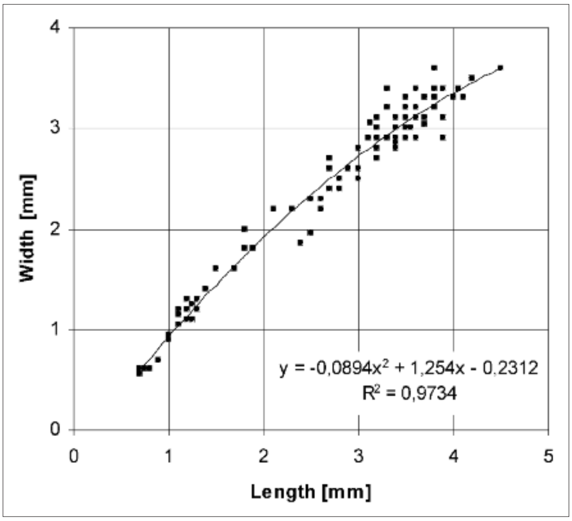

Fig. 2. Length/width ratio of shell of *Rioultina wapiennensis* sp. nov. (number of measured specimens – 91)

TYPE HORIZON: Upper Oxfordian, Hauffianum Subzone of the Bimammatum Zone to Planula Subzone (nearly at the base of the Galar Subzone) of the Planula Zone.

DERIVATION OF NAME: After the Wapienno Quarry, source locality of the holotype.

DIAGNOSIS: A species of *Rioultina* up to about 4.5 mm in length, 3.6 mm width and 2.6 mm thick; shell triangular in outline, with two rounded apices (anterior-lateral part); shell surface smooth, endopunctate, with poorly outlined growth lines; pseudodeltidium large, flat, occupying majority of interarea, poorly visible; ventral valve interior with distinct median ridge, elongate-triangular sessile hemispondylium and small hinge teeth; cardinal process large, distinctly trilobed; median septum very long, ornamented by tubercles in the anterior part; interbrachial lobes developed as perforated canopies, with one deep incision in the posterior part (near the end of the median septum) and one big, triangular to oval hole (much larger than other perforations) in the terminal, posterior part.

MATERIAL: 272 specimens, including 183 complete (100 well-preserved), 47 dorsal (35 well-preserved) and 42 ventral valves (28 well-preserved).

DESCRIPTION: **External morphology**: The shell is small, distinctly triangular in outline (Pl. 3, Fig. 4a). The length of the shell of juvenile specimens is more or less the same as the width; however, the adult forms are distinctly elongate (see Text-fig. 2).

The surface of the shell is smooth, endopunctate (Pl. 8, Figs 4, 6, 8), with poorly visible growth lines. The attachment scar is relatively large, triangular in outline, and the free ventral wall is high. Cases of shell asymmetry are very rare and related to adaptation to the substratum (Pl. 3, Fig. 1a-b). The cardinal margin is short and its length varies between 0.35-0.48 of the shell

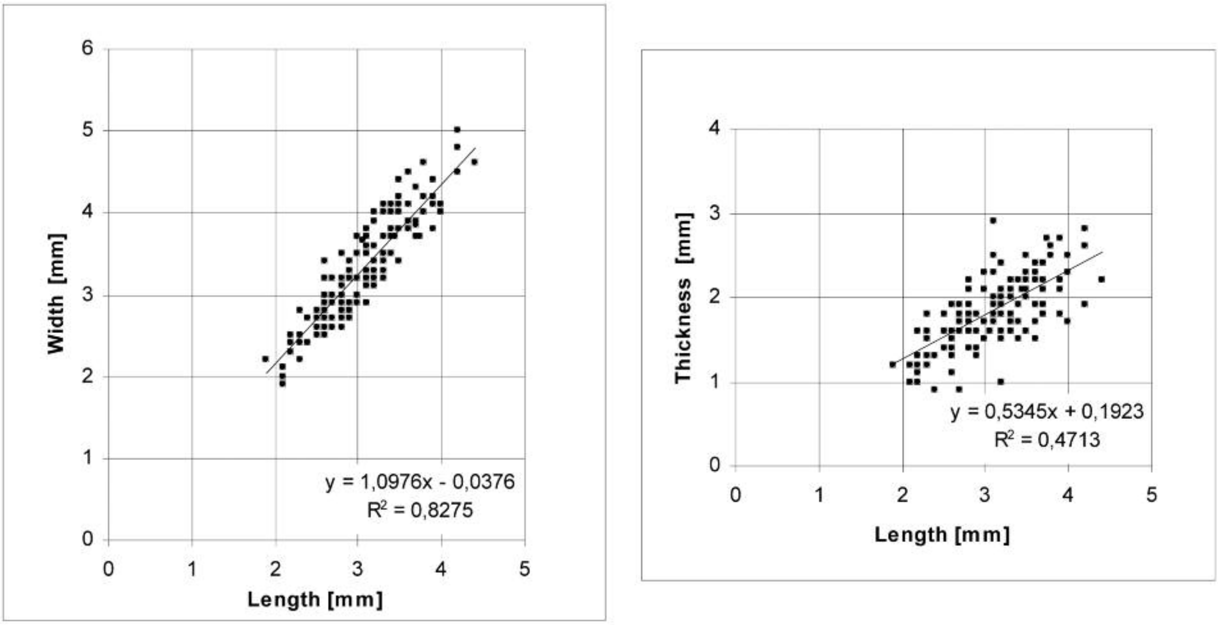

Fig. 3. Measurements of *Neothecidella ulmensis* (QUENSTEDT, 1858). A – Length/Width ratio (144 measured specimens). B – Length/Thickness ratio (139 measured specimens)

width. The interarea is flat and very well defined (Pl. 3, Fig. 4a). The pseudodeltidium occupies the majority of the interarea surface and is weakly demarcated. The ventral valve has a shallow median sulcus that is especially well seen near the anterior margin of large specimens. In such cases this sulcus is also visible on the dorsal valve, in the anterior part of the subperipheral rim (Pl. 1, Fig 3a).

Internal morphology

Ventral valve: The median ridge is distinctly marked in the posterior part of the valve (above the place of attachment) and divides the interior into two large oval depressions which are probably genital pits (Pl. 3, Fig. 3). The hemispondylium is visible in the posterior part of the median ridge and they form together an arrowhead-shaped structure (Pl. 3, Fig. 3; Pl. 8, Fig. 2), similar to that observed in *Stentorina sagittata* BAKER & WILSON, 1999. The hinge teeth are small and not widely separated (Pl. 3, Fig. 3; Pl. 8, Fig. 2). The marginal area of shell is ornamented by fine tubercles.

Dorsal valve: The cardinal process is large, protruding well beyond the cardinal margin, clearly trilobed and dorsally deflected (Pl. 1, Figs 1-3; Pl. 2, Figs 1-4, 6; Pl. 3, Fig. 1). The dental sockets are small, oval and lie close to the base of the cardinal process (Pl. 1, Fig. 2c). The lateral adductor muscle scars are very distinctly marked and form two kidney-shaped imprints near the base of the cardinal process, between the bridge (transversarium) and the dental sockets (Pl. 1, Fig. 2c). The tranversarium (Pl. 1, Figs 1-3; Pl. 2, Figs 2-4, 7; Pl. 3, Figs 1-2) is straight, strong, with a denticulate edge (Pl. 1, Figs 2b, 3b) and is frequently preserved even in damaged specimens. The outer surface of the subperipheral rim is very wide, ornamented by numerous fine tubercles (up to eight rows) and is strongly endopunctate (Pl. 8, Fig. 8). This ornamentation extends also onto the anterior part of the median septum. The interbrachial lobes have, as in other Thecidellinidae (see BAKER 1991, fig. 6) very characteristic, perforated canopies covering the interbrachial cavities (Pl. 1, Figs 1-3; Pl. 2, Figs 1-3). The canopies possess one deep incision, situated near the top of the septum and one big hole, much larger than the other perforations, located in the marginal, posterior part of the lobe (Pl. 1, Figs 1-3). The perforated canopies are relatively rarely preserved in the study material and usually the only evidence of their existence is provided by broken canopy skeletal supports, ringing the interbrachial cavities (Pl. 2, Fig. 2-6). The entry to each cavity is situated in the posterior part of the interbrachial lobe, near the top of the median septum (Pl. 1, Figs 2b). In adult forms, the interbrachial cavities most probably contained interbrachial sacs acting as brood pouches in which the larvae matured, as in Recent *Thecidellina* (see PAJAUD, 1970; LÜTER & *al*. 2003; LÜTER 2005). The interbrachial sac of present-day *Thecidellina* consists of a small posteriorly situated "*vestibule*" and a large anterior chamber (PAJAUD 1970). A similar duality appears also in the construction of the canopies (Pl. 1, Figs 1-3) and the interiors of the interbrachial cavities of *Rioultina wapiennensis* sp. nov. (Pl. 1, Fig. 2). Each interbrachial cavity has, moreover, a connection with the visceral cavity by a broad canal passing under the junction of the basal part of the posterior-lateral interbrachial canopy and the structure supporting the entrance to the cavity (Pl. 1, Fig. 2a-b; Pl. 2, Figs 1, 3-4; Pl. 3, Fig. 1). The lophophoral impression is visible in the form of a shallow groove running along the inner margin of the subperipheral rim, the surface of which is covered by numerous elongate lophophore muscle scars (Pl. 1, Figs 1-3; Pl. 2, Fig. 1).

Microstructure: The shell is endopunctate (Pl. 8, Figs 4, 6, 8); the diameter of particular endopunctae varies between 13 and 25 μm on the inner surface and between 13 and 20 μm on the outer. The punctae can be branched (Pl. 8, Fig. 6). Strong tuberculation occurs in the marginal zone of the shell (Pl. 8, Fig. 8). The fibrous secondary layer is well developed in both valves (Pl. 3, Fig. 4b). The primary layer of fine-grained calcite is usually relatively well preserved in the ventral valves, however it is mostly visible only as small residual patches in the dorsal valves.

REMARKS: *Rioultina wapiennensis* sp.nov. shows the greatest resemblance to the middle Oxfordian species *Rioultina matisconensis* PAJAUD, 1966, from which it differs in the triangular shape of the shell. Precise examination of the relationship between these two species is not possible because of the incomplete preservation of the specimens (especially the interbrachial lobes) illustrated by PAJAUD (1966, 1970). The same situation occurs in the case of *Rioultina ornata* (MOORE, 1861) from the upper Oxfordian of England and France (DAVIDSON 1874-1882, PAJAUD 1970).

Family Thecideidae GRAY, 1840
Subfamily Lacazellinae BACKHAUS, 1959

Genus *Neothecidella* PAJAUD, 1970

TYPE SPECIES: *Thecidea antiqua* GOLDFUSS, 1840

Neothecidella ulmensis (QUENSTEDT, 1858)
(Pl. 4, Figs 1-6; Pl. 5, Figs 1-6; Pl. 6, Figs 1-3; Pl. 7, Figs 1-5; Pl. 8, Figs 3, 5, 7, 9)

1858. *Thecidea ulmensis* QUENSTEDT.; F.A. QUENSTEDT, p. 749-750, pl. 91, fig. 17-18.
1868-1871. *Thecidea ulmensis* QUENSTEDT.; F.A. QUENSTEDT, p. 699, pl. 61, fig. 135-138.
1915-1916. *Thecidea ulmensis* QUENSTEDT.; L. ROLLIER, p. 56.
1963. *Thecidella ulmensis* (QUENSTEDT)., D. PAJAUD, p. 996.
1970. *Praelacazella ulmensis* (QUENSTEDT)., W. BARCZYK, p. 648-649, text-fig. 1, pl. 1, fig.1-9.
1970. *Neothecidella ulmensis* (QUENSTEDT)., D. PAJAUD, p. 112-113, text-fig. 43c.

MATERIAL: 761 specimens, including 328 complete (244 well-preserved), 225 dorsal valves (155 well-preserved) and 208 ventral valves (95 well-preserved).

DIAGNOSIS: Medium-sized thecideide brachiopod with deep ventral valve; attachment scar usually large; pseudodeltidium faintly marked; hemispondylium W-shaped; dorsal valve subtrapezoidal in outline; cardinal process large, trough-like in transverse section; subperipheral rim with fine tubercles; ramus of adult individuals with two extensive ramuli, connected by jugum with major interbrachial lobes; minor interbrachial lobes developed in the form of small processes.

DESCRIPTION: **External morphology**: Shell subtrapezoidal in outline, with distinct sulcus visible along the anterior commissure in the ventral valve (Pl. 7, Figs 1-4). The ventral valve is strongly convex; the dorsal valve is flat, with a very prominent umbo. Maximum length of the shell 4.4 mm, width 5 mm and thickness 2.9 mm. The shell is usually slightly wider than long (Text-fig. 3A). The thickness of the shell is very variable (Text-fig. 3B) depending on the substrate.

The cardinal margin is straight and its length reaches from half to two-thirds the width of the shell. The ventral interarea is large, flat, well defined, with a poorly marked pseudodeltidium. The dorsal interarea is very narrow but clearly visible. The shell surface is smooth, endopunctate, with faint growth lines (Pl. 7, Figs 1-4; Pl. 8, Figs 5, 7, 9).

Internal morphology:

Ventral valve: The shell interior is ornamented by numerous tubercles, which are particularly distinct in juvenile specimens (Pl. 7, Fig. 5). In adults the individual tubercles are visible only in the marginal zone of the valve (Pl. 8, Fig. 3). The hemispondylium is two-lobed, W-shaped and it has a very distinctly marked myophragm (Pl. 7, Fig. 5; Pl. 8, Fig. 3). The hinge teeth are relatively large and rather widely separated (Pl. 7, Fig. 5; Pl. 8, Fig. 3).

Dorsal Valve: The subperipheral rim is wide and ornamented by a few rows of small tubercles. The cardinal process is large, rectangular in outline and, with the exception of juvenile forms, emerges slightly beyond the cardinal margin (Pl. 4, Figs 1-5; Pl. 5, Figs 1-6; Pl. 6, Figs 1, 3). The dental sockets are very large, oval and close to the base of the cardinal process (Pl. 6, Figs 1a-c, 3a-b). The lateral adductor muscle scars are very distinctly marked close to the base of the transversarium. They are semicircular in shape and orientated nearly perpendicular to the commissural plane (Pl. 6, Figs 1c, 3b).

The transversarium shows clear evidence of sexual dimorphism. The bridge of males (Pl. 6, Fig. 1a-d) is straight, with a slightly denticulate posterior edge and a shallow depression in the central part, similar to that observed by LOGAN (2004, fig. 3E) in *Pajaudina atlantica* LOGAN, 1988. The females possess a large depression in the middle of the tranversarium with a marsupial notch (Pl. 6, Fig. 2a), through which would pass two specialized lophophoral tentacles, supporting larvae in the brood pouch. In some specimens the bridge of large females was additionally strongly deflected towards the anterior of the shell (Pl. 6, Fig. 3a-b). The major interbrachial lobes occupy most of the surface of the brachial cavities and their posterior part (reticulum) is strongly perforated and possesses a distinctly denticulate edge (Pl. 4, Fig. 5a-b; Pl. 6, Figs 1a, 2b). The minor interbrachial lobes appear late in ontogeny and take the form of two small rounded processes, diverging anteriorly from the reticulum (Pl. 5, Fig. 1; Pl. 6, Fig. 1a). The major interbrachial lobes are connected with the ramus by a small slat-like jugum (Pl. 4, Fig. 5a-b). The ramus arises at the base of the opening in the anterior part of the median septum (Pl. 4, Fig. 1-4), which similarly was observed by BAKER & LAURIE (1978, text-fig. 2f-i) in juveniles of the Aptian *Neothecidella parviserrata*. The posterior undivided part of the septum is hidden in the adults by the extensive ramuli (Pl. 4, Fig. 5; Pl. 5, Figs 1, 4, 6; Pl. 6, Figs 1-3) and is visible only in specimens with a damaged ramus (Pl. 5, Figs 2-3, 5).

Microstructure: The shell is endopunctate (Pl. 4, Figs 4-5; Pl. 7, Fig. 5; Pl. 8, Figs 5, 7). The diameter of particular endopunctae varies between 17-26 µm, on the inner and outer surface. The shell is built mainly of granular calcite. The fibrous secondary layer is present only in the ventral valve, and is often visible even with the naked eye in strongly abraded specimens (apparent ribbing of the valve).

REMARKS: The sexual dimorphism in *Neothecidella ulmensis* (Quenstedt, 1858) does not influence ventral valve morphology which, in females of other representatives of the Lacazellinae, may be strongly distended to accommodate the brood pouch (Logan 2004). The eventual differences in shell shape between males and females may be hidden by the large variability in shell thickness (Text-fig. 3B), which is greatly dependent on the substrate.

The final ramus construction and appearance of small "minor interbrachial lobes" suggests that the lophophore development of *Neothecidella ulmensis* (Quenstedt, 1858) stops at the early ptycholophe stage (see Logan, 2004; fig. 4D, I, p. 212).

ECOLOGY AND PALAEOECOLOGY

Bathymetry

Recent representatives of the Thecideida are most numerous at depths from 10 to about 100 m (Pajaud 1974; Logan 1979, 2004, 2005; Lee & Robinson 2003; Lüter & *al*. 2003; Lüter 2005). The only exception is the unusual species *Kakanuiella chathamensis* Lüter, 2005 from deep waters of New Zealand, where living individuals have been discovered at depths between 400 and 1000 m. However *Kakanuiella hedleyi* (Thomson, 1915), also from this area, is found in shallow-water Eocene – Oligocene deposits (Lee & Robinson 2003; Lüter 2005). The environmental changes which caused the migration of *Kakanuiella* to deeper waters are not understood (Lüter 2005). The other records of Recent thecideide brachiopods in deep

KIND OF SUBSTRATE				**NUMBER OF INDIVIDUALS**	
				Neothecidella	***Rioultina***
SPONGES			Hexactinellida	18	132 (surface of one sponge)
			„Lithistida"	8	3
			Calcispongea	2	
			Sclerospongea (*Neuropora* sp.)	22	4
BRACHIOPODS	Rhynchonellida		*Lacunosella*	227	28
			Torquirhynchia	6	
	Terebratulida	ribbed	*Dictyothyropsis*	1	
		smooth	*Juralina*	2	
			Delmontanella	1	
	Thecideida		*Neothecidella*	3	
			Rioultina		1
TUBES OF DWELLING POLYCHAETES				3	2
ECHINOIDS				1	
BRYOZOANS				1	
BIVALVES (OYSTERS)				3	

Table 1. Some kinds of substrate settled by *Neothecidella ulmensis* (Quenstedt, 1858) and *Rioultina wapiennensis* sp. nov.

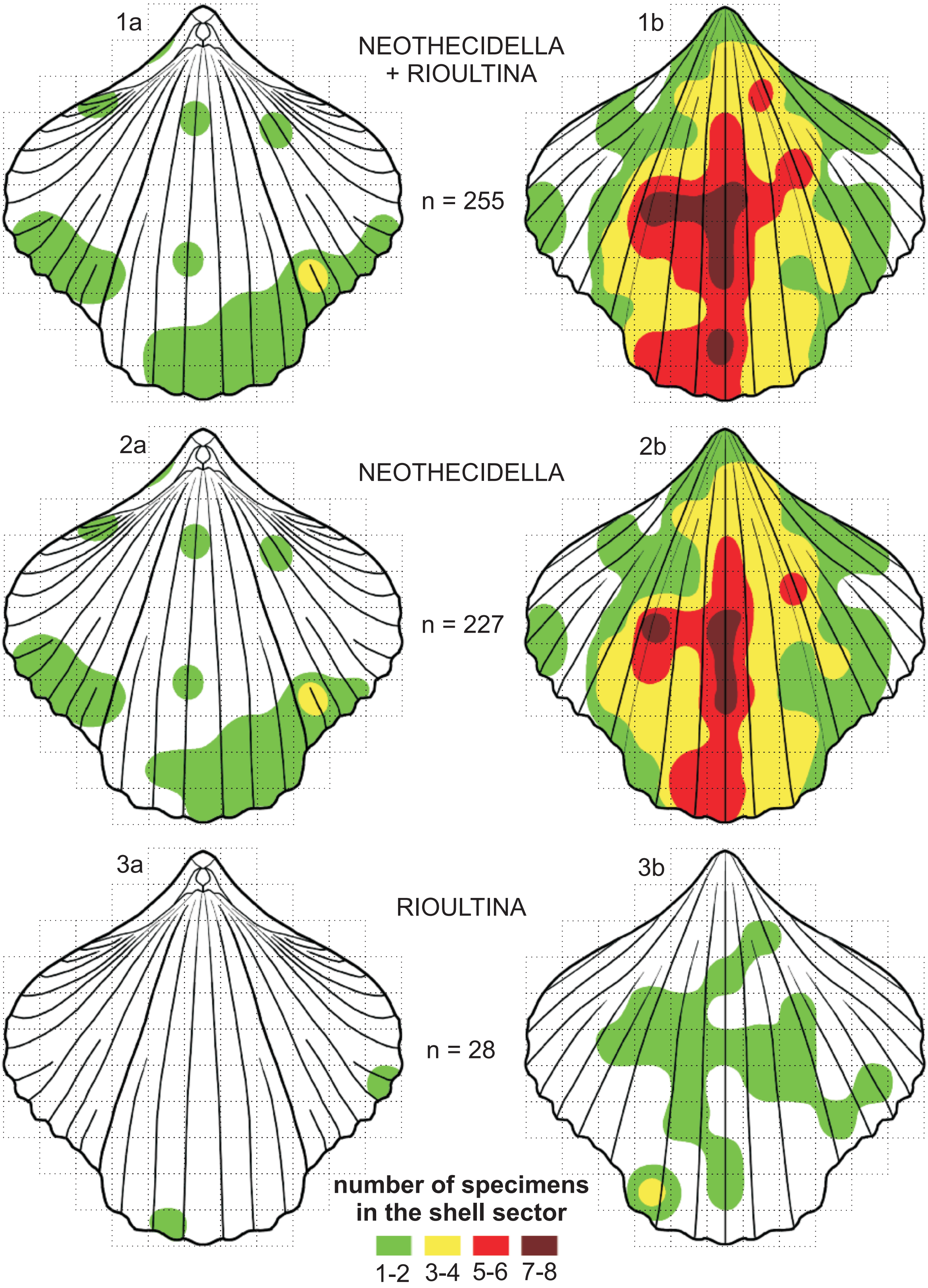

Fig. 4. Scheme of thecideide brachiopod distribution on the shells of *Lacunosella cracoviensis* (QUENSTEDT, 1871); 1a, 2a, 3a – dorsal side; 1b, 2b, 3b – ventral side

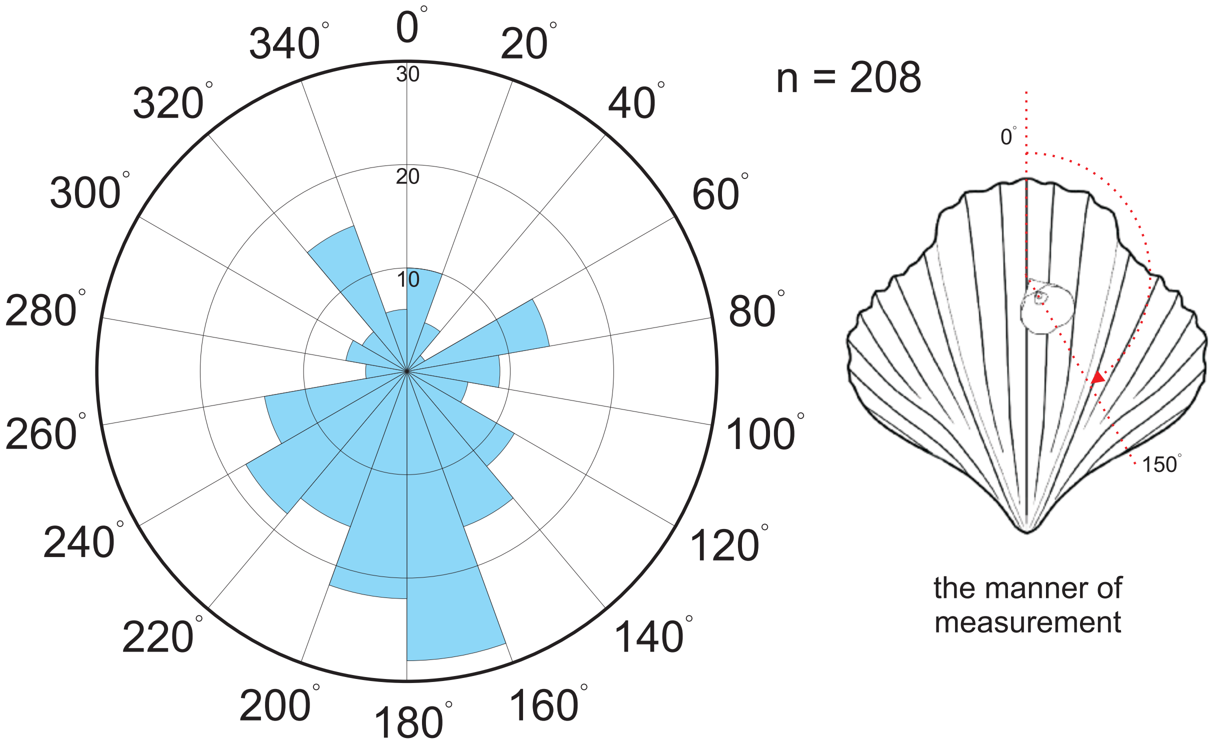

Fig. 5. Orientation of thecideide brachiopods cemented to the ventral valves of *Lacunosella cracoviensis* (Quenstedt, 1871); n – number of studied specimens

water have almost all resulted from post-mortem transportation of dead shells from original living sites (Logan 1988, 2004; Lee & Robinson 2003). The fossil record indicates that the trend to occupy shallow environments has been maintained during the whole evolutionary history of the group.

Depths estimations of horizons with *R. wapiennensis* sp. nov. and *N. ulmensis* in the area of the Zalesie Anticline are difficult but some facts shed light on this problem. The studied brachiopods come from the biohermal slope where, in addition to autochthonous elements, living and dead material is found that has been redeposited from the upper parts of the buildup (Matyja & Wierzbowski 1985). The thecideides are associated with a very rich sponge assemblage (Kołsut 1999) comprising 33.8% ± 3.2 Demospongea ("Lithistida"), 52.1% ± 3.4 Hexactinellida and 14.1% ± 2.3 Calcispongea. These numbers do not include a large amount of small sclerosponges (*Neuropora* sp). The large numbers of hexactinellids and lithistids and the relatively small number of calcisponges indicate rather deep waters, more than one hundred metres depth (see Leinfelder 1994, Pisera 1997). On the other hand, the central part of the bioherm in the late Oxfordian was settled by hermatypic corals and was probably situated above the wave base (Matyja & Wierzbowski 1985). The character of the environment occupied by corals ("hypothetical reef") of Matyja & Wierzbowski (1985) is, however, difficult to define because of substantial subsequent erosion of Upper Jurassic deposits in the centre of the Zalesie Anticline. The common occurrence and locally observed great density of *Rioultina* and *Neothecidella* populations in the Upper Oxfordian (Hauffianum – Planula Subzones) of Bielawy and Wapienno indicate that living depths did not exceed 100 m.

Substrate

The distribution of Recent thecideides is generally controlled by the availability of the hard substrates needed for shell cementation (see Pajaud 1970, 1974; Logan 1979, 2004, 2005; Logan & *al.* 2004; Richardson 1997; Lee & Robinson 2003; Lüter & *al.* 2003; Lüter 2005).

The various hard substrates on which *N. ulmensis* and *R. wapiennensis* sp. nov. from Bielawy and Wapienno have been found are compared in Table 1. Most specimens are cemented to the surfaces of sponges and large brachiopods. The siliceous sponge "mummies" represent the main hard substrates found in the late Oxfordian of the Zalesie Anticline, but the number of specimens found on them is probably much underestimated. This is caused by problems in the preparation of sponges without simultaneous damage of epibionts. Such difficulties do not occur in the case of the brachiopod shells. One good example of this underestimation is a single specimen of the sponge *Stauroderma lochense* (QUENSTEDT, 1858) from a marly layer (a deposit that is easy to remove), on which 132 specimens of *R. wapiennensis* sp.nov. have been counted (Tab. 1; Pl. 8, Fig. 1). The individuals of *Rioultina* occur on the upper surface of this flat plate-like sponge (Pl. 8, Fig. 1) and they are associated with other epifauna, such as: serpulids (see RADWAŃSKA 2004), bryozoans, and rare craniids (see KRAWCZYŃSKI 2005). The thecideides found on other siliceous sponges nearly always occur on their undersides, as in the case of the Late Bathonian *Rioultina triangularis* observed by PALMER & FÜRSICH (1981) on the surface of the sponge *Platychonia magna*.

Particularly interesting is the association of thecideides and the sclerosponge *Neuropora* sp. (Tab. 1; Pl. 7, Figs 1-2), which is similar to the Recent brachiopod-sclerosponge community observed by LOGAN (1977, 1981) in submarine reef caves of Grand Cayman. LOGAN described dense populations of *Thecidellina barretti* associated with (and attached to) the sclerosponges *Goreauiella auriculata* and *Ceratoporella nicholsoni*. Similar thecideide-sclerosponge communities were also observed in dark reef caves of Jamaica, Bahamas (LOGAN 1977), Palau and Saipan (LOGAN 2005). Thecideides from different locations in the Bielawy and Wapienno quarries have always been associated with large numbers of *Neuropora*. Twenty two individuals of *Neothecidella* and four of *Rioultina* were found still attached to specimens of *Neuropora* (Pl. 7, Figs 1-2; Tab. 1), and many more possess characteristic trough-like attachment scars indicating that these brachiopods were cemented to elongate, small substrates that were probably sclerosponges. Such convergence of association of *N. ulmensis* and *R. wapiennensis* sp.nov. with the sclerosponge *Neuropora* sp. indicates that these organisms probably inhabited similar cryptic environments to those in Recent forms.

Rioultina and *Neothecidella* have also often been found on shells of other brachiopods, especially large rhynchonellids. The most commonly encrusted species is *Lacunosella cracoviensis* (QUENSTEDT, 1871), which is also the most frequently represented large brachiopod associated with thecideides (Tab. 1). The preference for settling on this species is most probably related to its large size and the fact that brachiopods with strong-ribbed, non-punctate shells are more commonly encrusted by different kinds of epibionts (HURST 1974; TAYLOR & WILSON 2003; personal observations). For example, no thecideides have been found on the shells of the commonly-occurring, fine-ribbed, small terebratulids *Terebratulina substriata* (SCHLOTHEIM, 1820), and only single specimens on the large shells of *Juralina insignis* (SCHÜBLER, 1830). Representatives of *Neothecidella* and *Rioultina* settled mostly on still-living individuals of *Lacunosella cracoviensis* (QUENSTEDT, 1871), as indicated by their arrangement on the host's shells (Text-fig. 4), orientation (Text-fig. 5), and by the fact that only 2 specimens from 255 studied encrusted seemingly dead shells (growth across the lateral and anterior commissure respectively). Most of these epibionts occur on the ventral valves (89.4%) and in the anterior part of the dorsal valve of *L. cracoviensis*, and this situation corresponds with the life position of the above-mentioned brachiopods (Text-fig. 4). These areas of the shell, and especially the central part of the ventral sulcus where the thecideides are mostly concentrated (Text-fig. 4), were much exposed and easier to settle on. The almost complete absence of *Neothecidella* and *Rioultina* on the anterior-lateral areas of the shell of *L. cracoviensis* (Text-fig. 4) suggests that they did not use the inhalant currents of the host. Since most thecideides are found on the borders of ventral sulci, it is unlikely that these brachiopods used exhalant current produced in the mid-anterior part of the *L. cracoviensis* shell (Text-fig. 4). The orientation of *Neothecidella* and *Rioultina* on the ventral valves of *Lacunosella* is not random, and their anteriors are directed mostly to the shell posterior of the hosts (Text-fig. 5; Pl. 7, Fig. 4a-b). Such orientation suggests that on the living *Lacunosella* their shell gapes were pointed downward. A similar orientation has also been observed in *N. ulmensis* cemented to the small sclerosponge *Neuropora* sp. (Pl. 7, Figs 1-2), and analogous cases are known, for example, in the sponge *Platychonia magna* encrusted by *Rioultina triangularis* (PALMER & FÜRSICH 1981) or in *Neothecidella* sp. attached to corals (HOUŠA & NEKVASILOVÁ 1987). The downward orientation of the anterior commissure was an advantage during disposal of sedimentary particles and the products of metabolism from the shell interior (HOUŠA & NEKVASILOVÁ 1987).

The shell asymmetry is mostly related to an adaptation to the substrate and is more frequent in *N. ulmensis* than in *R. wapiennensis* sp.nov. This asymmetry is manifested by an increase or reduction in size of one brachial cavity (Pl. 3, Fig. 1a-b; Pl. 5, Figs 2, 4) and/or by curvature of the plane of symmetry related to a gradual change in the orientation of the brachiopod during ontogeny (often forced by substrate morphology). It has been observed in *Neothecidella* cemented to the shells of *Lacunosella cracoviensis* (QUENSTEDT, 1871) that the coarse ribs of the host sometimes controlled the direction of growth (Pl. 7, Fig. 4a-b).

Very rarely, the shells of thecideides may also be the substratum for other encrusting organisms. In the material studied such cases are rare but very interesting. The first example is a juvenile *N. ulmensis*, which settled on the dead shell of an adult representative of the same species (Pl. 7, Fig. 5). This type of occurrence may indicate a great population density and the fact that spatfalls of thecideides do not travel very far from the parent population. The juvenile is in such an early stage of development that the cementation area occupies the whole surface of its ventral valve. The second case is the polychaete ?*Metavermilia* sp. (see RADWAŃSKA 2004) encrusting the shell of *N. ulmensis* (Pl. 7, Fig. 3). This serpulid worm began its development on the ventral valve of the brachiopod (see white arrow Pl. 7, Fig. 3) and then grew across the cardinal margin to the dorsal valve, where it utilized this small surface to the maximum. There are three possible interpretation of this state:

- the polychaete settled on a dead shell
- the polychaete settled initially on the ventral valve of a living *Neothecidella* and, following the natural death of the brachiopod, extended its growth onto the dorsal valve.
- the development of the dwelling tube of this polychaete caused the death of the brachiopod resulting from overgrowth of the cardinal margin and blockage of the shell opening.

The third example is the dorsal valve of an adult *R. wapiennensis* sp.nov. (Pl. 3, Fig. 1a-b) colonized by a juvenile of the same species and a bryozoan colony of *Hyporosopora* sp.; the latter is developed mostly on the external surface (not visible on picture) but partially encroaches onto the outer surface of the subperipheral rim (Pl. 3, Fig. 1a – right-hand corner of the photo). This last fact indicates that the colony developed on a dead shell, at least in the last phase of growth. The *Rioultina* juvenile settled in the interior of a much-damaged (as a result of a long exposure on the bottom or/and transportation) dorsal valve that lacked both interbrachial canopies, and it died in consequence of blockage of the shell by a hooked element of the left interbrachial canopy support.

Temperature

Recent thecideides inhabit mostly tropical and subtropical waters: Caribbean Sea (LOGAN 1977; COOPER 1979), Coral Sea (LÜTER & *al*. 2003); coasts of Bahamas (PAJAUD 1974), Mauritius, Madagascar (COOPER 1973, 1981), Maldives (LOGAN 2005), etc. The most thermophilous is the genus *Thecidellina* THOMSON, 1915, the only Recent representative of the Thecidellinidae ELLIOTT, 1958, which occurs in waters with mean temperatures above 23°C (PAJAUD 1970). The coolest site in which this genus has been recorded is the Kermadec Islands (New Zealand), where the average water temperature ranges between 20 and 21°C, and reaches a maximum of 26°C (LEE & ROBINSON 2003). Recent representatives of the Lacazellinae BACKHAUS, 1959 also prefer very warm environments, but they also occur in the Mediterranean Sea (*Lacazella mediterranea*), with mean water temperatures of 18-20°C (PAJAUD 1970) or the the Canary Islands (*Pajaudina atlantica*), with a mean temperature of 17°C (JAECKS & *al*. 2001).

Reproduction

All Recent thecideides brood their offspring, resulting in the production of few eggs equipped with large amounts of yolk, and lecithotrophic larvae which are able to settle and metamorphose just after leaving the parent shell (PAJAUD 1970, LÜTER 2005). Brood protection is realized in a somewhat different manner by the two Recent families Thecideidae GRAY, 1840 and Thecidellinidae ELLIOTT, 1858.

In the Thecideidae the embryos are protected in a single brood pouch, situated in the ventral valve mantle (underneath the hemispondylium) of adult females. Larvae maturing in its interior are attached to the tips of two specialized lophophoral tentacles. These are supported by special, trough-like hollows in the transversarium of the dorsal valves – (marsupial notch). This feature is developed exclusively in females of all recent representatives of the Thecideidae GRAY, 1840 (PAJAUD 1970; LOGAN 1988, 2004, 2005; LÜTER & *al*. 2003; LÜTER 2005) and it enables discrimination of sexes even on the basis of skeletal material. In the fossil material sexual dimorphism has been observed e.g. by BAKER (2005) in his *Protolacazella scripta*, but it usually has been overlooked by researchers particularly because of the delicate structure of the transverarium, which is very easily destroyed during postmortem transportation, fossilization or preparation. In the case of *N. ulmensis* studied herein only 5.3% of the dorsal valves possess a well preserved transversarium, but features associated with sexual dimorphism are still visible (see systematic description for details; Pl. 6, Fig. 1b, 2a).

Recent Thecidellinidae protect their offspring in two brood pouches situated in the interior of the interbrachial lobes, but they do not possess any specialized lophophoral tentacles (PAJAUD 1970, LÜTER & *al*. 2003, LÜTER 2005). The interbrachial sacs acting as brood pouches are epidermal invaginations and up to five larvae can mature simultaneously in each sac (LÜTER & *al*. 2003). *R. wapiennensis* sp.nov. possesses interbrachial lobes enabling accommodation of brood pouches (see systematic description for details; Pl. 1, Figs 1-3; Pl. 2, Fig. 1). It is manifested by the characteristic duality of an interbrachial cavity and its canopy, which corresponds to the structure of the interbrachial sac (marsupium) of Recent *Thecidellina* (see PAJAUD 1970, fig. 19 B). The latter genus is probably hermaphroditic (WILLIAMS & *al*. 1997, LÜTER & *al*. 2003, LÜTER 2005). In the case of *Rioultina* the skeletal material does not allow for an unequivocal interpretation, however, hermafroditism cannot be excluded because there is no marked dimorphism. The bridge, in contrast to that of *Neothecidella,* is well preserved in the majority of specimens and is straight, denticulated, without any marsupial notch (Pl. 1, Fig. 1-3; Pl. 2, Fig. 2-4; Pl. 3, Fig. 1). In only one individual (Pl. 3, Fig. 2) has a structure resembling a marsupial notch been observed, but in view of the fact that it is an early juvenile form, this structure is probably not associated with any eventual "specialized tentacles".

Acknowledgments

Cordial thanks are due to Professors Urszula RADWAŃSKA and Andrzej RADWAŃSKI for valuable comments and access to their collections from the Wapienno and Bielawy quarries. I would like to thank also the journal referees, Prof. Dr. A. LOGAN and Prof. Dr. J. REITNER, for their constructive criticism and language corrections. The management of Lafarge Cement Polska S.A. is thanked for access to the Wapienno and Bielawy quarries and logistic help during fieldwork. The research was supported by the Faculty of Geology, University of Warsaw.

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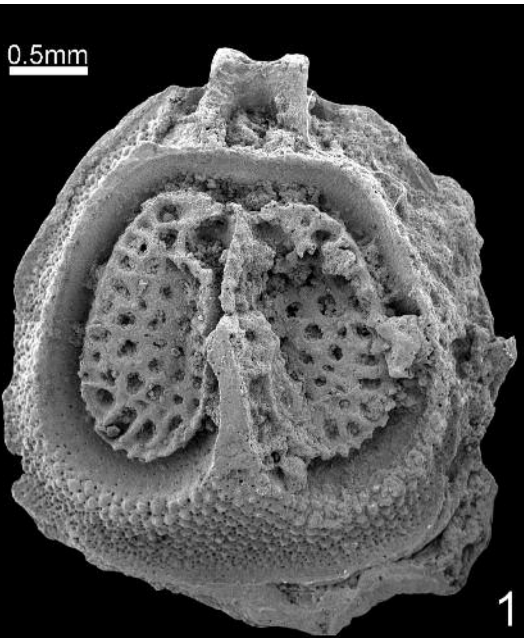
Manuscript submitted: 15th January 2007
Revised version accepted: 5th August 2008

PLATES 1-8

PLATE 1

Rioultina wapiennensis sp. nov.; specimens with perfectly preserved canopies of the interbrachial lobes, Upper Oxfordian, Wapienno

1 – paratype (RW6-P2-B4), general view of the dorsal valve interior; **2** – paratype (RW6-P2-B6), dorsal valve interior: 2a – general view of specimen with partly damaged left interbrachial canopy (part of the interbrachial cavity is clearly visible), 2b – oblique view (cardinal process digitally removed to show details of transversarium, two white arrows show openings of the interbrachial cavities, white triangle shows the canal connecting interbrachial cavity with visceral cavity), 2c – posterior view, cardinalia; **3** – holotype (RW6-P2-B5) interior of dorsal valve, 3a – general view (white arrow shows deep incision in posterior part of the canopy), 3b – oblique view showing details of transversarium and interbrachial canopies.



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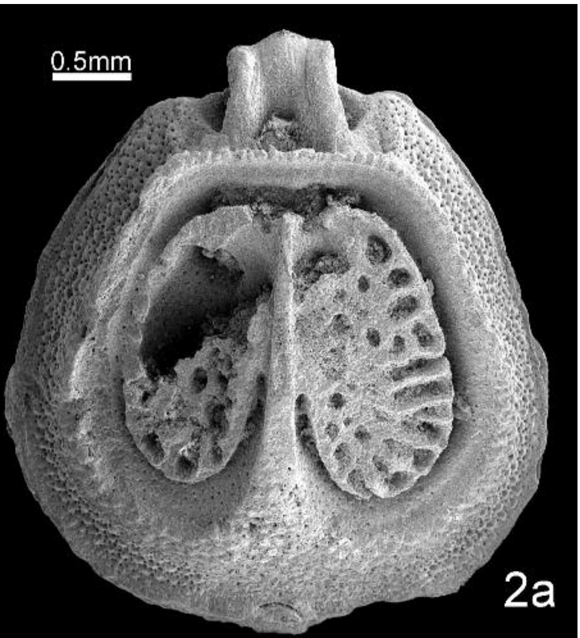

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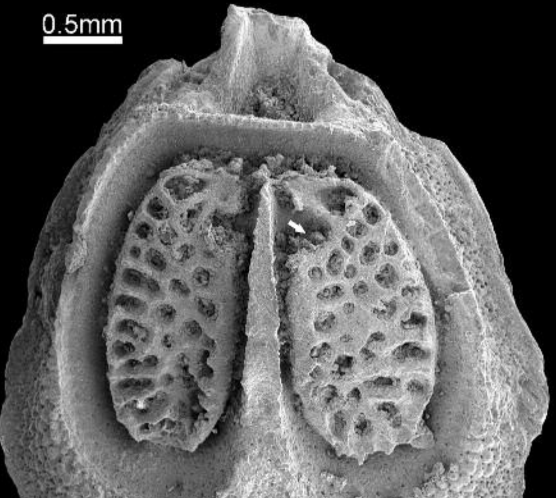

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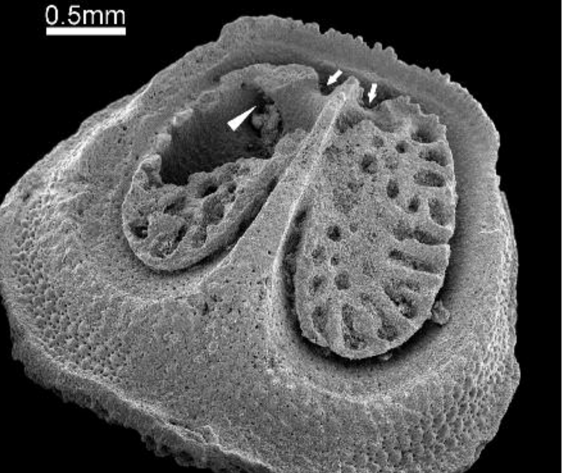

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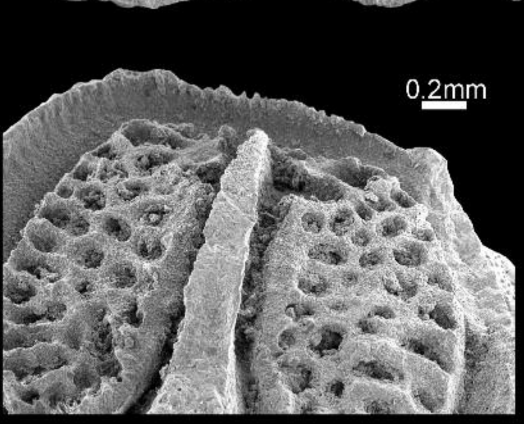

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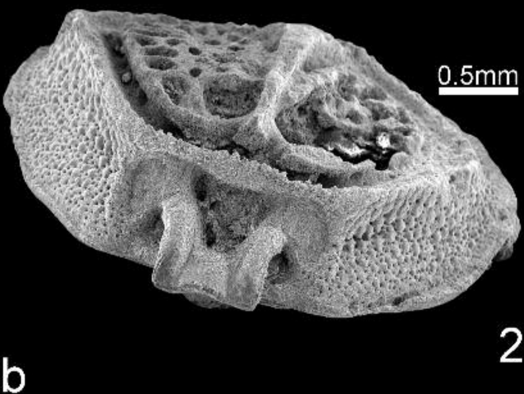
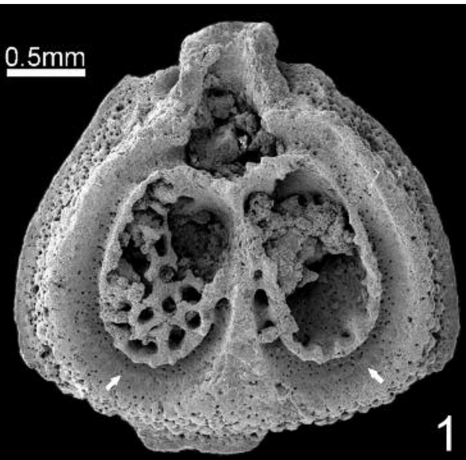


2c

PLATE 2

Rioultina wapiennensis sp. nov., interiors of dorsal valves in different stages of damage

1 – paratype (RB2-P1-D5), Upper Oxfordian, Planula Subzone, Bielawy, Specimen with partly damaged canopies of interbrachial lobes (white arrows show lophophoral groove); **2-3** – (RB2-P1-D6, D4), Upper Oxfordian, Planula Subzone, Bielawy, specimens with preserved remains of interbrachial canopies; **4** – (RW6-P2-A4), Upper Oxfordian, Wapienno, specimen with only canopy skeletal supports preserved (typical state of preservation); **5-7** – (RB2-P1-D2/1, RB2-P1-D3, RB2-P3-A3), Upper Oxfordian, Planula Subzone, Bielawy, strongly damaged specimens (5-6 – mechanically, 7 – chemically dissolved).



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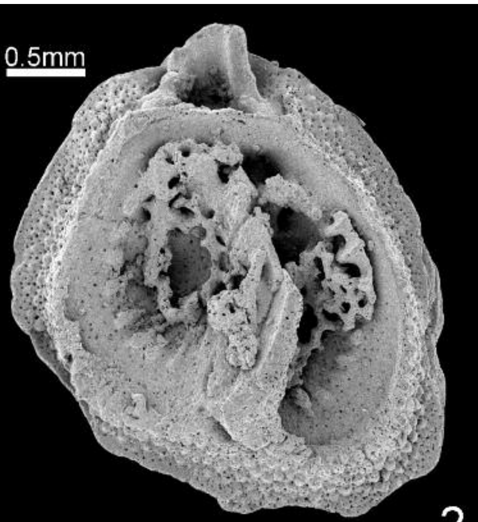

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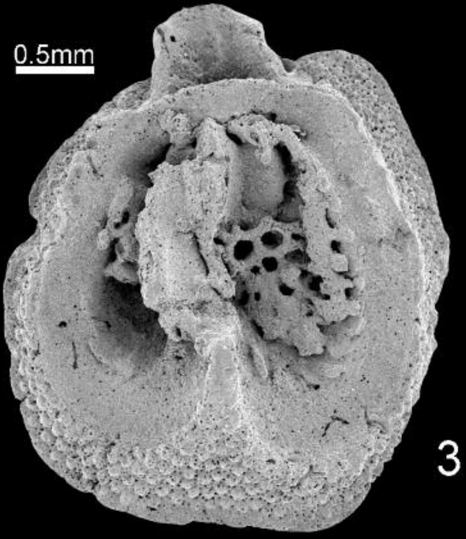

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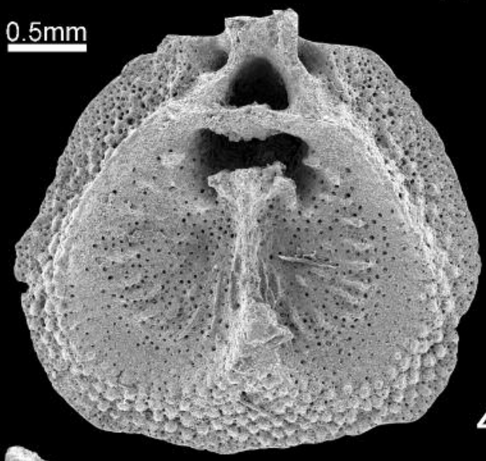

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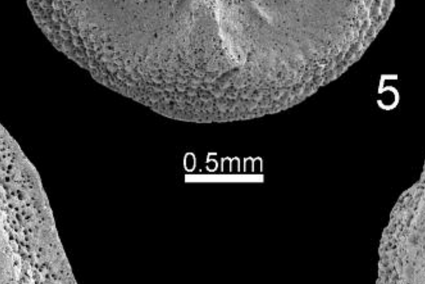

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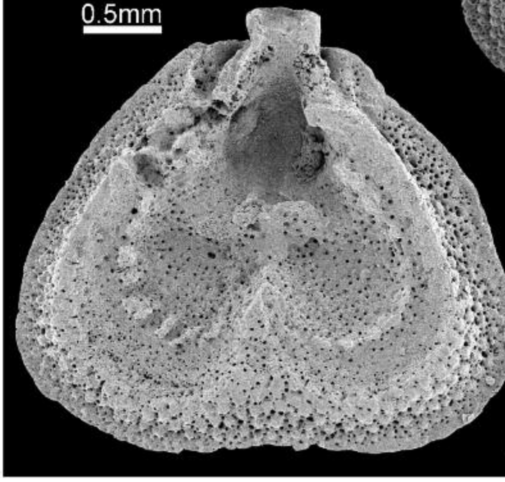

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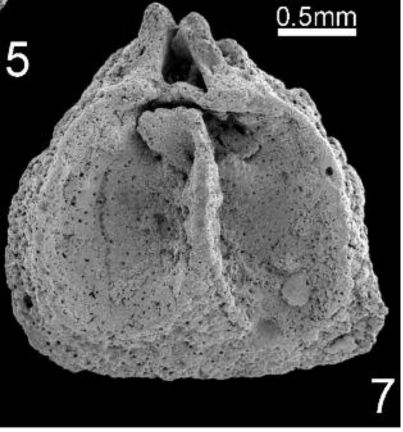

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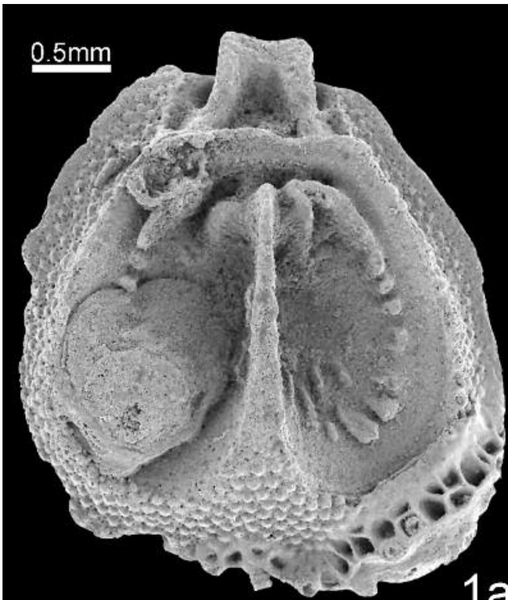
PLATE 3

Rioultina wapiennensis sp. nov.

1 – (RW6-P2-B2), Upper Oxfordian, Wapienno: 1a – dorsal valve encrusted posthumously by another individual of this species (left interbrachial cavity) and bryozoan *Hyporosopora* sp. (colony fragment is visible in right anterior part of the valve; the greater part of the colony occurs on the external; surface of the valve), 1b – enlargement of left interbrachial cavity, showing exact position of occupant and its possible cause of death as a result of shell blockage by a piece of the host's interbrachial canopy support; **2** – (RW6-P2-C5), Upper Oxfordian, Wapienno: 2a – juvenile individual, with structure similar to marsupial notch of Lacazellinae on the transversarium of the dorsal valve, 2b – enlargement of the same structure; **3** – paratype (RB2-P1-D1), Upper Oxfordian, Planula Subzone, Bielawy, ventral valve interior; **4** – paratype (RB2-P1-A5), Upper Oxfordian, Planula Subzone, Bielawy: 4a – complete specimen, dorsal view, white arrow shows enlarged fragment, 4b – fibrous secondary layer.



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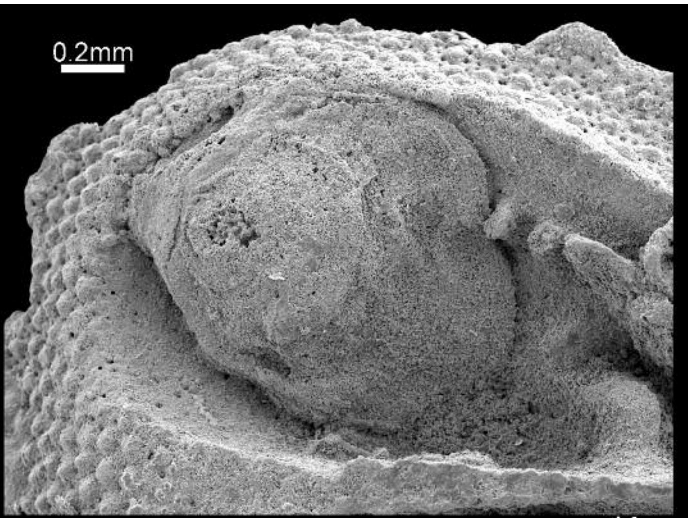

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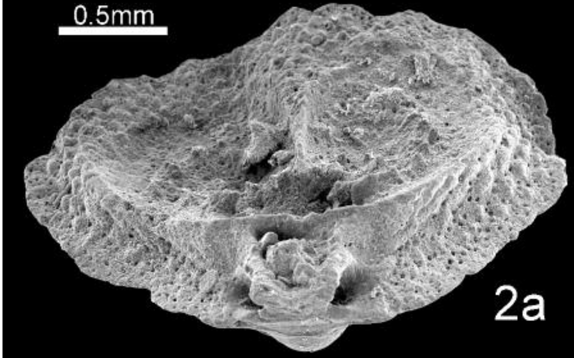

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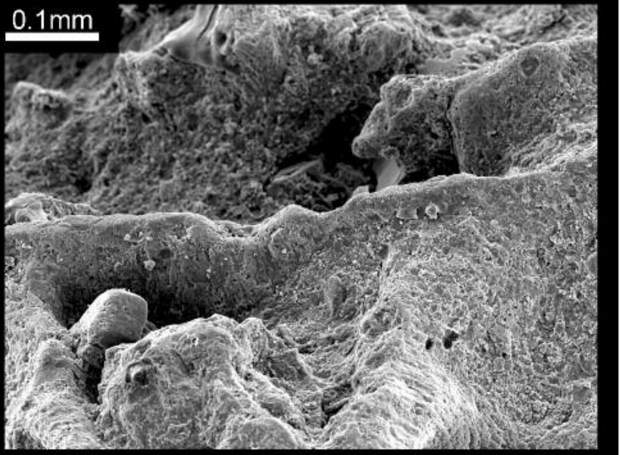

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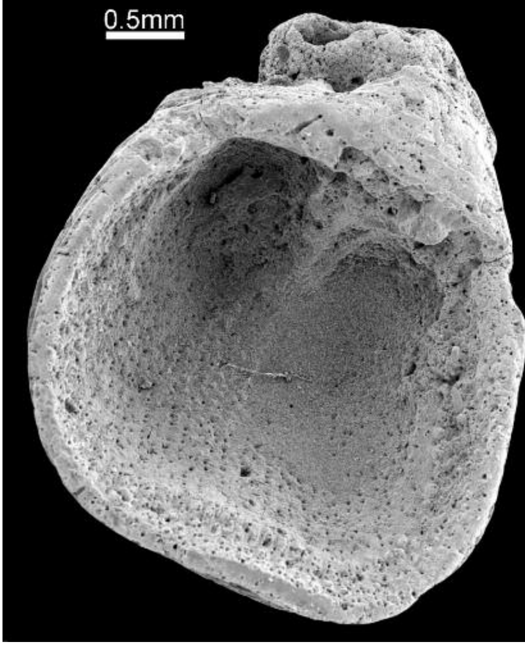

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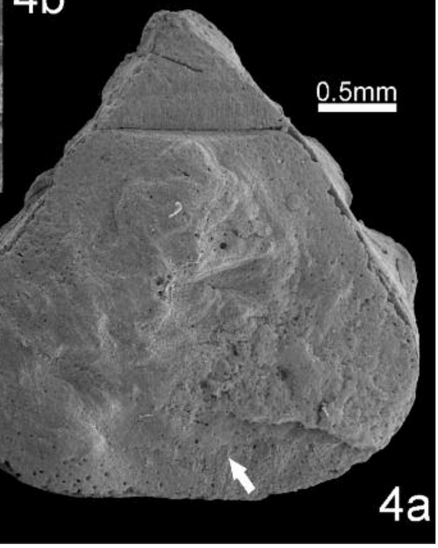

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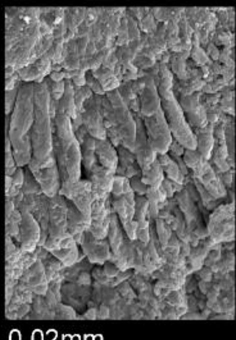

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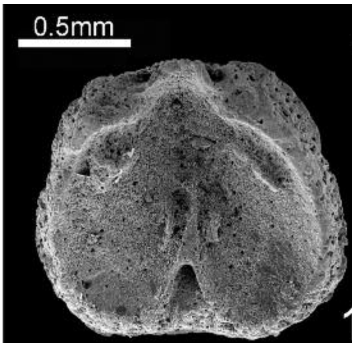
PLATE 4

Neothecidella ulmensis (QUENSTEDT, 1858), Upper Oxfordian, Planula Subzone, Bielawy

1-3 – (NB2-P3-B2, A1, B1) dorsal valves of early juvenile specimens. **4-5** – (NB2-P3-A6, A5) dorsal valves of juvenile specimens: 4a – general view, 4b – fragment of the subperipheral rim with visible endopunctae, 5a – general view of a specimen with well preserved interior, 5b – some elements of the brachidium (J – jugum, R – reticulum, RA – ramus, MA – major interbrachial lobe; **6** – (NB2-P3-D3) early adult specimen.



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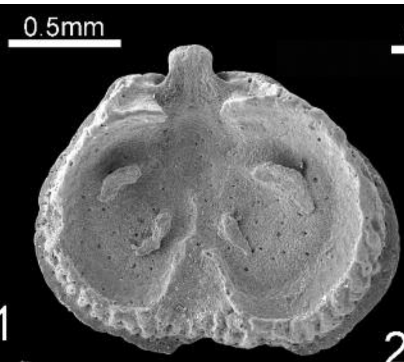

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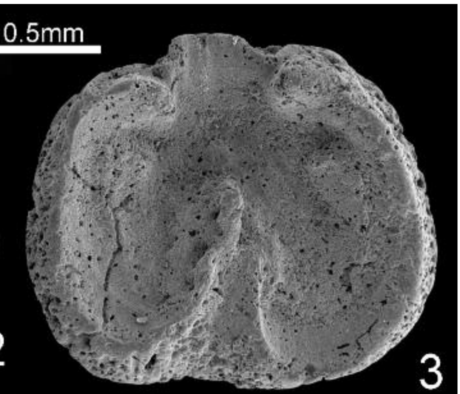

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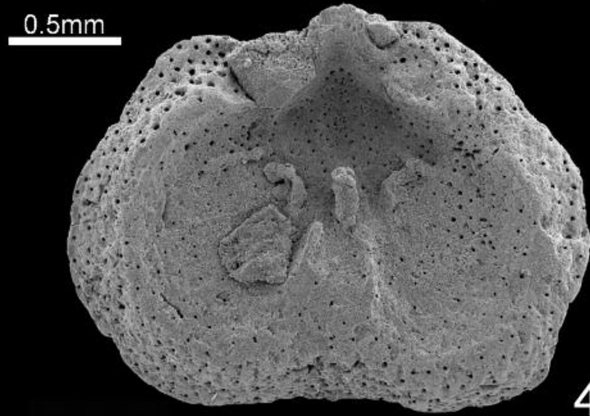

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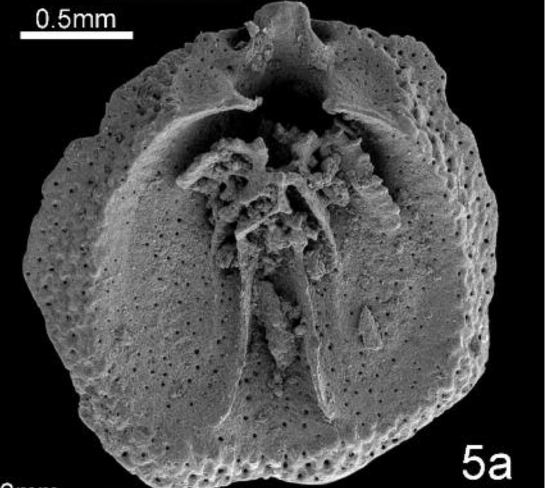

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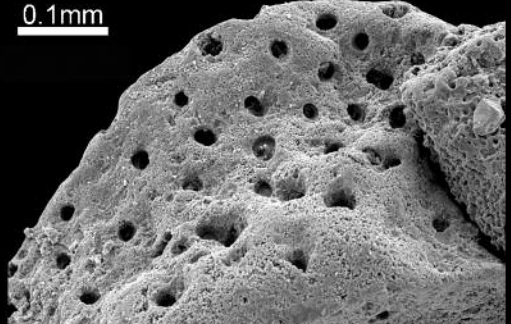

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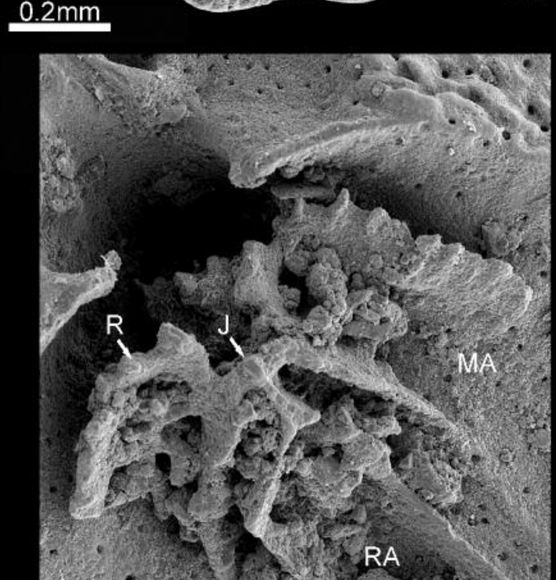

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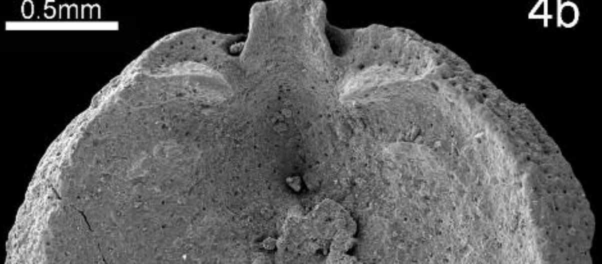

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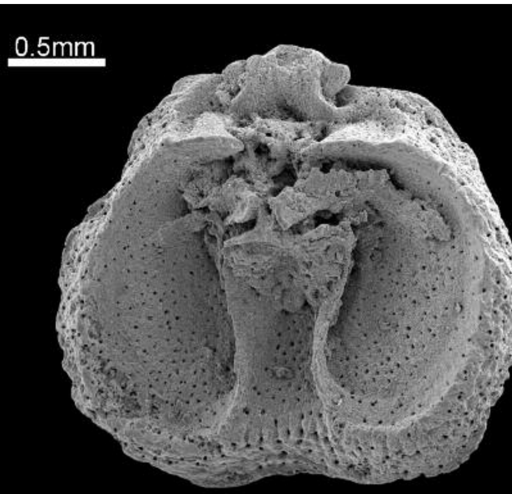
PLATE 5

1-6 – *Neothecidella ulmensis* (QUENSTEDT, 1858), Upper Oxfordian, Planula Subzone, Bielawy (NB2-P3-B3, C2, D5, B5, D2, NB2-P4-A1); early adult specimens.



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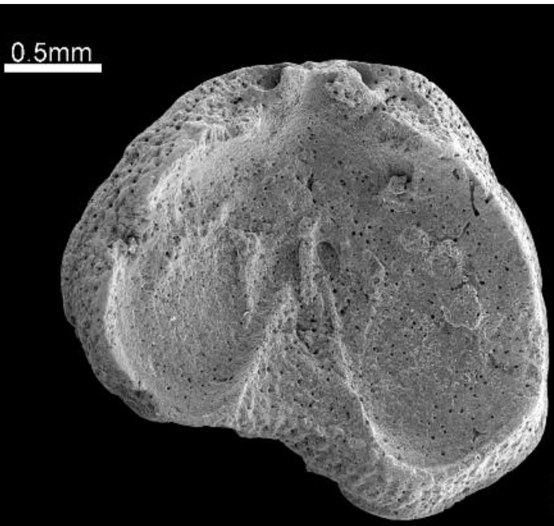

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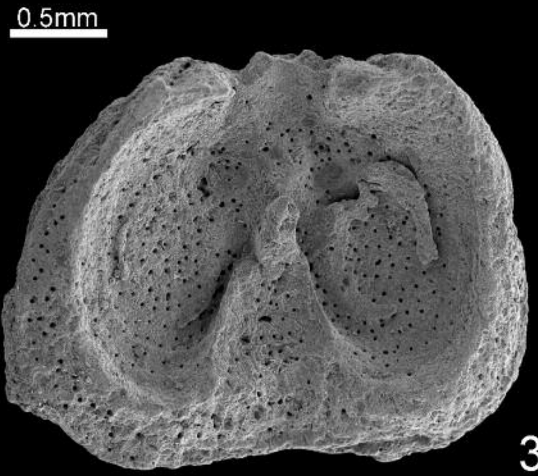

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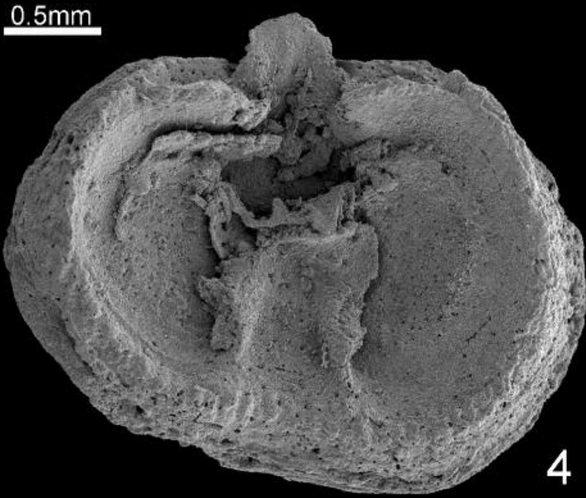

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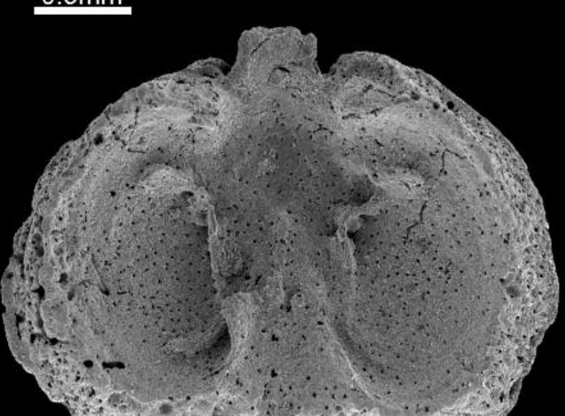

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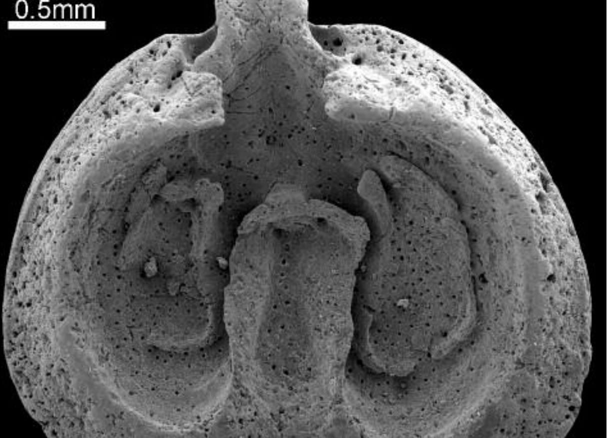

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PLATE 6

Neothecidella ulmensis (QUENSTEDT, 1858), Upper Oxfordian, Wapienno

1 – (NW6-P1-A3) perfectly preserved dorsal valve of an adult male: 1a – general view of valve interior, 1b – enlargement of the posterior part of the valve to show cardinal process, dental sockets and typical male transversarium (bridge), 1c – oblique posterior view of valve interior, 1d – enlarged posterior view of the transversarium; **2** – (NW6-P2-B1) dorsal valve of adult female: 2a –enlarged anterior view of the female transversarium, with distinct marsupial notch shown by arrows, 2b – general view of valve interior, **3** – (NW6-P2-A1) dorsal valve of adult female with very strongly deflected transversarium: 3a – general view of valve interior, 3b – oblique posterior view of valve interior.

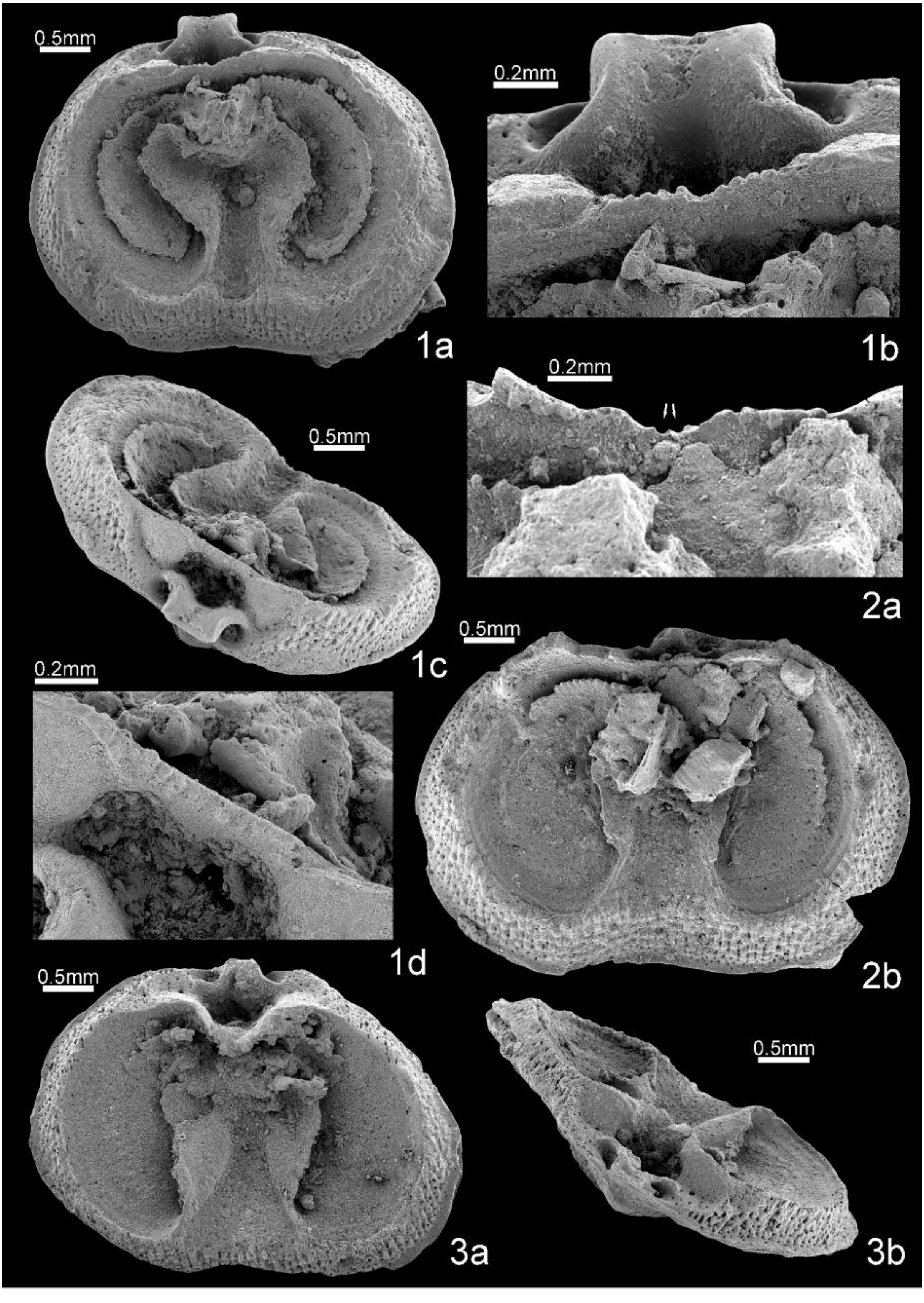
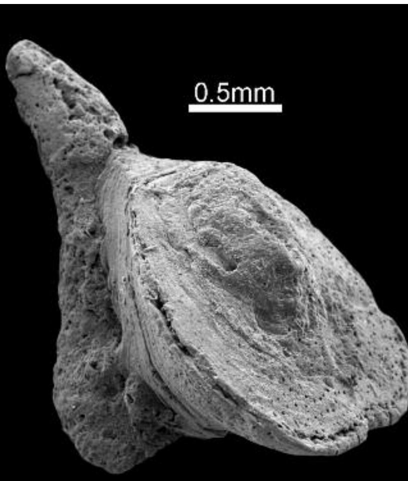

0.5mm
1a
0.2mm
1b
0.2mm
2a
0.5mm
1c
0.2mm
1d
0.5mm
2b
0.5mm
3a
0.5mm
3b

PLATE 7

Neothecidella ulmensis (QUENSTEDT, 1858)

1-2 – (NB2-P5-A1, A2), Upper Oxfordian, Planula Subzone, Bielawy, specimens in life position, attached to the basal skeletons of the sclerosponges *Neuropora* sp.; **3** – (NW6-P2-C4), Upper Oxfordian, Wapienno, specimen with adnate polychaete ?*Metavermilia* sp. (white arrow shows the beginning of its dwelling-tube); **4** – (LNW1/12), Upper Oxfordian, Wapienno, 4a – specimen cemented to the shell of the brachiopod *Lacunosella cracoviensis* (QUENSTEDT, 1871), white arrow shows position of the host's anterior, 4b – enlargement of the same specimen; **5** – (NW6-P1-A4), Upper Oxfordian, Wapienno, juvenile individual (ventral valve) which settled posthumously on the shell of an adult *Neothecidella ulmensis* (QUENSTEDT, 1858).



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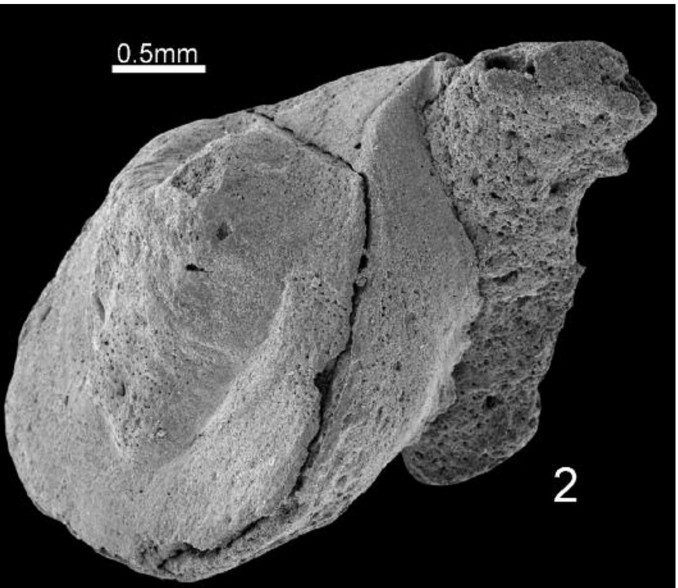

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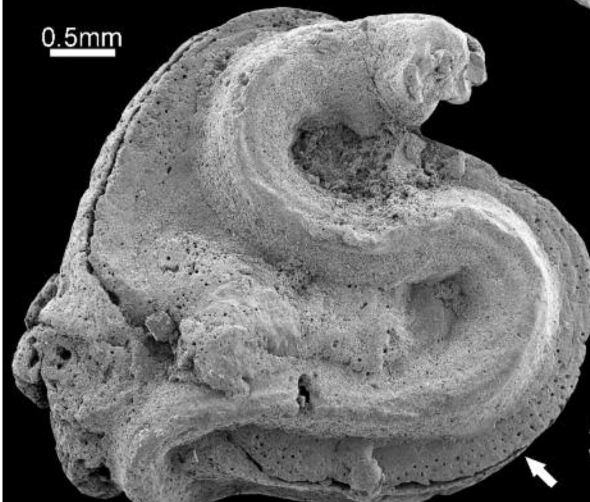

3

4a

4b

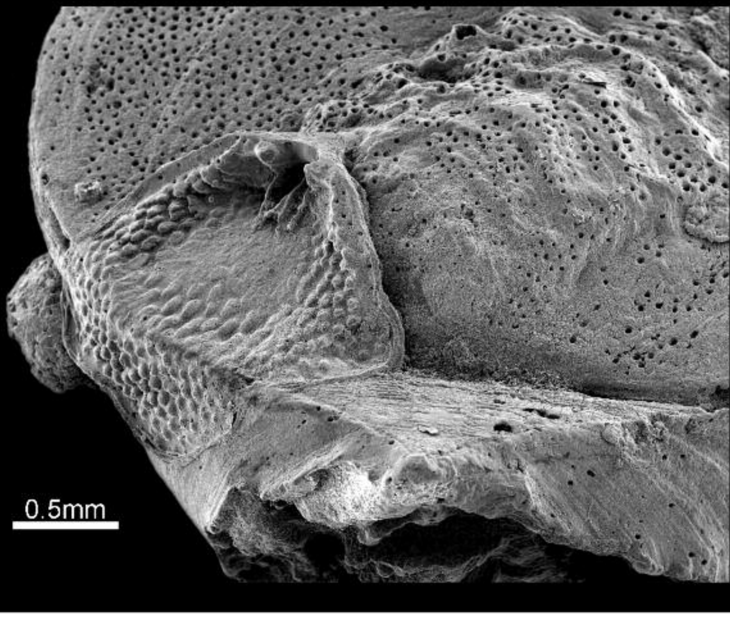

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PLATE 8

1 – (RW11-ST2), six juvenile individuals of *Rioultina* sp. attached to a fragment of the sponge *Stauroderma lochense* QUENSTEDT, 1858) and to the polychaete *Neovermilia limata* (MÜNSTER *in* GOLDFUSS, 1831), Bimammatum Zone, Wapienno.

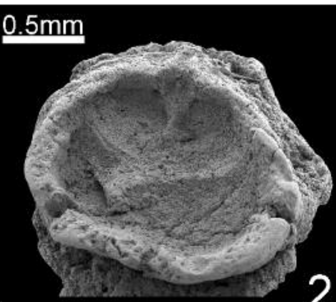
2 – (NB2-P3-A2), ventral valve interior of a juvenile *Rioultina wapiennensis* sp. nov., Upper Oxfordian, Planula Subzone, Bielawy.

3 – (NW11-P1-C6), ventral valve interior of an adult *Neothecidella ulmensis* (QUENSTEDT, 1858), Upper Oxfordian, Hauffianum Subzone, Wapienno.

4, 6, 8 – shell microstructure of *Rioultina wapiennensis* sp.nov.: 4 – (RW6-P1-A1) endopunctae in the floor of the left interbrachial cavity, 6 – (RB2-P1-D2/2) granular calcite and branched endopuncta (left side) in the floor of the right interbrachial cavity, 8 – (RB2-P1-D2/1) ornamentation of the subperipheral rim (outer surface).

5, 7, 9 – shell microstructure of *Neothecidella ulmensis* (QUENSTEDT, 1858): 5 – (NB2-P3-B3) endopunctae in the floor of the left brachial cavity, 7 – (NB2-P3-C5) longitudinal section of endopunctae, visible in a broken dorsal valve, 9 – (NW6-P1-B2) granular calcite (primary layer) and growth lines visible on the outer surface of a dorsal valve.

1



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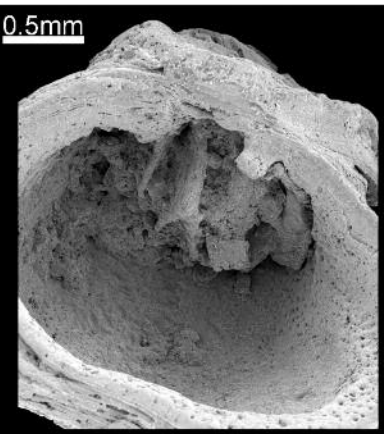

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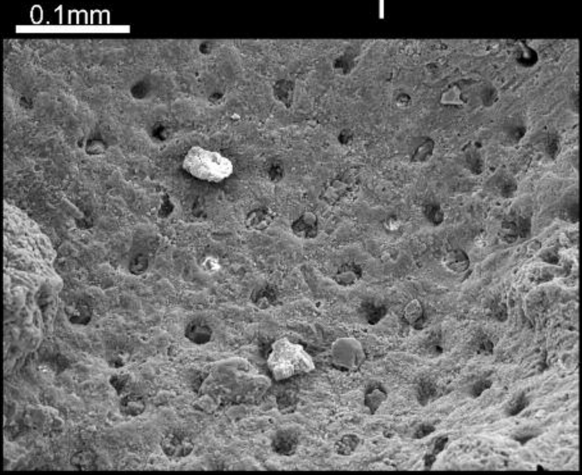

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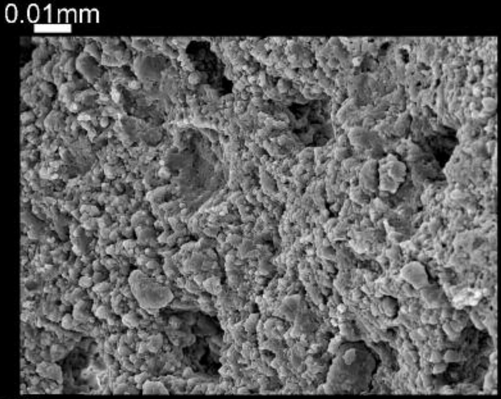

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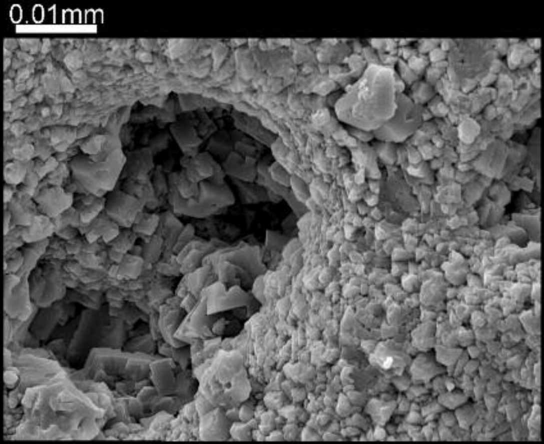

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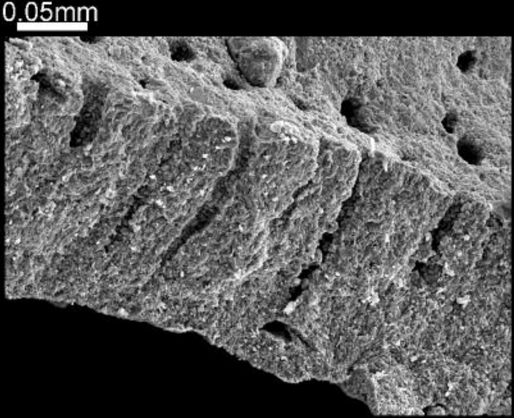

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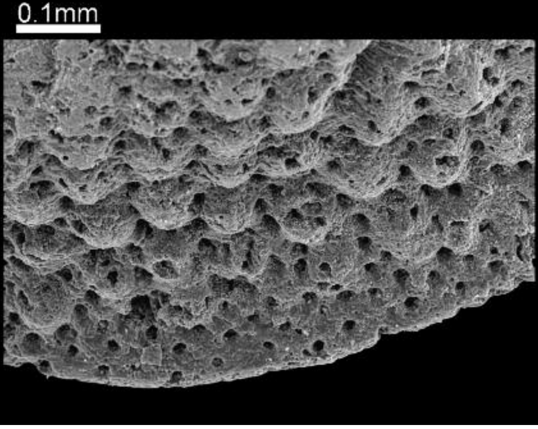

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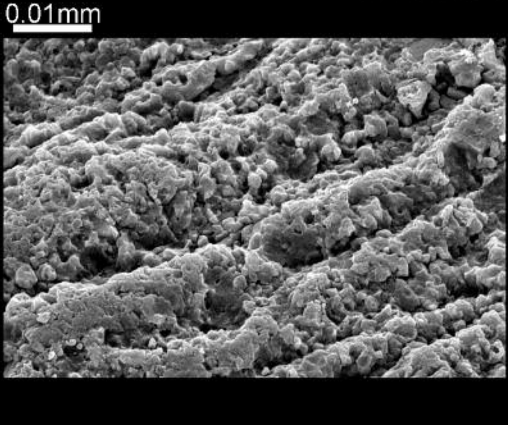

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