Selected Oxfordian brachiopods from Zalas
(Cracow Upland, Poland)

URSZULA RADWAŃSKA

Faculty of Geology, University of Warsaw, Żwirki i Wigury Str. 93; PL-02-089 Warszawa, Poland
E-mail: u.radwanska@uw.edu.pl

ABSTRACT:

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Small brachiopods of the families Craniidae Menke, 1828 and Thecidellinidae Elliott, 1958 were selected from the Oxfordian sequence which lies transgressively upon a Variscan rhyodacite laccolite exposed at Zalas in the Cracow Upland, southern Poland, a site which is well-known due to various kinds of ubiquitous fossils. The craniids include three species: *Craniscus bipartitus* (Münster in Goldfuss, 1837), *Craniscus tripartitus* (Münster in Goldfuss, 1837) and *Craniscus antiquior* (Jelly, 1843), and the thecidellinids – two species: *Rioultina zalasensis* sp. nov. and *Rioultina wapiennensis* Krawczyński, 2008. The species described herein indicate tropical or subtropical waters, and a moderately (?) deep character of the sea basin at Zalas.

Key words: Brachiopods; Craniidae; Thecidellinidae; Craniscus; Rioultina; Oxfordian; Poland.

INTRODUCTION

The Middle to Upper Jurassic strata exposed at Zalas (Text-fig. 1) in the Cracow Upland (some 20 km to the west of the town of Cracow) represent one of the most prolific fossiliferous sequences in Poland. The fame of the Zalas locality began in the early 19th century, to be continued ever since. Since the 1970's, the strata have been exposed in the topmost part of a huge quarry of rhyodacite, a Variscan laccolite of which makes up the basement.

The sedimentary sequence capping the laccolite developed during the mid-Jurassic (Callovian) transgression, which encroached upon eroded laccolite, exposed it as a hilly monadnock. The sequence begins with a Callovian cliff, bearing large blocks/ boulders of rhyodacite, and preserved as though just frozen in the surf zone (Dżułyński 1950, fig. 2), nowadays forming a protected site.

The Jurassic sequence of Zalas, has been a subject of numerous reports (e.g., Roemer 1870; Zaręczny 1894; Wójcik 1910; Gradziński 1960; Tarkowski 1989; Gradziński and Gradziński 1994).

The Oxfordian succession at Zalas, far-famed due to its content of ubiquitous ammonites, sponges, and echinoderms, overlies a sedimentary gap. It begins with variegated marls and marly limestones (about 2 m thick) of the Cordatum Zone, covered by a carbonate buildup (cyanobacteria-sponge bioherm) ,and by thin-bedded limestones and marls, or platy limestones (about 10 m thick) of the Middle Oxfordian Tenuicostatum Subzone of the Plicatilis Zone (see Matyja and Tarkowski 1981, figs 2–3).

The Jurassic sequence of Zalas has been the subject of numerous descriptions (e.g., Roemer 1870; Zaręczny 1894; Wójcik 1910; Gradziński 1960; Tarkowski 1989; Gradziński and Gradziński 1994).

During a systematic research of Upper Jurassic echinoids from Poland (see e.g., Radwańska 2003, 2005, 2014), the present author has recognized that amongst the undescribed material occur small craniid and thecidellinide brachiopods from Zalas.

Text-fig. 1. Location of the studied Oxfordian Zalas exposure yielding brachiopods in the Polish Jura Chain (insert shows location in Poland); adopted from Radwańska (2003, fig. 2)

Their state of preservation is usually a bit worse than that of specimens from other locations (see Barczyk 1968; Krawczyński 2005, 2008).

The brachiopod material studied herein spans the interval from the Cordatum Zone to the Tenuicostatum Subzone of the Plicatilis Zone (see Matyja and Tarkowski 1981). The more precise horizon of particular specimens cannot be determined, as all specimens were collected from scree and/or rainfall outwash.

SYSTEMATIC ACCOUNT

The classification used herein follows the second and fifth volume of the revised *Treatise on Invertebrate Paleontology*, *Part H, Brachiopoda* (Bassett 2000; Baker 2006). The investigated brachiopods of Zalas belong to two families: Craniidae Menke, 1828 and Thecidellinidae Elliott, 1958.

The terminology used in the description of the studied brachiopods is after Barczyk (1968), Schülke and Helm (2000) and Krawczyński (2005). To avoid any misunderstanding, the adapted nomenclature is shown in Text-figs 2–3.

Repositories

All specimens described herein are housed in the Stanisław Józef Thugutt Geological Museum of the Faculty of Geology, University of Warsaw (prefixed with MWGUW ZI/76/..).
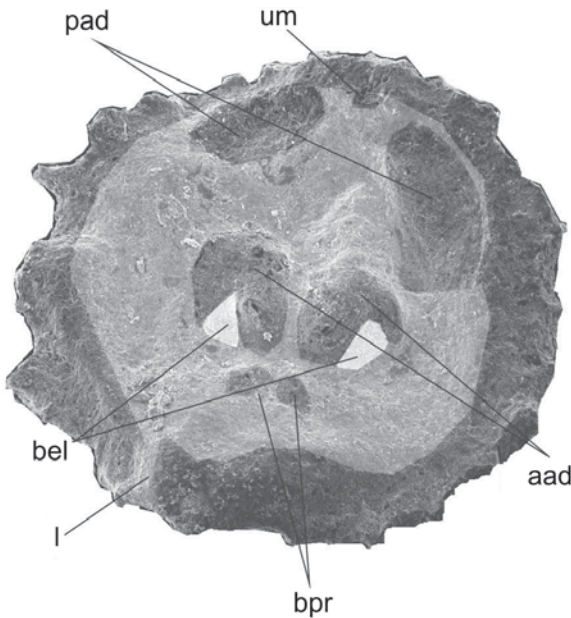
Text-fig. 2. Internal morphology of the dorsal valve of *Craniscus* Dall, 1871, exemplified on *Craniscus antiquior*. Abbreviations: l – limbus, bel – brachial elevator muscle scars; bpr – brachial protractor muscle scars; aad – anterior adductor muscle scars; pad – posterior adductor muscle scars, um – unpaired median muscle scar
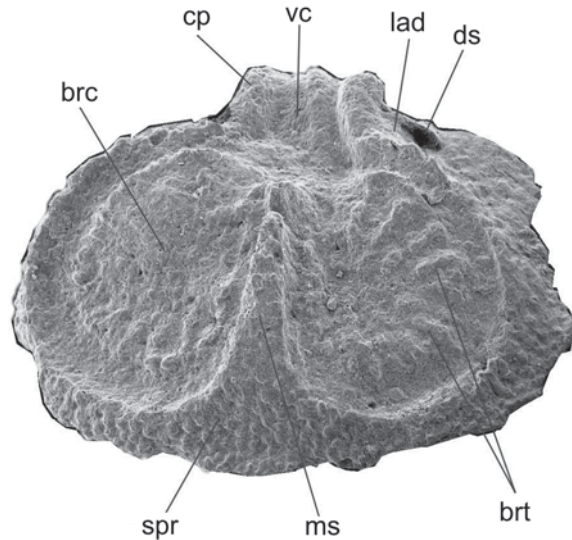
Text-fig. 3. Internal morphology of the dorsal valve of *Rioultina* Pajaud, 1966, exemplified on *Rioultina zalasensis*. Abbreviations: spr – subperipheral rim; ms – median septum; brt – brachial tubercles; ds – dental socket; lad – lateral adductor muscle scars; vc – visceral cavity, cp – cardinal process; brc – brachial cavity

Phylum Brachiopoda Duméril, 1806
Subphylum Craniiformea Popov *et al.*, 1993
Class Craniata Williams *et al.*, 1996
Order Craniida Waagen, 1885
Superfamily Cranioidea Menke, 1828
Family Craniidae Menke, 1828
Genus *Craniscus* Dall, 1871

TYPE SPECIES: *Crania tripartita* Münster, 1840; OD.

Craniscus bipartitus (Münster in Goldfuss, 1837)
(Pl. 1, Figs 5–6)

1837. *Crania bipartita* Münster; A. Goldfuss, p. 296, pl. 163, fig. 5.
1968. *Craniscus bipartitus* (Münster, 1837); W. Barczyk, pp. 179–181, text-fig. 2 and pl. 1, figs 1–4.
2005. *Craniscus bipartitus* (Münster, 1837); C. Krawczyński, p. 78, pl. 1, figs 1, 2.

MATERIAL: 15 poorly preserved dorsal valves.

DESCRIPTION: The shell is thin, subrectangular in outline, with straight or slightly concave posterior margin (Pl. 1, Figs 5–6). The outer surface is without distinctly marked apex, smooth with a fine growth line.

The dorsal valve is moderately convex. The limbus is narrow (Pl. 1, Fig. 6), and irregularly developed. Three pairs of muscle scars are relatively well-preserved. Posterior adductor muscles are large, rounded or oval in outline, and lie near the posterior margin of the valve. Anterior adductor muscle scars are large, distinctly elevated and laterally elongated. The outline of the anterior adductor muscles is falciform. They include two subtriangular brachial elevator scars (Pl. 1, Fig. 5). Other muscle scars, the median septum and the pallial sinuses are not preserved.

Ventral valves not preserved.

REMARKS: The studied brachiopods are slightly abraded, but despite this, they are consistent with the figures and description presented by Münster in Goldfuss (1837, p. 296, pl. 163, fig. 5). Such forms have already been reported twice from the Oxfordian deposits of Poland by Barczyk (1968) and Krawczyński (2005).

Craniscus tripartitus (Münster in Goldfuss, 1837)
(Pl. 1, Figs 1–4).

1837. *Crania tripartita* Münster; A. Goldfuss, p. 297, pl. 163, fig. 6.
1965. *Craniscus tripartitus* (Münster, 1837); A.J. Rowell, p. 290, fig. 181/3a–c.
2000. *Craniscus tripartitus* (Münster, 1840); M.G. Bassett, p. 173, fig. 98/1a–c.
2005. *Craniscus tripartitus* (Münster, 1840); C. Krawczyński, pp. 78, 79, pl. 1, figs 3, 4.

MATERIAL: Five dorsal valves, badly preserved.

DESCRIPTION: The dorsal valve is moderately convex, subtriangular or subrectangular in outline (Pl. 1, Figs 1–4). The outer surface (Pl. 1, Fig. 4) is irregular, with weakly developed growth lines. An eccentric apex is situated near the posterior margin of the valve.

The inner surface is very characteristic with anterior adductor scars developed as two strong ridges united with a median septum, which subdivides the valve into three chambers (Pl. 1, Figs 1–3). Other muscle scars are not distinguished. The limbus is weakly developed.

Ventral valves are not preserved.

REMARKS: The studied brachiopods are compatible with those figured and described by Münster in Goldfuss, 1837 as "*Crania tripartita* (p. 297, pl. 163, fig. 6)". The date of the establishment of this species is 1837 (the same as for *C. bipartitus*) and not 1840, because pages 225–312 and plates 147–165 from Part 2 of Goldfuss' monograph were published in 1837.

The studied species is the closest to *Craniscus bipartitus* (Münster, 1837), from which it differs in the presence of two strong ridges united with the median septum, which subdivides the ventral part of the dorsal valve into three characteristic deep chambers. Such forms have already been reported from the Oxfordian of Poland (recently recognized as Lower Kimmeridgian, see Wierzbowski *et al.* 2014, fig. 6), by Krawczyński (2005).

Craniscus antiquior (Jelly, 1843)
(Pl. 2, Figs 1–5)

1851. *Crania antiquior* Jelly; T. Davidson, p. 11, pl. 1, figs 4–8.
1874. *Crania antiquior* Jelly; T. Davidson, p. 89, pl. 9, figs 36, 37.
1968. *Craniscus antiquior* Jelly, 1843; W. Barczyk, pp. 181, 182, text-fig. 3 and pl. 2, figs 1, 2.
2005. *Craniscus antiquior* (Jelly, 1843); C. Krawczyński, p. 79, pl. 1, fig. 5 and pl. 2, figs 1, 2 and 4.

MATERIAL: 98 dorsal valves and two ventral valves.

DESCRIPTION: The shell is biconvex, subrectangular or trapezoidal in outline (Pl. 2). The outer surface is ornamented by thick and irregular ribs varying between 20–40 in number. The distinctly marked apex is positioned centrally or eccentrically near the posterior rim (Pl. 2, Fig. 1b).

The dorsal valve is relatively concave, but in some cases almost flat (Pl. 2, Figs 1a, 2). The limbus is narrow. The posterior adductor scars are rounded or ellipsoidal in outline, and positioned close to the posterior rim in the corner of the valve (Text-fig. 2 and Pl. 2, Figs 2–4). Near the posterior rim of the valve, the oval, unpaired, median adductor scar is weakly marked (Text-fig. 2 and Pl. 2, Fig. 4). Two falciform anterior adductor scars are placed centrally on a small elevation, and they include two subtriangular brachial elevator scars (Text-fig. 2 and Pl. 2, Figs 2–4). Two small, oval in outline brachial protractor scars are present in the anterior part of the valve near the axis (Text-fig. 2 and Pl. 2, Figs 2–4). The median septum is weakly developed. Other muscle scars and pallial sinuses are not preserved.

The ventral valve is moderately convex. The outer surface is ornamented by distinct ribs and a relatively large attachment scar is visible (Pl. 2, Fig. 5). Only two pairs of adductor scars are preserved on the ventral side of the valve. Rounded posterior adductor scars are placed near the posterior rim, and falciform anterior adductor scars occur in the central part of the valve.

REMARKS: The studied brachiopods are compatible with those figured and described by Davidson (1851) as "*Crania antiquior*". The species is closest to the species *Craniscus corallinus* (Quenstedt, 1852), from which it differs in the general shape of the dorsal valve and its profile. From *Corallinus bipartitus* and *C. tripartitus* it differs in the distinct ornamentation (ribs) developed on the outer surface of the valves. The species has been reported previously by Barczyk (1968) and Krawczyński (2005).

Subphyllum Rhynchonelliformea Williams *et al.*, 1996
Class Rhynchonellata Williams *et al.*, 1996
Order Thecideidea Elliott, 1958
Superfamily Thecideoidea Gray, 1840
Family Thecidellinidae Elliott, 1958
Subfamily Thecidellininae Elliott, 1953
Genus *Rioultina* Pajaud, 1966

TYPE SPECIES: *Thecidea triangularis* (d'Orbigny, 1847); OD.

Rioultina wapiennensis Krawczyński, 2008
(Pl. 3, Figs 1–2)

2008. *Rioultina wapiennensis* sp. nov.; C. Krawczyński, pp. 396–398, pl. 1, figs 1–3; pl. 2, figs 1–7, pl. 3, figs 1–4, and pl. 8, figs 2, 4, 6, 8).

MATERIAL: 43 dorsal valves.

DESCRIPTION: The dorsal valve is small, distinctly triangular in outline (Pl. 3, Figs 1, 2). The cardinal process is large, trilobed and often protruding well beyond the cardinal margin (Pl. 3, Figs 2, 3). The hinge line is relatively short. The dental sockets are small, oval and lie close to the base of the process (Pl. 3, Fig. 3). The transversarium is broken in all specimens. The surface of the subperipheral rim is very wide and ornamented by numerous fine tubercles (up to 8 rows), and shows an endopunctate microstructure (Pl. 3, Fig. 2a–2c). The median septum is long and its anterior part is covered by tubercles, which are the same as on the subperipheral rim (Pl. 3, Fig. 2a, 2b). The characteristic perforated covering of the interbrachial cavities (see Krawczyński 2008, pl. 1, figs 1–3) is not preserved. The interbrachial cavities (Pl. 3, Figs 1–3) show skeletal supports of the canopy. The supports are auriform and each consists of a ring of small tubercles (Pl. 3, Fig. 1). These tubercles are often connected and form oblique rows (Pl. 1, Figs 2–3).

Ventral valves are not preserved.

REMARKS: The studied brachiopods are compatible with those figured and described by Krawczyński (2008) as "*Rioultina wapiennensis* sp. nov.". The studied specimens are closest to those illustrated by Krawczyński (2008, pl. 2, figs 4, 6) and represent a typical state of preservation, without the transversarium and a perforated canopy.

Rioultina zalasensis sp. nov.
(Pl. 3, Fig. 4, Pl. 4, Figs 1–5, Pl. 5,
Figs 1–5 and Pl. 6, Figs 1–4)

HOLOTYPE: Specimen MWGUWZI/76/016, illustrated in Pl. 4, Fig. 1.

PARATYPES: Seven specimens: five dorsal valves – MWGUW ZI/76/017 (Pl. 4, Fig. 2), MWGUW

ZI/76/018 (Pl. 4, Fig. 3), MWGUW ZI/76/019 (Pl. 4, Fig. 4), MWGUW ZI/76/020 (Pl. 4, Figs 5a–5b), MWGUW ZI/76/021 (Pl. 5, Fig. 1); one ventral valve – MWGUW ZI/76/023 (Pl. 5, fig. 3); one complete shell – MWGUW ZI/76/025 (Pl. 5, Figs 5a–5b).

TYPE LOCALITY: Zalas Quarry in the Cracow Upland, southern Poland.

TYPE HORIZON: Middle Oxfordian, Tenuicostatum Subzone of the Plicatilis Zone.

DERIVATION OF NAME: Referred to the Latinized name of the Zalas Quarry, the type locality of the holotype.

DIAGNOSIS: Shell transversally oval in outline, with two rounded apices in the anterior part of the shell; outer surface of shell smooth, endopunctate with poorly visible growth lines; interarea flat, with a scarcely visible pseudodeltidium, which occupies the majority of its surface; ventral valve interior with weakly developed median ridge, dental hinge moderately wide; dorsal valve with large cardinal process, weakly trilobed; very long median septum, ornamented by tubercles almost on the entire length; interbrachial lobes developed as auriform rings consist of densely spaced, small tubercles, these tubercles often connect and form rows oblique to the median septum.

MATEREIAL: Seven complete shells, 268 dorsal valves, 10 ventral valves (poorly preserved).

DESCRIPTION

External morphology: The endopunctate shell (Pl. 4, Fig. 5b) is distinctly transversely oval in outline with a shallow median sulcus on the anterior part of the margin (Pl. 4, Figs 1–4 and Pl. 5, Fig. 4). The outer surface of the shell is almost smooth, with poorly visible growth lines (Pl. 6, Figs 1–4). In some cases the surface of the dorsal valve may be centrally elevated (Pl. 6, Figs 2a, 2b). The attachment scar is variously developed and its outline is clearly related to the character of the substrate (Pl. 5, Figs 4, 5 and Pl. 6, Figs 1b, 2b, 3, 4). Free ventral wall is low (Pl. 5, Fig. 5b) to very high (Pl. 5, Fig. 4). The cardinal margin is moderately wide and the interarea is flat, well defined (Pl. (Pl. 5, Fig. 5a and Pl. 6, Figs 1a, 2a). The pseudodeltidium is weakly demarcated and occupies the majority of the interarea surface (Pl. 6, Figs 1a, 2b).

Internal morphology: Ventral valve: The median ridge is weakly developed (preserved?), the hemispondylium is not visible. The dental hinge is moderately wide with two knob-like denticles (Pl. 5, Figs 2, 3). The marginal area is smooth.

Dorsal valve: The valve is transversely oval in outline and slightly convex in lateral profile. The cardinal process is well defined and large, weakly trilobed (Pl. 4, Figs 1–5a). The dental sockets are small, oval and placed close to the base of the cardinal process (Text-fig. 3 and Pl. 4, Figs 1–5a, Pl. 5, Fig. 1). The lateral adductor muscle scars are weakly marked (Pl. 4, Figs 3, 5a and Pl. 5, Fig. 1). The transversarium is not observed (Pl. 4, Figs 1–5a). The subperipheral rim (Text-fig. 3 and Pl. 4, Fig. 1–5b) is wide and ornamented with numerous (up to six rows), fine tubercles. The median septum is long (extends to the base of the visceral cavity), distinctly elevated, and covered by tubercles along almost the entire length (Text-Fig. 3 and Pl. 4, Fig. 1). The interbrachial cavities are filled with densely spaced, small tubercles. These tubercles often connect and form rows oblique to the median septum (Text-Fig. 3 and Pl. 4, Figs 1–a). The perforated canopy is not preserved.

REMARKS: Specimens of the newly established species *Rioultina zalasensis* sp. nov. are close to other fossil species, previously described from the Oxfordian sequences in Europe. There include: *Rioultina wapiennensis* Krawczyński, 2008; *Rioultina pustulosa* Schülke and Helm, 2000; *Rioultina matisconensis* (Pajaud, 1966); *Rioultina virudinensis* (Buvinier, 1851) cf. *ornata* (Moore, 1861); and *Rioultina ornata* (Moore, 1861).

Rioultina wapiennensis Krawczyński, 2008 differs from *R. zalasensis* sp. nov. by its distinctly triangular shell outline, the tuberculate ornamentation on the median septum limited to the anterior part of the septum, and the character of the skeletal supports, which form only one auriform ring of the tubercles.

Rioultina pustulosa Schülke and Helm, 2000 is distinguished from *R. zalasensis* sp. nov. by its dorsal valve with a bilobed cardinal process, a shorter median septum with a dichotomously developed split of the posterior termination, a lower number of tubercle rows on the subperipheral rim, and by the character of the brachial apparatus limited only to a few tubercles.

Rioultina matisconensis (Pajoud, 1966) is distinguished from *R. zalasensis* sp. nov. by its elongated, subtriangular outer shape, and by the character of the skeletal supports, which form only one auriform ring of tubercles.

The taxon *Rioultina virudinensis* (Buvinier, 1851) cf. *ornata* (Moore, 1861) differs from *R. zalasensis* sp. nov. by a shorter median septum, the presence of the transversarium and lack (not preserved?) of the brachial apparatus.

Rioultina ornata (Moore, 1861) is distinguished from *R. zalasensis* sp. nov. by its shorter median septum, one ring of large tubercles developed on the subperipheral rim, and the presence of the transversarium. The hemispondylium and a well defined median septum is present within the ventral valve.

A more precise examination of the relationship between the newly established species and the species mentioned above is strongly limited due to the incomplete state of preservation of the specimens (especially the incompleteness or lack of the brachial apparatus) as illustrated by Pajaud (1966) and Gaillard and Pajaud (1971).

FINAL REMARKS

The material presented herein comes from the fossil-rich slope deposits of the cyanobacterial-sponge bioherm from Zalas Quarry in the Cracow Upland, southern Poland. This bioherm is almost exclusively composed of lithistid sponges, whereas the other settled benthic fauna is represented by a few brachiopods; however, this group contributes to only 1% of the entire benthic assemblage (see Trammer 1985). Characteristic is the lack of stromatolites and algae, and this fact is interpreted by Trammer (1982, 1985) as suggesting that the bioherm developed on a local slope of the bottom below the photic zone. Such position of the bioherm (on the slope) improved the water circulation, which supports the intensive growth of the sponges (Trammer 1982).

The studied small brachiopods from the Oxfordian deposits at Zalas are assigned to two genera: *Craniscus* Dall, 1871 and *Rioultina* Pajaud, 1966, and are represented by five species. The Jurassic Craniidae Menke, 1828 and Thecidellinidae Elliott, 1958 have hitherto been recognized twice from the territory of Poland, from Bałtów in the north-eastern Mesozoic margin of the Holy Cross Mountains (Barczyk 1968, 1970) and from the Wapienno-Bielawy Quarry in the south-eastern part of the Zalesie Anticline in the Kujawy area (Krawczyński 2005, 2008). All the described species are considered characteristic of warm and shallow-water sea environments. The studied assemblage from Zalas is taxonomically comparable with those described by Barczyk (1968, 1970) and Krawczyński (2005,

2008), but additionally comprises one new species, viz. *Rioultina zalasensis* sp. nov.

Among the Oxfordian deposits in Europe, the most numerous species of the genera *Craniscus* Dall, 1871 and *Rioultina* Pajaud, 1966 were described from Germany, France, Romania and England (Münster in Goldfuss 1837; Davidson 1851, 1874; Quenstedt 1858, 1871; Rollier 1915–1916; Pajaud and Patrulius 1964; Pajaud 1966; Gaillard and Pajaud 1971). This rather low-abundance community comprises small but very characteristic brachiopods whose distribution is generally controlled by the availability of hard substrates needed for shell cementation (ventral valves in all cases), and by exposition to the water current (see Pajaud 1970, 1974; Gaillard and Pajaud 1971; Logan 1979, 2005; Lüter *et al.* 2003; Lüter 2005; Krawczyński 2005, 2008).

Substrate

The type of the hard substrate, to which the brachiopods were cemented, is in many cases unknown. Because the craniid and thecidellinid brachiopods are associated with a very rich sponge assemblage (see Trammer 1982, 1985), it is possible that most specimens were attached to the surface of the sponges, which has also been described by Gaillard and Pajaud (1971) and Krawczyński (2005). The different morphologies of the thecidellinid shell, from very flat (see Pl. 5, Fig. 5b), moderately raised (Pl. 6, Figs 1b, 2b), to vertically erect (Pl. 5, Fig. 4), may indicate the relationship of the thecidellinid shell shape with the water turbulence. Very flat specimens with wide attachment scars (Pl. 5, Fig. 5b) may represent brachiopods adapted to turbulent waters, since they were very resistant to destruction by current energy. The moderately raised ones (Pl. 6, Figs 1b, 2b) were able to live in somewhat quieter habitats. The vertically erect shells (Pl. 5, Fig. 4) represent a group of thecidellinids that were able to live in very quiet waters, as they exposed the brachial apparatus vertically to the water current, and its relatively narrow attachment scar on the ventral valve was strong enough to keep the shell vertically erect. The morphological types of the shell may indicate the existence of different "micro-habitats", probably on a local scale amongst the settled sponges.

An almost identical variation in the shape of the ventral valves of *Thecidiopsis* (*T.*) *bohemica imperfecta* nov. subsp. is presented by Nekvasilová (1966, fig. 9) from the Upper Cretaceous of Bohemia, but in this case its is ascribed to ontogenetic changes. All

the studied complete shells of *Rioultina zalasensis* sp. nov. from Zalas represent adult stages, and the ontogenetic cause of the ventral valve shape changes must be rejected in this case.

On the other hand, of interest is the association of thecidellinids and the sclerosponge ?*Neuropora* sp. (Pl. 6, Figs 3, 4), which is similar to the Recent brachiopod-sclerosponge community described by Logan (1977, 1981) from submarine caves. An identical relation between thecidellinids and sclerosponges has been noted from the Oxfordian deposits (recently recognized as Lower Kimmeridgian, see Wierzbowski *et al.* 2014, fig. 6) of the Zalesie Anticline by Krawczyński (2008). Such convergence of the association of *Rioultina zalasensis* sp. nov. with some sclerosponges indicates that these organisms inhabited cryptic environments similar to those of Recent forms. Adaptation to a cryptic environment may have resulted from the bioherm "model", very commonly referred to (see Trammer 1982) as a "sloping sea bottom", where the water circulation is strong.

Bathymetry

Depth estimation of the horizons with *Craniscus* and *Rioultina* in the Zalas bioherm is difficult. Of the two groups of brachiopods recognized in the Oxfordian of Zalas, the Thecideidea are more indicative. Recent representatives of this group are most numerous at depths from 10 to about 100 m (Pajaud 1974; Logan 1979, 2005; Lüter *et al.* 2003; Lüter 2005; Krawczyński 2008). Records of Recent thecideide brachiopods from larger depths have almost always resulted from the *post-mortem* transportation of dead shells (Logan 1988, 2005; Lee and Robinson 2003). However, the Zalas bioherm is composed almost exclusively of lithistid sponges, which indicate rather deep waters, exceeding one hundred meters in depth (Trammer 1982; Pisera 1997). All collected specimens of *Craniscus* and *Rioultina* have probably been redeposited from the upper parts of the bioherm. This is indicated by the poor state of preservation of the specimens and by the fact that 97.7% of the specimens are represented by dorsal valves, *post-mortem* moved by water currents. The fossil record also indicates that the trend to occupy shallow environments has been maintained during the whole evolutionary history of the group (Krawczyński 2008). Summarizing, the studied brachiopods probably settled in the upper part of the bioherm, where the depth may have reached about 100 m.

Temperature

Of the two groups of brachiopods recognized in the Oxfordian of Zalas, the thecidellinids are more indicative of the temperature of the environment. Most of the Recent and fossil thecidellinids inhabit tropical and subtropical waters (see Barczyk 1968, 1970; Cooper 1973, 1979, 1981; Pajaud 1970; Krawczyński 2008).

Acknowledgments

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PLATES 1–6

PLATE 1

1-4 – *Craniscus tripartitus* (Münster in Goldfuss, 1837); 1-3 – internal view of dorsal valves (1 – specimen No. MWGUW ZI/76/001; 2 – specimen No. MWGUW ZI/76/002; 3 – specimen No. MWGUW ZI/76/003); 4 – outer surface of dorsal valve (specimen No. MWGUW ZI/76/004).
5-6 – *Craniscus bipartitus* (Münster in Goldfuss, 1837), internal view of dorsal valves; (5 – specimen No. MWGUW ZI/76/005; 6 – specimen No. MWGUW ZI/76/006).
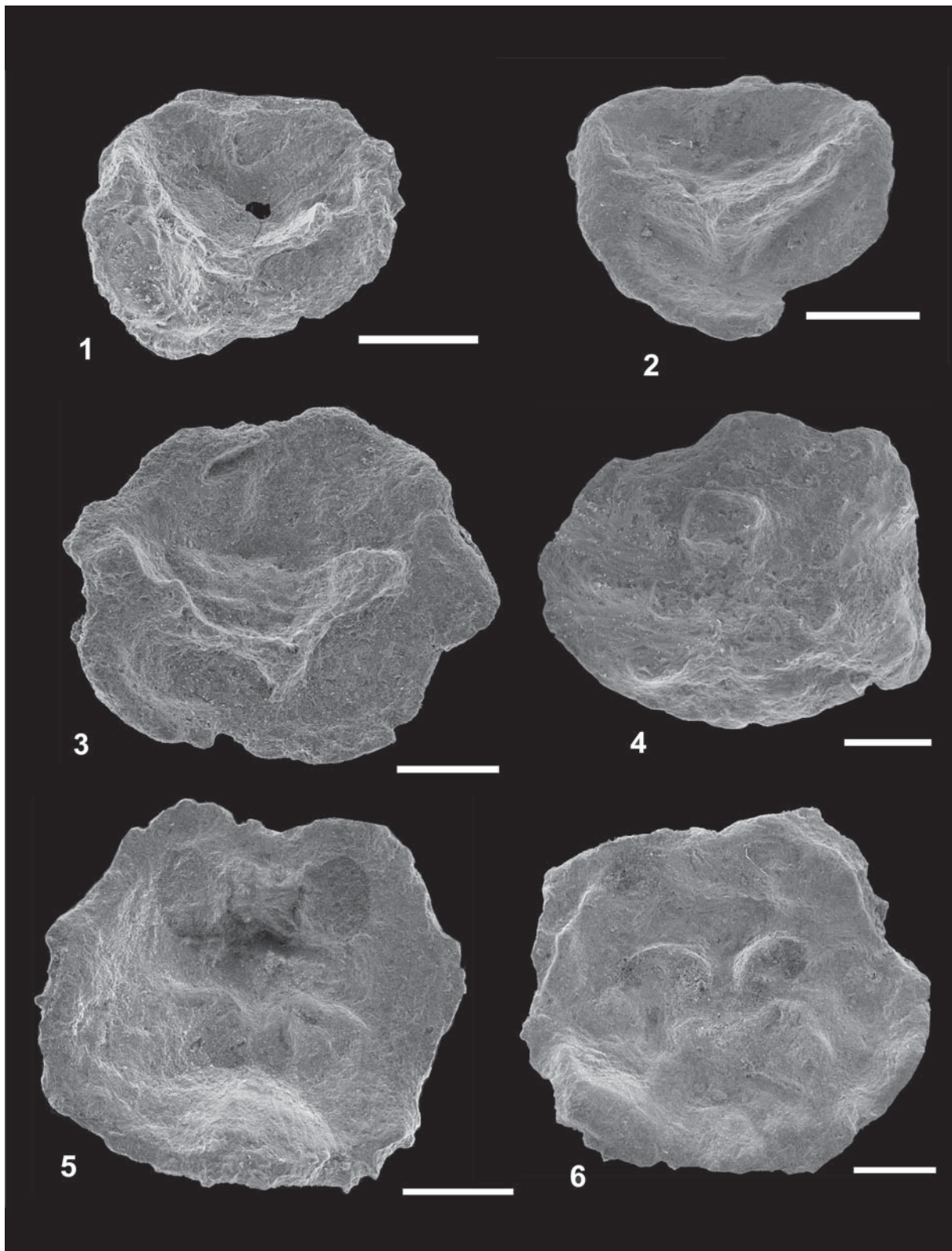
Scale bars are 1 mm

PLATE 2

Craniscus antiquior (Jelly, 1843)

1a – lateral view of dorsal valve; **1b** – outer view of dorsal valve (specimen No. MWGUW ZI/76/007); **2-4** – internal view of dorsal valves (2 – specimen No. MWGUW ZI/76/008; 3 – specimen No. MWGUW ZI/76/009; 4 – specimen No. MWGUW ZI/76/010); **5** – outer view of ventral valve, to show the attachment scar (specimen No. MWGUW ZI/76/011).
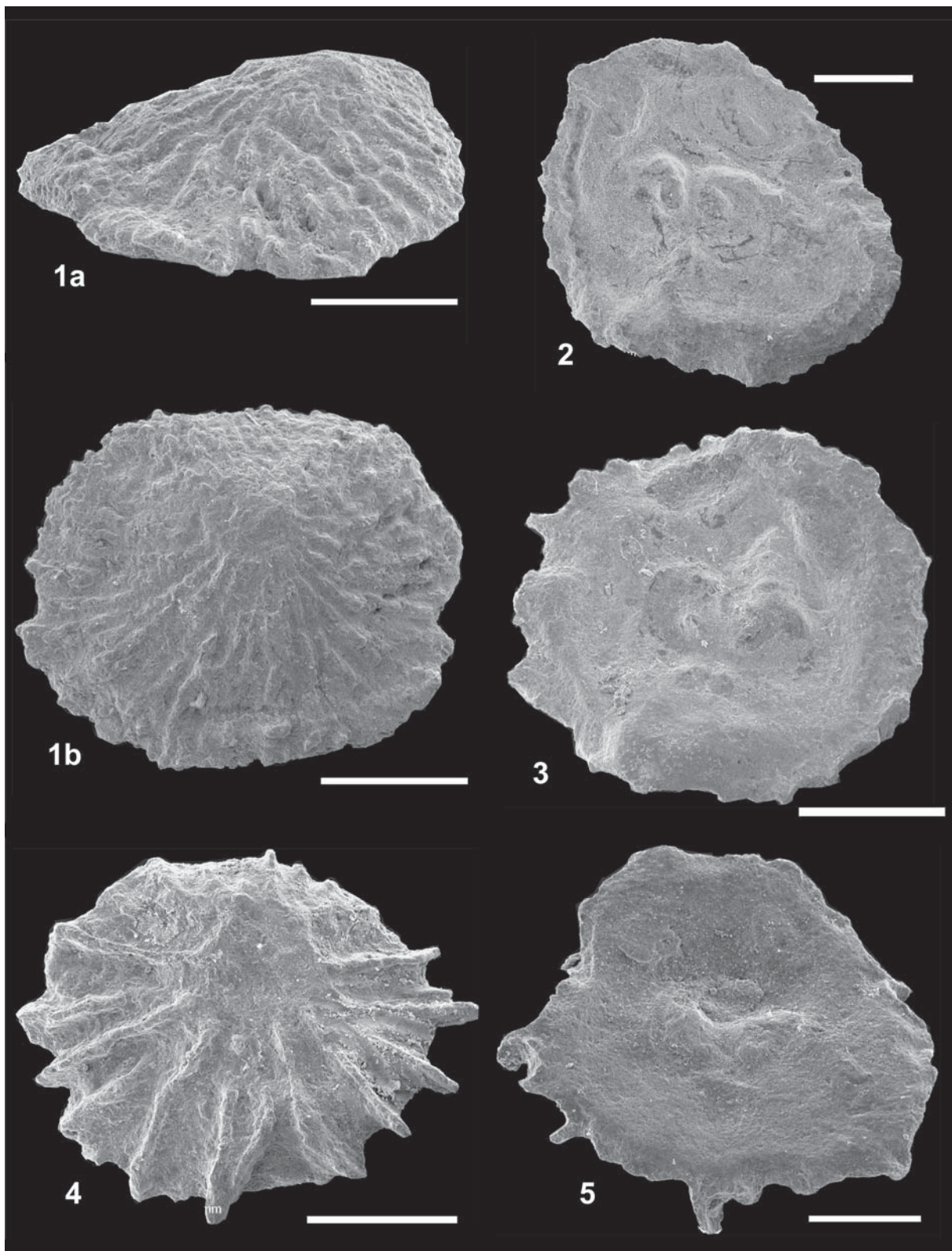
Scale bars are 1 mm

PLATE 3

1-3 – *Rioultina wapiennensis* Krawczyński, 2008; 1 – internal view of dorsal valve, specimen with auriform arranged interbrachial tubercles (specimen No. MWGUW ZI/76/012); 2a – internal view of dorsal valve, specimen with connected interbrachial tubercles; 2b – close-up view of sub-peripheral rim, to show ornamentation; 2c – close-up view to show endopunctate microstructure of the shell (specimen No. MWGUW ZI/76/013); 3 – internal view of dorsal valve, specimen with connected interbrachial tubercles (specimen No. MWGUW ZI/76/014). **4** – *Rioultina zalasensis* sp. nov., outer view of open shell (specimen No. MWGUW ZI/76/015).

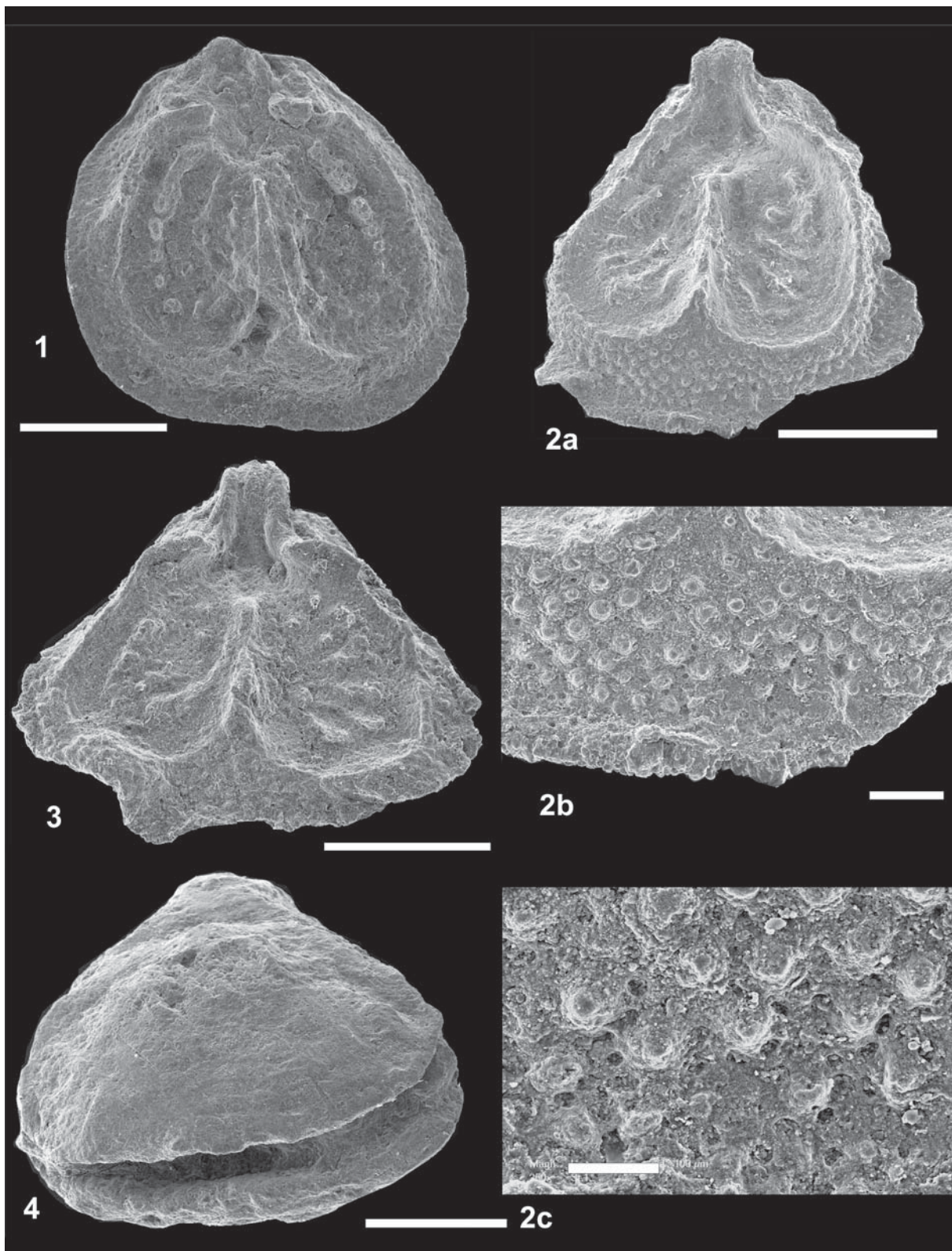Scale bars are 1 mm, but 2b which is 0.2 mm and 2c which is 0.1 mm

PLATE 4

Rioultina zalasensis sp. nov.

1 – holotype (specimen No. MWGUW ZI/76/016), internal view of dorsal valve; **2-4** – paratypes, internal view of dorsal valves, visible are brachial structures supporting the canopy (2 – specimen No. MWGUW ZI/76/017; 3 – specimen No. MWGUW ZI/76/018; 4 – specimen No. MWGUW ZI/76/019); **5a** – paratype (specimen No. MWGUW ZI/76/020), posterior view of dorsal valve, to show trilobed cardinal process and lateral adductor scar (arrowed), **5b** – close-up of subperipheral rim to show ornamentation.

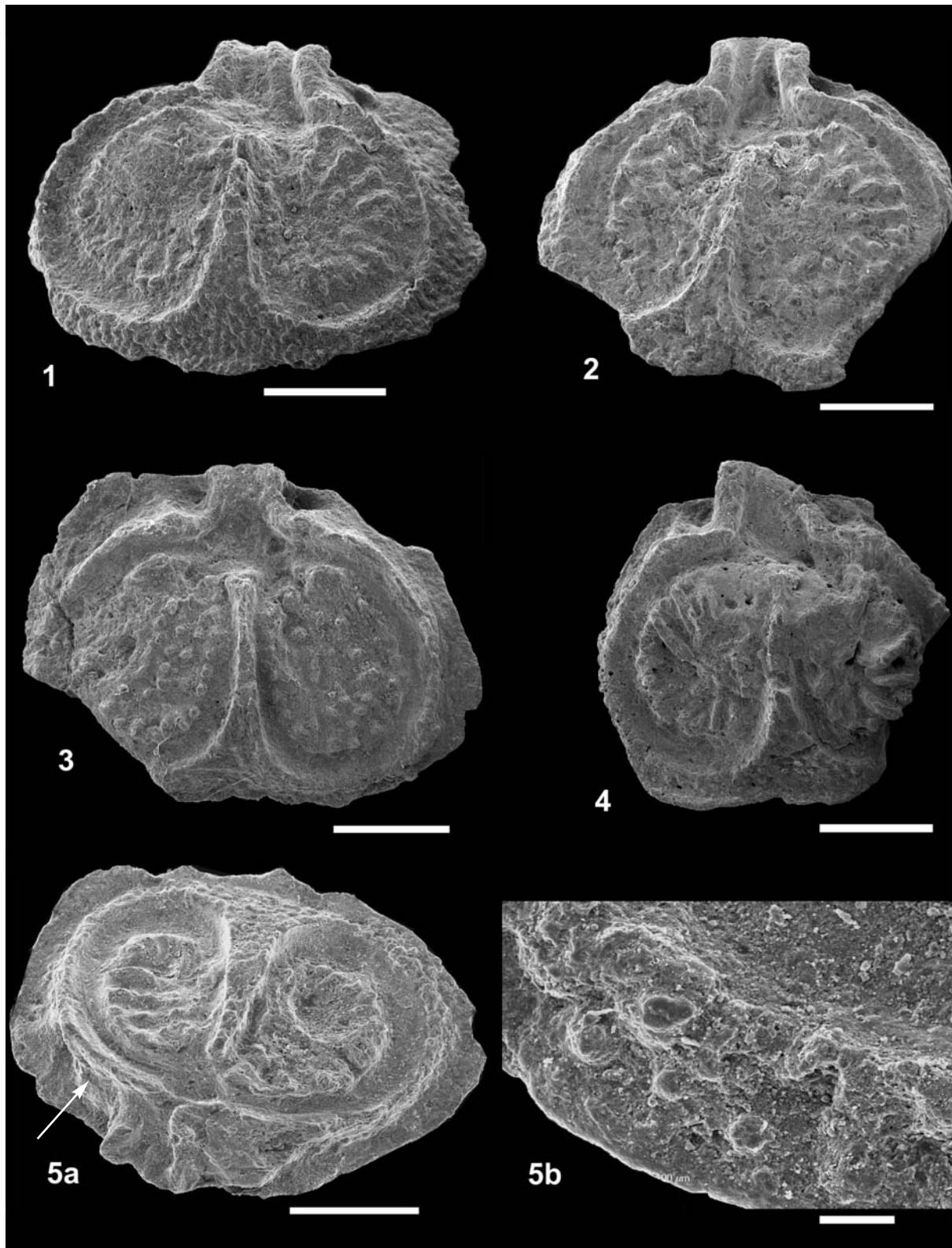Scale bars are 1 mm, but 5b which is 0.1 mm

PLATE 5

Rioultina zalasensis sp. nov.

1 – posterior view of dorsal valve (specimen No. MWGUW ZI/76/021) to show dental sockets and lateral adductor scars (arrowed); **2** – internal view of ventral valve (specimen No. MWGUW ZI/76/022); **3** – paratype (specimen No. MWGUW ZI/76/023), internal view of ventral valve, to show median rim and denticles (arrowed); **4** – complete specimen, dorsal view (specimen No. MWGUW ZI/76/024), **5** – paratype (No. MWGUW ZI/76/025), 5a – complete specimen, dorsal view with flat interarea visible, 5b – lateral view.
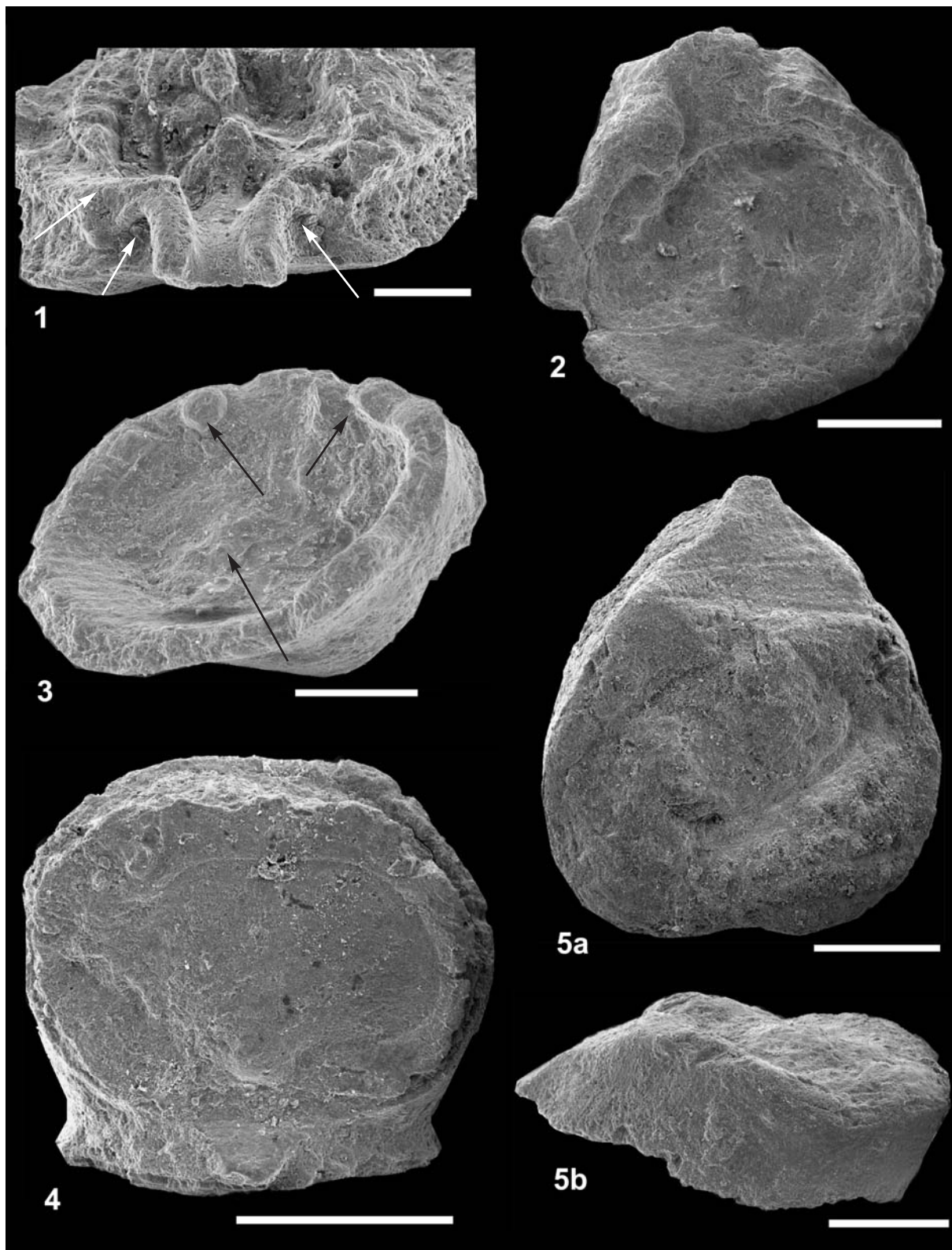
Scale bars are 1 mm, but 1 and 3 which are 0.5 mm

PLATE 6

Rioultina zalasensis sp. nov.

1a – complete specimen, dorsal view; white arrow shows pseudodeltidium, **1b** – lateral view (specimen No. MWGUW ZI/76/026); **2a** – complete specimen, dorsal view with centrally elevated rim visible, **2b** – lateral view (specimen No. MWGUW ZI/76/027); **3-4** – complete specimens attached to the basal skeletons of the sclerosponge *Neuropora* sp. (3 – specimen No. MWGUW ZI/76/028; 4 – specimen No. MWGUW ZI/76/029).

Scale bars are 1 mm