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Tube-dwelling polychaetes from the Upper Oxfordian of Wapienno/Bielawy, Couiavia region, north-central Poland

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ABSTRACT:

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A relatively rich assemblage of tube-dwelling polychaetes is recognized in the talus facies of the Late Jurassic (Late Oxfordian) biohermal, sponge-cyanobacterial buildup from the Wapienno/Bielawy succession exposed in a salt-dome cored anticline of the Couiavia region, north-central Poland. Fourteen taxa are described belonging to 12 genera: *Glomerula* BRÜNNICH NIELSEN, 1931, *sensu* REGENHARDT, 1961; *Cementula* BRÜNNICH NIELSEN, 1931, *sensu* REGENHARDT, 1961; *Ditrupula* BRÜNNICH NIELSEN, 1931, *sensu* HOWELL, 1962; *Filogranula* LANGERHANS, 1884; *Laqueoserpula* LOMMERZHEIM, 1979; *Metavermilia* BUSH, 1904; *Mucroserpula* REGENHARDT, 1961; *Neovermilia* DAY, 1961; *Pannoserpula* JÄGER, KAPITZKE & RIETER, 2001; *Parsimonia* REGENHARDT, 1961; *Placostegus* PHILIPPI, 1844; *Serpula* LINNAEUS, 1758. Only very few, or no representatives of these genera have formerly been reported from the Jurassic of Poland. Five species are established as new: *Ditrupula meandrica* sp.nov., *Laqueoserpula intumescens* sp.nov., *Mucroserpula jaegeri* sp.nov., *Pannoserpula couiaviana* sp.nov., *Placostegus conchophilus* sp.nov. The ecology of this assemblage, which comprises typically epizoans of sponges, and of brachiopods upon whose shells they often formed 'serpulid gardens', is discussed. In the case of the brachiopods, live specimens were favoured, to which the tube-dwelling polychaetes became commensals located preferably on their ventral valves. Some of the polychaetes had their own commensal, the hydroid *Protulophila gestroi* ROVERETO, 1901, whose stolonal network was embedded in their tubes. The lithology of the source deposits indicates their transport by storm agitation and/or mass movements. Consequently, rapid burial affected all biota, including the living brachiopods, some of which were bearing living polychaetes.

Key words: Polychaeta, Sedentaria, Taxonomy, New species, Eco-taphonomy, Upper Jurassic, Poland.

INTRODUCTION

The tube-dwelling polychaetes from the Jurassic of Poland have hitherto been rather neglected by students of the abundant, high diversity Jurassic faunas. Only a few authors contributed to the taxonomic recognition of polychaetes more precisely than just 'serpulid worms', 'serpulids', or '*Serpula* sp.'. The exception to this was a thin Late Jurassic ('Bononian', 'Volgian', or Tithonian) serpulite exposed in Brzostówka at Tomaszów Mazowiecki (NW margin of the Holy Cross Mountains), composed of the rock-building tubes of *Serpula coacervata* BLUMENBACH, 1804, a species long known from this now inaccessible locality and some nearby ones (RADWAŃSKA

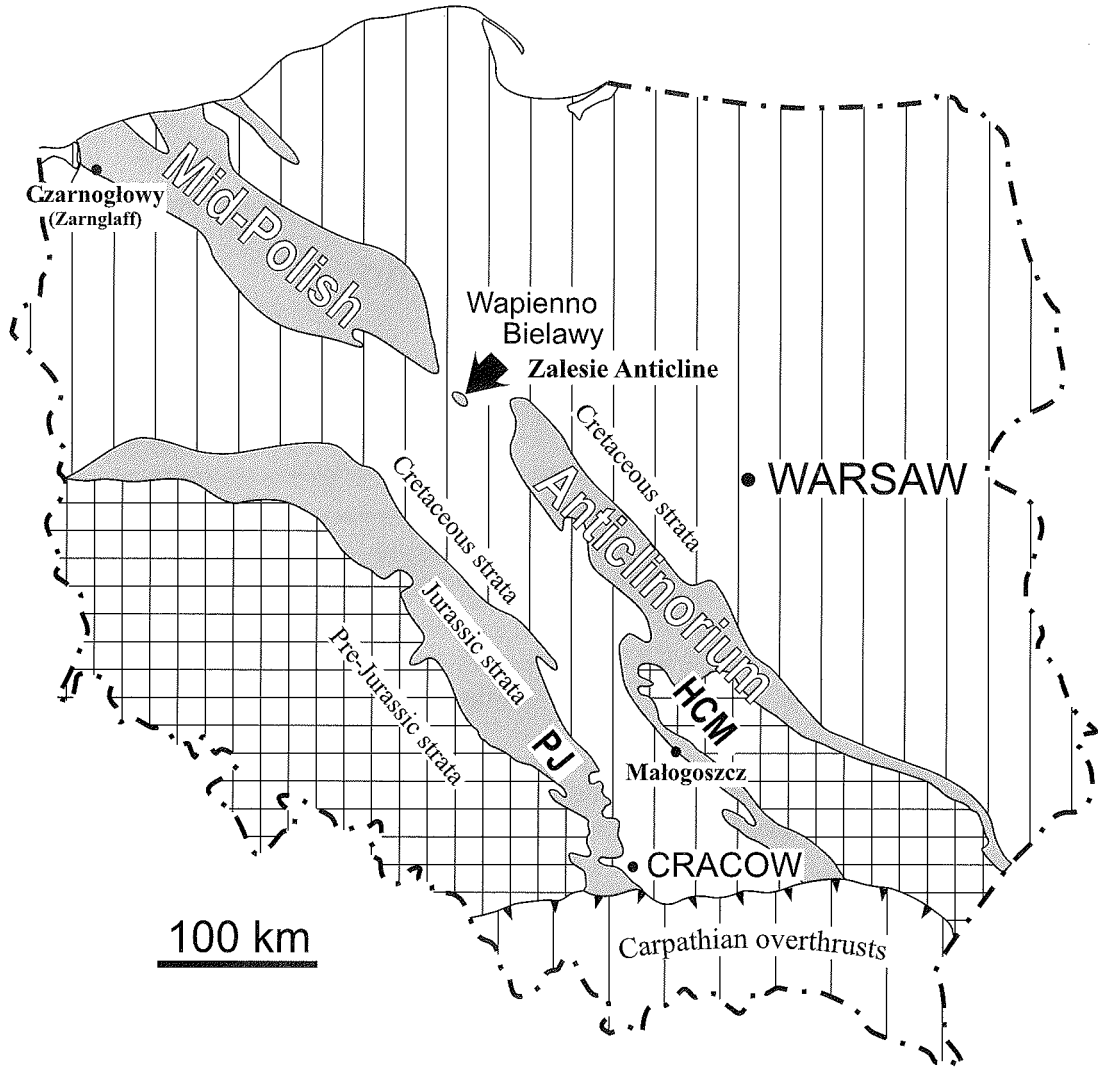

Fig. 1. Geological map of Poland, without Cenozoic cover, to show location of the Wapienno and Bielawy quarries, in the Zalesie Anticline in the Couiavia region, yielding the studied tube-dwelling polychaetes. The main regions where the Upper Jurassic succession is exposed are indicated: PJ – Polish Jura, HCM – Holy Cross Mountains, as well as some cited localities yielding Oxfordian and/or Lower Kimmeridgian faunas (cf. RADWAŃSKA 2003a, fig. 1); *adopted from* MATYJA & WIERZBOWSKI (2000, fig. 1)

2003c). The lithology and stratigraphical position of the serpulite was compared to that of the 'Purbeck Beds' or 'Portlandian' serpulite in NW Germany and England (LEWIŃSKI 1923; KUTEK 1962, 1967, and 1994, pp. 5-6; KUBIATOWICZ 1977; TEN HOVE & VAN DEN HURK 1993).

The few instances of taxonomic recognition of serpulid polychaetes in the Jurassic of Poland that may be verified by illustrations and/or by specimens in collections are as follows. MAKOWSKI (1952) noted three serpulid taxa: *Serpula tetragona* SOWERBY, *S. convoluta* GOLDFUSS, and *S. lumbricalis* SCHLOTHEIM, the latter being an epibiont on ammonite shells, all from the world-famous Callovian clays of Łuków. KUTEK & RADWAŃSKI (1965) noted *Cycloserpula* sp. commonly overgrowing blue-green-algal onkolites from around the Oxfordian/Kimmeridgian boundary in the Holy Cross Mountains. PUGACZEWSKA (1970) reported five species from the Middle Jurassic through Volgian, such as *Sarcinella sarcinella* REGENHARDT, 1961; *Glomerula gordialis* (SCHLOTHEIM, 1820); *Serpula* (*Tetraserpula*) *tetragona* SOWERBY, 1829; *Serpula* (*Tetraserpula*) *quinquangularis* GOLDFUSS, 1831; *Serpula* (*Tetraserpula*) *quadrilatera* GOLDFUSS, 1831. WIŚNIEWSKA-ŻELICHOWSKA (1971) reported three indeterminable serpulid taxa from an Oxfordian sponge-cyanobacterial bioherm of the Polish Jura.

Of the taxa in the reports cited above, only those species studied by the present author are included into synonymy and/or discussion.

In respect of the number of serpulid taxa recognized, the locality Wapienno /Bielawy in the Couiavia region of the Polish Lowland (Text-fig. 1) is exceptional. Here a sponge-cyanobacterial bioherm (salt-dome cored Zalesie Anticline) was known, over a century ago, to GALLINEK (1896), who reported the occurrence of seven taxa: *Serpula perrugosa* GALLINEK 1896 (newly described), *S. quinqueangularis* GOLDFUSS, *S. gordialis* SCHLOTHEIM, *S. deshayesi* MÜNSTER, *S.* cf. *limata* MÜNSTER, *S. convoluta* GOLDFUSS, *S.* cf. *laufonensis* ETALLON. The material from this locality, represented by the huge Wapienno and Bielawy quarries, over 1.5 km long and over 100 m deep, complements the author's previous recognition of tube-dwelling polychaetes in the younger sequences of Poland, namely the upper Lower and Upper Cretaceous (RADWAŃSKA 1996) and the Tertiary (Middle Miocene, Badenian; RADWAŃSKA 1994a, b; see also TEN HOVE & NISHI 1996).

The history of the investigation of the Wapienno/ Bielawy sequence, its facies structure and stratigraphy was presented recently (MATYJA & WIERZBOWSKI 2002, RADWAŃSKA & RADWAŃSKI 2003a). The polychaete-bearing strata are represented primarily by a talus of the sponge-cyanobacterial calcareous buildup, composed of marly interbeds, overloaded locally with detrital material (over a metre in diameter), and larger olistholiths slumped from the bioherm core. Apart from polychaetes, the talus locally yields common fossils of various kinds, including brachiopods (GALLINEK 1896, KRAWCZYŃSKI 2003), enigmatic crinoids *Cyclocrinus* and their hash (RADWAŃSKA & RADWAŃSKI 2003a), the aberrant starfish *Sphaeraster* (RADWAŃSKA 2003b), cidaroid echinoids (RADWAŃSKA 2000, 2003a) and rare ammonites (MATYJA & WIERZBOWSKI 2002), all associated with ubiquitous siliceous sponges (KOŁSUT, in prep.).

STRATIGRAPHY

The Upper Jurassic succession of the Zalesie Anticline (see MATYJA, MERTA & WIERZBOWSKI 1985), exposed in the quarries studied, is represented by Lower to Upper Oxfordian in the Wapienno Quarry and by Upper Oxfordian only in the Bielawy Quarry (Text-fig. 2). The tube-dwelling polychaetes have been found exclusively in the Upper Oxfordian. The majority of the polychaete species from either of these two quarries are treated consequently in the following systematic account as from Wapienno/Bielawy, and as of Late Oxfordian age (Bimammatum to Planula zones). The exception to this

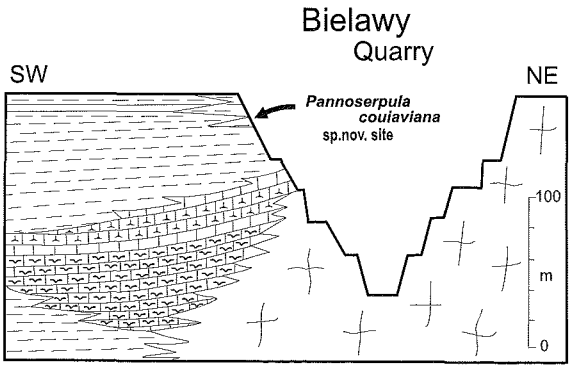

Fig. 2. Sketch of facies distribution of the Upper Jurassic (Oxfordian) succession exposed at Bielawy Quarry, to show the position of the site with *Pannoserpula couiaviana* sp.nov.; adopted from MATYJA & *al.* (1985, fig. 4)

are obviously, single specimens reported from one of these quarries, the same as the largest and peculiarly shaped species *Pannoserpula couiaviana* sp.nov. The occurrence of this species is restricted to the uppermost part of the section in Bielawy Quarry (see Text-fig. 2), referred to Member B_5 (MATYJA & *al.* 1985) and assigned to the upper Planula Zone, close to the base of the Galar Subzone (just beneath Unit I of MATYJA & WIERZBOWSKI 2002, p. 412 and figs 3-4).

Repositories

The material studied herein is housed in the Department of Palaeontology, Faculty of Geology, University of Warsaw, where it is registered under collection numbers preceded by the character **P** (Polychaeta) and **Ox** indicative of Oxfordian age, followed by **W** for the locality Wapienno/Bielawy.

SYSTEMATIC ACCOUNT

The taxonomy of the polychaete genus names used in the present account follows that by BRÜNNICH NIELSEN (1931), REGENHARDT (1961), HOWELL (1962), LOMMERZHEIM (1979), and recently by JÄGER & *al.* (2001). The proposal of JÄGER (1983, 1993), followed by PILLAI (1993), to reject the genus names introduced by BRÜNNICH NIELSEN (1931) is not accepted.

The authorship of the genus names *Glomerula*, *Cementula* and *Ditrupula* is ascribed herein to BRÜNNICH NIELSEN (1931, p. 85), followed by REGENHARDT (1961), HOWELL (1962), and LOMMERZHEIM (1979).

The author is aware of the fact that BRÜNNICH NIELSEN (1931) did not indicate the type species of his genera. Consequently – as stressed by JÄGER (1983) and

PILLAI (1993) the genera in question are invalidated according to Articles 13.1 and 50 of ICZN 1999 (4th Edition) for genus names published after 1930. Nevertheless, it should be remembered that in many papers and monographs published in the early 1930s this Code was not treated as obligatory. Furthermore, it is important to avoid the ridiculous situation that the species names introduced by BRÜNNICH NIELSEN, and accepted by all subsequent authors (REGENHARDT 1961, LOMMERZHEIM 1979, JÄGER 1983, PILLAI 1993), should be associated with the name BRÜNNICH NIELSEN in brackets, as if to suggest that the genus names had not been introduced by himself.

Class Polychaeta GRUBE, 1850
Order Sedentaria LAMARCK, 1818
Family Serpulidae RAFINESQUE, 1815
Subfamily Filograninae RIOJA, 1923
(see JÄGER 1993, JÄGER & *al.* 2001)

Genus *Glomerula* BRÜNNICH NIELSEN, 1931, *sensu* REGENHARDT, 1961

TYPE SPECIES: *Serpulites gordialis* SCHLOTHEIM, 1820; *SD* REGENHARDT, 1961

Glomerula gordialis (SCHLOTHEIM, 1820)
(Pl. 1, Figs 1-10)

1831. *Serpula gordialis* SCHLOTH.; A. GOLDFUSS, p. 234, pl. 69, fig. 8a-c.
1831. *Serpula Ilium* nobis; A. GOLDFUSS, p. 234, pl. 69, fig. 10a-d.
1831. *Serpula gordialis* SCHLOTH. *Varietas serpentina*; A. GOLDFUSS, p. 240, pl. 71, fig. 4.
partim 1858. *Serpula gordialis*; F.A. QUENSTEDT, p. 776, pl. 97, fig. 33 [*non* pl. 40, fig. 1].
1896. *Serpula gordialis* v. SCHLOTH.; E. GALLINEK, p. 406, pl. 1, fig. 7.
1896. *Serpula* cf. *Laufonensis* ETALLON; E. GALLINEK, p. 410, pl. 1, figs 6, 8.
1903. *Serpula gordialis* GOLDF.; K. ZITTEL, p. 227, text-fig. 426b-c.
1911. *Serpula gordialis*, var. *serpentina*; A. FRIČ, p. 72, text-fig. 304.
1931. *Glomerula gordialis* v. SCHLOTH. sp.; K. BRÜNNICH NIELSEN, p. 88, pl. 1, figs 9-11.
1956. *Serpula* (*Cycloserpula*) *gordialis* (SCHLOTHEIM) 1820; K.O.A. PARSCH, p. 214, pl. 20, figs 15-16.
1961. *Glomerula gordialis* (SCHLOTHEIM, 1820); H. REGENHARDT, p. 26, pl. 1, fig. 2.
1961. *Glomerula scitula* n.sp.; H. REGENHARDT, p. 27, pl. 1, fig. 1.
1961. *Glomerula solitaria* n.sp.; H. REGENHARDT, p. 28, pl. 9, fig. 11.
1961. *Glomerula saucia* n.sp.; H. REGENHARDT, p. 28, pl. 1, fig. 3.
1961. *Protula rasilis* n.sp.; H. REGENHARDT, p. 33, pl. 1, fig. 7.
1961. *Omasaria funiculis* (WOLLEMANN); H. REGENHARDT, p. 45, pl. 3, fig. 1.
1961. *Omasaria omnivaga* n.sp.; H. REGENHARDT, p. 45, pl. 5, fig. 7.
1962. *Glomerula gordialis* (VON SCHLOTHEIM); B.F. HOWELL, p. *W*157, text-fig. 97/3.
1963b. *Glomerula gordialis* v. SCHLOTH.; A.H. MÜLLER, text-fig. 517.
1964b. *Glomerula gordialis* v. SCHLOTH.; A.H. MÜLLER, p. 621, text-figs 5-6.
1965. *Glomerula gordialis* (SCHLOTHEIM); H. NESTLER, p. 74, pl. 4, figs 6, 8-10.
1965. *Glomerula saucia* REGENHARDT; H. NESTLER, p. 74, pl. 4, fig. 11.
1965. *Glomerula solitaria* REGENHARDT; H. NESTLER, pl. 4, fig. 7.
1965. *Serpula* (*Cycloserpula*) *gordialis* (SCHLOTHEIM, 1820); H. PUGACZEWSKA, p. 82, pl. 6, fig. 1a-b.
1966. *Glomerula gordialis* (v. SCHLOTHEIM); A.H. MÜLLER, p. 1060, text-fig. 13.
1967. *Glomerula gordialis* (SCHLOTHEIM, 1820); H. PUGACZEWSKA, p. 180, pl. 1, figs 5-10; pl. 2, fig. 4 and pl. 3, fig. 1.
1968. *Glomerula gordialis* (VON SCHLOTHEIM 1820); G. BIGNOT, p. 18, pl. 1, fig. 1; pl. 2, figs 1-4.
1970. *Glomerula gordialis* (SCHLOTHEIM, 1820); H. PUGACZEWSKA, p. 434, pl. 3, fig. 10.
1973. *Glomerula gordialis* (SCHLOTHEIM), 1820; S. PASTERNAK, p. 9, text-fig. 1, pl. 1, figs 3-5.
1973. *Glomerula solitaria* REGENHARDT, 1961; S. PASTERNAK, p. 10, pl. 1, figs 6-7.
? 1973. *Protula rasilis* REGENHARDT, 1961; S. PASTERNAK, p. 12, pl. 1, fig. 9.
1975. *Glomerula gordialis* (SCHLOTHEIM, 1820); H. NESTLER, p. 64, text-fig. 98.
1975. *Glomerula saucia* REGENHARDT, 1961; H. NESTLER, text-fig. 99.
1979. *Glomerula gordialis* (SCHLOTHEIM, 1820); A. LOMMERZHEIM, p. 130.
1983. *Glomerula gordialis* (SCHLOTHEIM, 1820); M. JÄGER, p. 26, pl. 2, figs 1-18.
1987. *Glomerula gordialis* (SCHLOTHEIM, 1820); M. JÄGER, p. 40, pl. 1, figs 17-20.
1987. Serpulids, probably *Glomerula gordialis* (SCHLOTHEIM); A. PISERA, p. 86 and pl. 34, figs 5-6.
1996. *Cycloserpula gordialis* (SCHLOTHEIM, 1820); U. RADWAŃSKA, p. 66, pl. 1, figs 1-4.

DIAGNOSIS: A species of *Glomerula* with moderately large, solitary tube, coiled variably.

MATERIAL: Twenty specimens from the Wapienno/Bielawy Quarry.

DESCRIPTION: The solitary tube is coiled variably, either trochospirally (Pl. 1, Figs 1a-1c, 4) or meander-like (Pl. 1, Figs 2-3, 5-10), with the whorls arranged in groups (partially overlapping) or separate. The majority of the specimens are attached (Pl. 1, Figs 2-10) to the substrate (sponges, brachiopods, or other polychaetes); some are free (Pl. 1, Figs 1a-1c). The cross-section of the tube is circular, from 1 to 3 mm in diameter. The tube increases very gradually in diameter. The thickness of the tube wall reaches about a quarter of the tube diameter. The outer surface is smooth, without any peristomes.

REMARKS: Tubes of this species were reported from the Wapienno/Bielawy Quarry by GALLINEK (1896) as *Serpula gordialis* v. SCHLOTH. and *Serpula* cf. *Laufonensis* ETALLON. GALLINEK's (1896) specimens of the species *laufonensis* fall within the intraspecific variability of *S. gordialis*, as described in the present paper. It is noteworthy that this species is one of the commonest polychaetes of the Wapienno/Bielawy succession.

The species *Glomerula gordialis* was reported by PUGACZEWSKA (1970) from other Jurassic localities (Łęczyca, Czarnogłowy), as well as by PUGACZEWSKA (1965) and RADWAŃSKA (1996) from the Upper Cretaceous, and by PUGACZEWSKA (1967) from the lowest Tertiary of Poland. Moreover, PISERA (1987) noted it as an epibiont of erratic Upper Jurassic coral colonies in glacial deposits of northern Poland. In Europe, it is widespread in the Jurassic and the Cretaceous (see synonymy).

Subfamily Serpulinae MACLEAY, 1840

Genus *Cementula* BRÜNNICH NIELSEN, 1931, *sensu* REGENHARDT, 1961

TYPE SPECIES: *Cementula sphaerica* BRÜNNICH NIELSEN, 1931; *SD* REGENHARDT, 1961

Cementula spirolinites (MÜNSTER *in* GOLDFUSS, 1831) (Pl. 2, Figs 6-8)

1831. *Serpula spirolinites* MÜNSTER; G. MÜNSTER, p. 229, pl. 68, fig. 5a-c.

1956. *Serpula spirolinites* MÜNSTER 1831; K.O.A. PARSCH, p. 221, pl. 21, fig. 29.

DIAGNOSIS: A species of *Cementula* with tube of triangular cross-section, small diameter (less than 1 mm), and outer surface sculptured by distinct median keel.

MATERIAL: Six specimens from the Wapienno Quarry.

DESCRIPTION: The tube is attached to the substrate (sponge wall). The posterior part of the tube is planispirally coiled and then passes into the uncoiled, meandering anterior part (Pl. 2, Figs 7a-7b, 8). The umbilicus is situated at the centre of the coil (Pl. 2, Figs 6, 7a). The cross-section of the tube is triangular, 0.9 mm in diameter. Internal longitudinal ridges are absent. The diameter of the tube increases very gradually, but in the uncoiled part it is constant (Pl. 2, Figs 7a-7b, 8). The outer surface of the tube is sculptured by a distinct median keel (Pl. 2, Figs 7a, 7b), but the lateral walls are smooth. Very rare peristomes are alate.

REMARKS: The specimens studied compare well with those described by MÜNSTER (in GOLDFUSS 1831, pl. 68, figs 5a-b). The characteristic mode of coiling, and the absence of internal longitudinal ridges, fit well into the diagnosis of the genus *Cementula* BRÜNNICH NIELSEN, 1931. The species has not hitherto been reported from Poland.

Cementula? sp. (Pl. 2, Fig. 1)

MATERIAL: Two specimens (one of these poorly preserved) from the Wapienno Quarry.

DESCRIPTION: The small tube is attached to the substrate (shell of the brachiopod *Lacunosella*) along its whole length (Pl. 2, Fig. 1). The mode of coiling is typical of species of the genera *Cementula* and *Spiraserpula*. The very narrow, straight initial part passes into one whorl, then continues into straight portions, and finally forms a coiled part. During growth, the tube diameter increases gradually, to reach 1.4 mm. The cross-section of the tube is subtriangular, with distinctly convex lateral walls. The outer surface is sculptured by a weakly developed keel, and delicate corrugations composed of small tubercles.

REMARKS: The mode of coiling and character of ornamentation of the specimens studied suggest their assignment to the genus *Cementula* BRÜNNICH NIELSEN, 1931, or to *Spiraserpula* REGENHARDT, 1961. The transverse cross-section of the tube appears to be devoid of the internal structures characteristic of *Spiraserpula* species (see PILLAI 1993; PILLAI & TEN HOVE 1994), but this was observed on the badly preserved specimen, and thus it is

uncertain whether it was an effect of preservation or an original feature.

Genus *Ditrupula* BRÜNNICH NIELSEN, 1931, *sensu* HOWELL, 1962

TYPE SPECIES: *Serpula canteriata* VON HAGENOW, 1840; *SD* HOWELL, 1962

Ditrupula quadrisulcata (PARSCH, 1956) (Pl. 6, Fig. 4a-4c)

1956. *Serpula* (*Tetraserpula*) *quadrisulcata* n.sp.; K.O.A. PARSCH, p. 227, pl. 21, fig. 15.

DIAGNOSIS: A species of *Ditrupula* with relatively prominent, sharply-pointed ridges, and lateral walls of the tube sculptured by a relatively deep furrow.

MATERIAL: One fragmentary specimen (attached to the substrate) from the Wapienno Quarry, infested by the hydroid *Protulophila gestroi* ROVERETO, 1901 (see SCRUTTON 1975).

DESCRIPTION: The arcuate tube (Pl. 6, Fig. 4a) with a quadrangular to trapezoidal cross-section is attached to the substrate along its whole length (the free part is broken). The thick-walled tube (Pl. 6, Fig. 4b) increases in diameter very gradually, to reach a maximum of 2.3 mm. The prominent, sharply-pointed ridges (Pl. 6, Figs 4a-4b) border the concave upper surface (Pl. 6, Fig. 4a). The lateral walls are flat and bear a relatively deep longitudinal furrow. The outer surface of the tube is ornamented by relatively distinct corrugations, which may be associated with a delicate constriction (Pl. 6, Fig. 4a).

REMARKS: The specimen studied agrees with those described by PARSCH (1956, pl. 21, fig. 15) as his new species, *Serpula* (*Tetraserpula*) *quadrisulcata*. The specimen from Wapienno represents an attached tube only, whereas PARSCH's (1956) specimen is a fragment of the free part.

The species *D. quadrisulcata* (PARSCH, 1956) differs from *D. tetragona* (SOWERBY, 1829) in its much longer attached part, and by distinctly sharp-pointed ridges.

Ditrupula meandrica sp.nov. (Pl. 6, Figs 1-3)

HOLOTYPE: The specimen POx/W-058, illustrated in Pl. 6, Fig. 1.

PARATYPES: Two specimens, POx/W-059 (Pl. 6, Fig. 2) and POx/W-060 (Pl. 6, Fig. 3).

TYPE LOCALITY: Bielawy Quarry, Couiavia region, north-central Poland.

TYPE HORIZON: Upper Oxfordian

DERIVATION OF THE NAME: Named for the meander-like course of the tube (neo-Latinized adjective *meandricus* – shaped like a river-bed meander).

DIAGNOSIS: A species of *Ditrupula* with meander-like tube, sculptured by two distinct, strongly undulated keels.

MATERIAL: Four specimens from the Wapienno Quarry.

DESCRIPTION: The meander-like tube (Pl. 6, Figs 1-3) is attached to the substrate (sponge wall) along its whole length. The tube wall is moderately thick. The tube diameter increases very fast, to reach 2 mm at the length of the aperture 32 mm. The cross-section of the tube is quadrangular in the posterior part and may pass into trapezoidal in the most anterior part (Pl. 6, Fig. 2). The outer surface of the tube (in uncorroded specimens) is glossy (Pl. 6, Fig. 1), and covered by corrugations which become more pronounced close to the aperture (Pl. 6, Figs 2-3). The tube is sculptured by two distinct, strongly undulate keels, which border the distinctly concave upper surface (Pl. 6, Figs 1-3).

REMARKS: In its quadrangular cross-section and the presence of distinct rims bordering the upper surface of the tube, *Ditrupula meandrica* sp.nov fits the characters of the genus *Ditrupula* BRÜNNICH NIELSEN, 1931. From the other Jurassic species, *D. quadrisulcata* (PARSCH, 1956) and *D. tetragona* (SOWERBY, 1829), it differs in its meandering tube, strongly undulate keels bordering the upper surface, and by the more rapid increase in the tube diameter. From the Cretaceous species of the genus (see JÄGER 1983) it differs also in the long portion attached to the substrate.

Genus *Filogranula* LANGERHANS, 1884

TYPE SPECIES: *Filogranula gracilis* LANGERHANS, 1884

Filogranula gibbosa (GOLDFUSS, 1831) (Pl. 6, Figs 7a-7b)

1831. *Serpula gibbosa* nobis; A. GOLDFUSS, p. 229, pl. 68, figs 3a-b.

MATERIAL: Two poorly preserved specimens from the Bielawy Quarry.

DIAGNOSIS: A species of *Filogranula* with tube attached to the substrate along its whole length, and bearing numerous, regularly spaced, thick alate peristomes, separated by deep incisions; upper surface sculptured by median keel.

DESCRIPTION: The small, arcuate tube is attached to the substrate (sponge wall) along its whole length (Pl. 6, Figs 7a-7b), and has a subtriangular cross-section. The tube increases in diameter very slowly (Pl. 6, Fig. 7b). The base of the tube is thick and massive, lacking holes or cells. The lumen is large and circular. The tube bears throughout its entire length, numerous, regularly spaced, thick alate peristomes, separated by deep incisions (Pl. 6, Figs 7a-7b). These peristomes consist of two lobes, which are covered by distinct corrugations. The upper surface of the tube is sculptured by a median keel (in studied specimens heavily corroded).

REMARKS: The specimens studied agree with those described by GOLDFUSS (1831, p. 229, pl. 68, figs 3a-b) as *Serpula gibbosa*. The generic assessment of this species has not hitherto been established. The presence of numerous, regularly spaced peristomes developed throughout the length of the tube suggests its affiliation to *Filogranula* LANGERHANS, 1884. This feature does not appear so clearly in other genera. Although in *Neovermilia*, *Placostegus*, and *Vermiliopsis* relatively numerous peristomes may develop in the terminal part of the tube, they never arise in regular sectors along the whole tube.

Regularly spaced peristomes are present in the Jurassic monospecific genus *Genicularia* QUENSTEDT, 1858, however, the tube is not attached to the substrate. The relationship of this genus to *Filogranula* LANGERHANS, 1884, is unclear and needs further study.

Genus *Laqueoserpula* LOMMERZHEIM, 1979

TYPE SPECIES: *Laqueoserpula litoralis* LOMMERZHEIM, 1979; *OD*

Laqueoserpula? intumescens sp.nov.
(Pl. 3, Figs 10-14)

HOLOTYPE: The specimen POx/W-035, illustrated in Pl. 3, Figs 14a-14b.

TYPE SERIES: Four specimens, POx/W-031 to POx/W-034, illustrated in Pl. 3, Figs 10-13.

TYPE LOCALITY: Bielawy Quarry, Couiavia region, north-central Poland.

TYPE HORIZON: Upper Oxfordian (Bimammatum to Planula zones).

DERIVATION OF THE NAME: Referring to its intumescent (Latin *intumescens*) peristome.

DIAGNOSIS: A species of *Laqueoserpula?* with low-trochospirally coiled tube; outer surface sculptured by alate incisions, a longitudinal, centrally placed furrow, and delicate corrugations developed on the basal part of whorls; peristome very intumescent, dissected by a furrow.

MATERIAL: Seven specimens from the Wapienno/ Bielawy Quarry.

DESCRIPTION: The solitary tube attached to the substrate is composed of few whorls. The tube is either regularly coiled planispirally (Pl. 3, Figs 10, 11, 13) or tends to coil trochospirally (Pl. 3, Figs 12a, 12b, 14a, 14b). The sutures between whorls are more or less distinct (Pl. 3, Figs 12b, 14a). The umbilicus is either wide (Pl. 3, Figs 10, 11, 13) or narrow and very deep (Pl. 3, Fig. 14a). The tube-wall is thick (Pl. 3, Fig. 13), and more or less flattened. The short, anterior part is erect (Pl. 3, Figs 12b, 14b). The outer surface of the tube is scuptured by alate incisions (Pl. 3, Figs 10, 11, 13, 14b), the longitudinal, centrally placed furrow (Pl. 3, Figs 10, 13, 14a, 14b), and delicate corrugations developed on the basal part of the whorls (Pl. 3, Figs 12a, 12b, 13, 14a, 14b). The alate incisions, correspond to the preceding peristomes, all of which form very distinct swellings dissected by a furrow (Pl. 3, Fig. 12a). The terminal part of the peristome is distinctly narrowed (Pl. 3, Figs 12a, 14b).

REMARKS: The generic affiliation of *Laqueoserpula? intumescens* sp.nov is not obvious, because the differences between *Laqueoserpula* LOMMERZHEIM, 1979, and *Cementula* BRÜNNICH NIELSEN, 1931, are not distinct. In the author's opinion, the new species, in the character of the peristomes (accentuated by distinct swellings) and a tendency to grow vertically from the substrate, falls into *Laqueoserpula* LOMMERZHEIM, 1979, rather than into *Cementula* BRÜNNICH NIELSEN, 1931. The new species is close to the Jurassic species *Serpula macrocephala* GOLDFUSS (1831) [which should probably be referred to *Laqueoserpula* LOMMERZHEIM, 1979], from which it differs in its outer sculpture (distinct vertical corrugations, but a lack of three distinct keels).

Genus *Metavermilia* BUSH, 1904

TYPE SPECIES: *Vermilia multicristata* PHILIPPI, 1844; *OD*

Metavermilia? *tricarinata* (GOLDFUSS, 1831)
(Pl. 2, Figs 2-5)

1831. *Serpula tricarinata* nobis; A. GOLDFUSS, p. 230, pl. 68, fig. 6a-c.
1956. *Serpula* (*Tetraserpula*) *tricarinata* GOLDFUSS 1831; K.O.A. PARSCH, p. 224, pl. 19, fig. 12 and pl. 21, fig. 21.

DIAGNOSIS: Small tube of trapezoidal cross-section, almost flat outer surface sculptured by three not very prominent keels and relatively distinct transverse corrugations.

MATERIAL: Eight specimens from the Bielawy/ Wapienno Quarry.

DESCRIPTION: The tube is attached to the substrate (sponges, other serpulids, brachiopods) along its whole length, and may be variously curved: *S*-shaped (Pl. 2, Fig. 4), slightly meander-like (Pl. 2, Fig. 5b), or loop-like (Pl. 2, Figs 2, 3b). The length of the tube reaches 12 mm, with the tube diameter gradually increasing to a maximum of 1.5 mm. The outer surface of the tube is sculptured by three, slightly undulate keels (Pl. 2, Figs 2, 3a-3b, 4, 5b) of identical thickness and height. Transverse corrugations are present, the best developed at the lateral walls (Pl. 2, Figs 2, 4, 5b). A weakly annular peristome may appear in some specimens (Pl. 2, Figs 2, 4, 5a-5b). The tube wall is moderately thick, but its base (observable at the aperture) is distinctly thicker (Pl. 2, Fig. 5a). The cross-section of the tube is trapezoidal. The peripheral keels form the upper edges of the trapezium. The upper surface of the tube is almost flat (Pl. 2, Figs 2, 3a-3b, 4, 5b).

REMARKS: The generic affiliation of this species has not hitherto been definitely recognised, but some suggestions are presented by JÄGER (1983, p. 63; 1993, p. 94).

The small forms studied herein, in their overall shape and the presence of three keels, resemble some Recent and fossil species (see BIANCHI 1981; JÄGER 1983, 1993) of such genera as, e.g. *Vermiliopsis*, *Janita*, *Filogranula*, *Metavermilia*, or *Serpula*. Because of the small size, a relatively fast increase in the tube diameter, and the presence of weakly developed ring-like peristomes, the species *tricarinata* is ascribed tentatively to the genus *Metavermilia* BUSH, 1904.

Genus *Mucroserpula* REGENHARDT, 1961

TYPE SPECIES: *Mucroserpula mucroserpula* REGENHARDT, 1961; *OD*

Mucroserpula jaegeri sp.nov.
(Pl. 2, Figs 9-10 and Text-fig. 3)

HOLOTYPE: The specimen No. POx/W-021, illustrated in Pl. 2, Fig. 10 and Text-fig. 3.

PARATYPE: The specimen No. POx/W-020, illustrated in Pl. 2, Fig. 9.

TYPE LOCALITY: Bielawy Quarry, Couiavia region, north-central Poland.

TYPE HORIZON: Upper Oxfordian (Bimammatum to Planula zones).

DERIVATION OF THE NAME: To honour Dr. Manfred JÄGER (Dotternhausen, Germany), whose comments allowed recognise nature of this species.

DIAGNOSIS: A species of *Mucroserpula* with strongly flattened tube, sculptured by delicate corrugations, a distinct median keel and two delicate parallel crests; long, terminal part of the arcuate tube.

MATERIAL: Three specimens (two of them largely corroded) from the Wapienno/Bielawy Quarry.

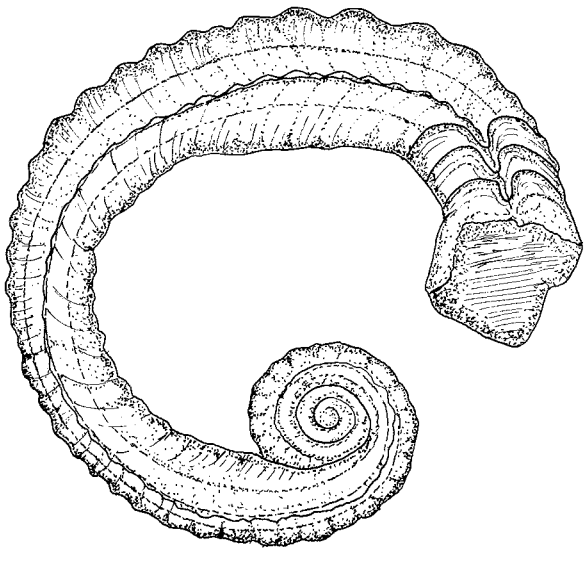

Fig. 3. Sketch drawing of the holotype of *Mucroserpula jaegeri* sp.nov. (see Pl. 2, Fig. 10); No. POx/W-021, × 3

DESCRIPTION: The tube is attached to the substrate (sponge wall) along its whole length. The posterior part is spirally coiled; the successive whorls slightly overlapping the preceding ones (Text-fig. 3 and Pl. 2, Fig. 9). The uncoiled, anterior part may be very long and distinctly arcuate (Pl. 2, Fig. 10). The umbilicus is deep and slightly eccentrically placed (Pl. 2, Fig. 9). The strongly flattened tube is wide and increases fastly in diameter. The wall of the tube is extremely thick (Pl. 2, Fig. 9). The outer surface of the tube is sculptured by delicate alate corrugations and a distinct, slightly undulating median keel, as well as by two delicate parallel crests. Narrow, bird wing-shaped incisions are present towards the end of the tube (Text-fig. 3).

REMARKS: The species *Mucroserpula jaegeri* sp.nov., in its trapezoidal cross-section and characteristic ornamentation (a median keel, parallel crests, and bird wing-shaped corrugations), agrees well with the diagnosis (see REGENHARDT 1961) of the genus *Mucroserpula* REGENHARDT, 1961. *M. jaegeri* sp.nov. is the closest to the type species of the genus *Mucroserpula* REGENHARDT, 1961, however, the mode of coiling of the latter is distinctly less regular. No closely allied Jurassic species is known.

Genus *Neovermilia* DAY, 1961

TYPE SPECIES: *Neovermilia capensis* DAY, 1961; *OD*

Neovermilia limata (MÜNSTER in GOLDFUSS, 1831) (Pl. 5, Figs 10-14; Pl. 6, Figs 5-6)

1831. *Serpula limata* MÜNSTER; G. MÜNSTER, p. 229, pl. 68, fig. 1a-c.
1831. *Serpula plicatilis* MÜNSTER; G. MÜNSTER, p. 229, pl. 68, fig. 2a-b.
1956. *Serpula* (*Dorsoserpula*) *limata* MÜNSTER 1831; K.O.A. PARSCH, p. 220, pl. 19, fig. 20a-20c and pl. 20, fig. 11.
1956. *Serpula* (*Dorsoserpula*) *plicatilis* MÜNSTER 1831; K.O.A. PARSCH, p. 220, pl. 19, fig. 22 and pl. 21, fig. 20.

MATERIAL: Twelve specimens from the Bielawy/ Wapienno Quarry.

DIAGNOSIS: A species of *Neovermilia* with moderately large tube attached to the substrate, and with subtriangular cross-section; outer surface sculptured by a distinct, undulate median keel and delicate irregular vesicles; peristomes alate, distinctly multiplied in the terminal part of the tube.

DESCRIPTION: The *S*-shaped tube is attached to the substrate (sponge wall) along its whole length, and has a subtriangular cross-section (Pl. 5, Figs 10-13; Pl. 6, Figs 5-6); the lateral walls are convex (Pl. 5, Fig. 13a). The tube-wall is moderately thick, and the base in apertural view displays two holes, which correspond to the densely spaced cells (Pl. 5, Fig. 14). The tube length of the largest specimen reaches about 90 mm, with the tube diameter increasing rather rapidly to a maximum of 7 mm (Pl. 5, Fig. 10). The outer surface of the tube is sculptured by a distinct, slightly undulate, median keel, and delicate, irregular vesicles developed in adult specimens (Pl. 5, Figs 10-13), but absent from the juveniles (Pl. 6, Figs 5, 6b). The alate peristomes (Pl. 6, Fig. 6a) in the proximal tube-part appear relatively rarely, but in the most terminal part they are distinctly multiplied (Pl. 5, Fig. 10).

REMARKS: Included into the synonymy of the species *limata* is the species *plicatilis* which differs only in its less regular distribution of transverse corrugations; according to the present author, this is not enough to distinguish separate taxa.

The specimens studied agree with those described by MÜNSTER (1831, pl. 68, figs 1a-c, 2a-b) as *Serpula limata* and as *Serpula plicatilis*. PARSCH (1956) ascribed the species *limata* to his new subgenus *Dorsoserpula* PARSCH, 1956, the diagnosis of which appears to be so arbitrary (the presence of a keel) that it may relate to many species of several different genera. If the diagnosis of *Dorsoserpula* was reduced to the features shown by the type species, *Serpula delphinula* GOLDFUSS, 1831, then the species *limata*, characterised by a smaller size and distinctly developed ornamentation, should clearly be excluded.

In its moderately large tube, alate peristomes that are more distinct and numerous in the terminal part of the tube, the relatively distinct sculpture and the structure of the tube-base, the species *limata* fits the characters of the genus *Neovermilia* DAY, 1961. This genus was originally used to describe Recent species, including *Neovermilia flacigera* (ROULE, 1898), that have subsequently been recognized in Plio-Pleistocene strata (see ZIBROWIUS & TEN HOVE 1987). JÄGER (1993, p. 81) has pointed out the great similarity between the tube characters of the Recent genus *Neovermilia* DAY, 1961, and those of the fossil genus *Proliserpula* REGENHARDT, 1961, and has suggested *Proliserpula* REGENHARDT, 1961, to be a junior synonym of *Neovermilia* DAY, 1961. The material studied fully justifies this suggestion, and if this is so, it extends the stratigraphical range of the genus *Neovermilia* DAY, 1961, to the Upper Jurassic (Upper Oxfordian).

The genus *Pomatoceros* PHILIPPI, 1844, to which the species could alternatively be assigned, is characterised by a more triangular cross-section, a lack of distinct peristomes, and by having its base adorned with longitudinal hollows.

Genus *Pannoserpula* JÄGER, KAPITZKE & RIETER, 2001

TYPE SPECIES: *Serpula spiralis* MÜNSTER *in* GOLDFUSS, 1831; *OD*

Pannoserpula couiaviana sp.nov.
(Pl. 4, Figs 1-8 and Text-fig. 6)

HOLOTYPE: The specimen No. POx/W-043, illustrated in Pl. 4, Figs 8a-8b.

TYPE SERIES: The specimens No. POx/W-036–POx/W-042, illustrated in Pl. 4, Figs 1-7.

TYPE LOCALITY: Bielawy Quarry, Couiavia region, north-central Poland.

TYPE HORIZON: Upper Oxfordian, Idoceras planula Zone, nearly at the base of the Galar Subzone.

DERIVATION OF THE NAME: Neo-Latinized adjective *couiaviana* of the Couiavia region in north-central Poland.

DIAGNOSIS: A species of *Pannoserpula* with barrel-like coiled posterior part; outer surface of tube sculptured by delicate corrugations and two distinct furrows placed on either side of the tube.

MATERIAL: Twenty five specimens (of which 17 are free tube parts only) from the Bielawy Quarry.

DESCRIPTION: The moderately thick-walled tubes are peculiarly coiled and attached to the substrate along their early (2-3) whorls. The whole specimens are moderately large and the height from the base to the top of the tube (in completely preserved specimens) varies from 30 to 44 mm. The initial part of the tube is relatively short and straight, but is observable on one specimen only (Pl. 4, Fig. 5b); in others it is not preserved (Pl. 4, Fig. 7c). This part continues into a group of 2-3 more or less planispirally coiled whorls, each of which is overgrown by the next one. These whorls (forming a basal platform), pass into barrel-like, coiled (3-4) whorls (Pl. 4, Figs 1a-1b, 5a, 6, 8a-8b), which are cemented together albeit the sutures are more or less readily discernible. All specimens are sinistral. The anterior, erect part is characteristically twisted like a corkscrew (Pl. 4, Figs 2, 3, 8a-8b). This part has a variable length in relation to the remainder of the tube (Pl. 4, Figs 1a-1b, 3, 8a-8b). The diameter of the free part varies from 5 to 7 mm. The outer surface of the whole tube is sculptured by more or less distinct corrugations (Pl. 4, Figs 1b, 2-3) and by two, deeply incised furrows, developed on either side of the tube (Pl. 4, Figs 1b, 2-3, 8a-8b, 7b). The peristome is circular and tapered (Pl. 4, Fig. 1a).

REMARKS: The newly established species, *Pannoserpula couiaviana* sp.nov., in its overall shape, straight course of the initial part and corkscrew-like anterior part, agrees well with the characters of the genus *Pannoserpula* JÄGER, KAPITZKE & RIETER, 2001. The specimens studied are generally more massive (thick-walled) than the other two species ascribed to this genus. Moreover, *Pannoserpula couiaviana* sp.nov. differs from *P. spiralis* (MÜNSTER *in* GOLDFUSS, 1831) in the barrel-like, coiled posterior part and the pronounced ornamentation (corrugations and furrows); and from *P. pannosa* (QUENSTEDT, 1857) in the distinctly smaller size, the barrel-like, coiled posterior part (comprising 3-4 whorls), and the shorter and less corkscrew-like erect part.

The specimens of *Pannoserpula couiaviana* sp.nov. were found free in the sediment. Two of them bear a fragment of the oyster shell to which they were attached; this is discussed hereafter (see Text-fig. 6).

Genus *Parsimonia* REGENHARDT, 1961

TYPE SPECIES: *Parsimonia parsimonia* REGENHARDT, 1961; *OD*

Parsimonia deshayesi (MÜNSTER in GOLDFUSS, 1831)
(Pl. 5, Figs 1-6)

1831. *Serpula Deshajesii* MÜNSTER; G. MÜNSTER, p. 232, pl. 68, fig. 18a-e.
1858. *Serpula deshayesii* GOLDFUSS; F.A. QUENSTEDT, p. 664, pl. 81, figs 53-56.
1956. *Serpula* (*Tetraserpula*) *deshayesi* MÜNSTER 1831; K.O.A. PARSCH, p. 225, pl. 19, figs 19a-19b; pl. 20, fig. 17.

MATERIAL: Fifteen fragments, represented mostly by free parts, from the Bielawy/Wapienno Quarry.

DIAGNOSIS: A species of *Parsimonia* with tube of large diameter, posterior part inverse-trochospirally coiled, attached to the substrate, and relatively short erect anterior part; sculptured by distinct corrugations, three longitudinal furrows and a median keel; ring-like peristomes rare.

DESCRIPTION: The tube is relatively massive, and the thickness of its wall in the largest specimen reaches 2 mm at 12 mm tube diameter. The cross-section is circular or subquadrangular (Pl. 5, Fig. 6a). The posterior part is attached to the substrate (terebratulid shell) and coiled inverse-trochospirally, sinistral or dextral (Pl. 5, Figs 1a-1b, 2a-2b). The anterior part is erect (Pl. 5, Figs 3, 4a-4b, 5, 6b). The outer surface is sculptured by distinct corrugations, three longitudinal furrows (Pl. 5, Figs 3, 5) and a median keel (Pl. 5, Figs 1a, 2a, 4a-4b). The indistinct, ring-like peristomes appear very rarely (Pl. 5, Figs 4b, 6b).

REMARKS: The studied specimens compare well with those described by MÜNSTER (1831, p. 232, pl. 68, fig. 18a-e) as *Serpula Deshajesii*. This species fits the diagnostic features of the genus *Parsimonia* REGENHARDT, 1961, in the large tube diameter, character of ornamentation, and the occurrence of rare ring-like peristomes.

Genus *Placostegus* PHILIPPI, 1844

TYPE SPECIES: *Serpula tridentatus* FABRICIUS, 1779; *SD* HOWELL, 1962

Placostegus conchophilus sp.nov.
(Pl. 3, Figs 1-9)

HOLOTYPE: The specimen No. POx/W-030, illustrated in Pl. 3, Figs 9-9a.

TYPE SERIES: The specimens No. POx/W-022–POx/W-029, illustrated in Pl. 3, Figs 1-8.

TYPE LOCALITY: Bielawy Quarry, Couiavia region, north-central Poland.

TYPE HORIZON: Upper Oxfordian (Bimammatum to Planula zones).

DERIVATION OF THE NAME: Referring to its settlement on shells of the brachiopod *Lacunosella cracoviensis* (QUENSTEDT, 1871); neo-Latinized adjective *conchophilus* – favouring the shell.

DIAGNOSIS: A species of *Placostegus* with tube of subtriangular cross-section, spirally coiled posterior part and short, erect anterior part; outer surface sculptured by thick keel forming a distinct ridge; peristome provided with three teeth.

MATERIAL: Eighteen specimens from the Wapienno Quarry.

DESCRIPTION: The unique substrate of all specimens (see Text-fig. 4.1-4.8) consists of shells of the brachiopod *Lacunosella cracoviensis* (QUENSTEDT, 1871). The posterior part of the tube is coiled planispirally, more or less regularly (Pl. 3, Figs 2-3, 6, 8-9), but the last whorl often lies upon the former ones (Pl. 3, Figs 1a, 4b, 5a, 7). In this last case, the whorls are cemented by tube material, and the sutures are weakly accentuated (Pl. 3, Figs 1b, 4a, 5b). The umbilicus is either wide (Pl. 3, Figs 2-3, 6, 9a), or narrow and very deep (Pl. 1a, 3, 4b, 5a, 7). The tube-wall is thick (Pl. 3, Fig. 9), and its transverse section is subtriangular (Pl. 3, Fig. 9a) to subquadrangular (Pl. 3, Figs 2, 8). The short, terminal part is erect (Pl. 3, Figs 8, 9, 9a), but in the majority of specimens this part is broken (Pl. 3, Figs 1a, 4b, 5a, 6, 7). Only one specimen (Pl. 3, Fig. 2) shows the anterior part cemented to the substrate. The outer surface of the tube is sculptured by the thick, marginal keel which forms a distinct ridge (Pl. 3, Figs 1a, 2-3, 4b, 5a, 6-8, 9a), and by delicate corrugations. The peristome (preserved only in the holotype) is provided with three teeth (Pl. 3, Figs 9, 9a).

REMARKS: In its mode of coiling, thick tube wall, cross-section, a tendency to grow vertically from the substrate, and a peristome provided with three teeth, *Placostegus conchophilus* sp.nov. falls in the diagnosis of the genus *Placostegus* PHILIPPI, 1844. A similar overall shape and size is found in the genus *Laqueoserpula* LOMMERZHEIM, 1979, which is characterised by a less regular mode of coiling, as well as by the absence of a distinct longitudinal keel and a peristome with three teeth.

The newly established species, *P. cochophilus* sp.nov., is close to the Jurassic forms described by MÜNSTER (*in* GOLDFUSS 1831) as *Serpula trochleata*, from which it differs in the presence of a distinct marginal keel and a peristome provided with three teeth. The species *Serpula trochleata* MÜNSTER *in* GOLDFUSS, 1831 should probably be ascribed to the genus *Laqueoserpula* LOMMERZHEIM, 1979.

Genus *Serpula* LINNAEUS, 1767

TYPE SPECIES: *Serpula vermicularis* LINNAEUS, 1767; *SD* HOWELL, 1962

? *Serpula* sp.
(Pl. 5, Figs 7-9)

MATERIAL: Four specimens from the Wapienno Quarry.

DESCRIPTION: The moderately large, thin-walled tubes (Pl. 5, Figs 7-9) are partly cemented to the substrate, exclusively to shells of the brachiopod *Lacunosella cracoviensis* (QUENSTEDT, 1871). The cross-section of the tube is circular (Pl. 5, Fig. 8). The mode of coiling is generally irregular, but three specimens display some regularity in the course of the tube. In such a case (Pl. 5, Figs 7-8), the posterior part is inverse-trochospirally coiled and attached to the substrate. In this part, the diameter of the tube increases relatively fast. The tube then changes its direction, and grows up vertically from the substrate (Pl. 5, Figs 7-8). This anterior part is trochospirally coiled and its diameter increases very slowly to reach 3.5 to 5 mm. The terminal part is erect. In one specimen (Pl. 5, Fig. 9), the loop-like coiled posterior part is attached to the substrate, and then passes into the trochospirally coiled anterior part, which is also attached by its side. The outer surface of the tube in all specimens is sculptured by weakly developed corrugations (Pl. 5, Figs 7-9) and widely spaced ring-like peristomes.

REMARKS: In the mode of coiling, the ornament composed exclusively of weakly developed corrugations, and the widely spaced ring-like peristomes, the specimens studied resemble representatives of both the genus *Serpula* LINNAEUS, 1758, and the genus *Hydroides* GUNNERUS, 1768. Both genera include species, e.g. *Hydroides pseudounicata*, *Serpula lobiancoi* (see BIANCHI 1981, fig. 7), with tubes that exhibit these same characters. Because ring-like peristomes occur more frequently in *Serpula* than in *Hydroides*, the specimens studied are assigned tentatively to the genus *Serpula* LINNAEUS, 1758. No species attribution is proposed.

From the similarly coiled species of *Glomerula* the studied specimens differ in their larger tube dimensions, the presence of corrugations, and the distinctly thinner wall.

Among Jurassic species the closest are those described by MÜNSTER (in GOLDFUSS 1831) as *Serpula canaliculata* and *Serpula substriata*, from which the studied specimens differ in their mode of coiling and sculpture.

ECO-TAPHONOMIC REMARKS

The tube-dwelling polychaetes studied are inferred to have lived at shallow depths, around and at the top of the biohermal buildup (cf. MATYJA & *al.* 1985). As the bottom was commonly muddy and/or soupy, all the species in question grew as epibionts of variable organic substrates, primarily sponges and brachiopods (see Text-fig. 4), rarely oysters. Some specimens were infested by and grew simultaneously with the symbiotic hydroid *Protulophila gestroi* ROVERETO, 1901 (see below).

Of the organic substrates, only the brachiopod shells enable inferences to be made regarding the relationships of the serpulids and brachiopods during life. Serpulids that grew as far as the shell commissure (see Text-fig. 4.3, 4.7, 4.8) evidently grew when the commissure was functioning, that means during the life of the brachiopod (see CUFFEY & *al.* 1995; RADWAŃSKA & RADWAŃSKI 2003b). The same may be said of serpulids that grew as far as a definite growth band of the brachiopod shell (see Text-fig. 4.2a), indicating a temporary stop in shell accretion during which the serpulid died; further growth of the shell was then devoid of serpulids. Of other instances of epizoic growth, serpulids attached to sponge skeletons and oyster shells provide no information about the life of the host, but those upon some brachiopod shells may provide indirect evidence. Such indirect evidence is twofold: (*i*) from having a preference for particular brachiopod species, and (*ii*) from settlement on a preferred valve of the brachiopod shell.

Ad (*i*): One of the species, *Placostegus conchophilus* sp.nov., has been found exclusively on shells of *Lacunosella cracoviensis* (QUENSTEDT, 1871), to which it may thus be claimed to have been a commensal. In other words, those brachiopods with epizoic serpulids on any part of their shells (Text-fig. 4.1, 4.4-4.6) were then alive, as were those overgrown either to their commissure or to a definite growth band (Text-fig. 4.2-4.3, 4.7-4.8).

Ad (*ii*): Most of the tube-dwelling polychaetes, regardless of their species attribution, growing upon brachiopod shells, as exemplified by *Lacunosella cracoviensis* (QUENSTEDT, 1871), were located on the ventral valves (Text-fig. 4.1-4.8).

An analysis by STUDENT's *t*-test reveals (see Text-fig. 5) a statistically significant ($p < 0.01$) dominance of serpulid-inhabited ventral valves over dorsal valves. There was thus a preference for the serpulid larvae to settle on the more readily accessible ventral valves. It is reasonable to conclude that these must have been valves of living brachiopods, since these tended to lie on the bottom by their dorsal valves, with their ventral valves exposed. If this is the case, it can then be suggested that all serpulids growing upon shells of brachiopods and forming 'serpulid gardens' (Text-fig. 4)

were commensal, to benefit (see AGER 1961, 1963; SCRUTTON 1975, pl. 42, fig. 11; MICHALIK 1976, fig. 10) from food-supplying suspension streams induced by the host brachiopod.

A response of serpulid morphology to bottom conditions other than live/dead biotic material is demonstrated by *Pannoserpula couiaviana* sp.nov., the only species whose spectacular specimens (see Pl. 4, Figs 1-8)

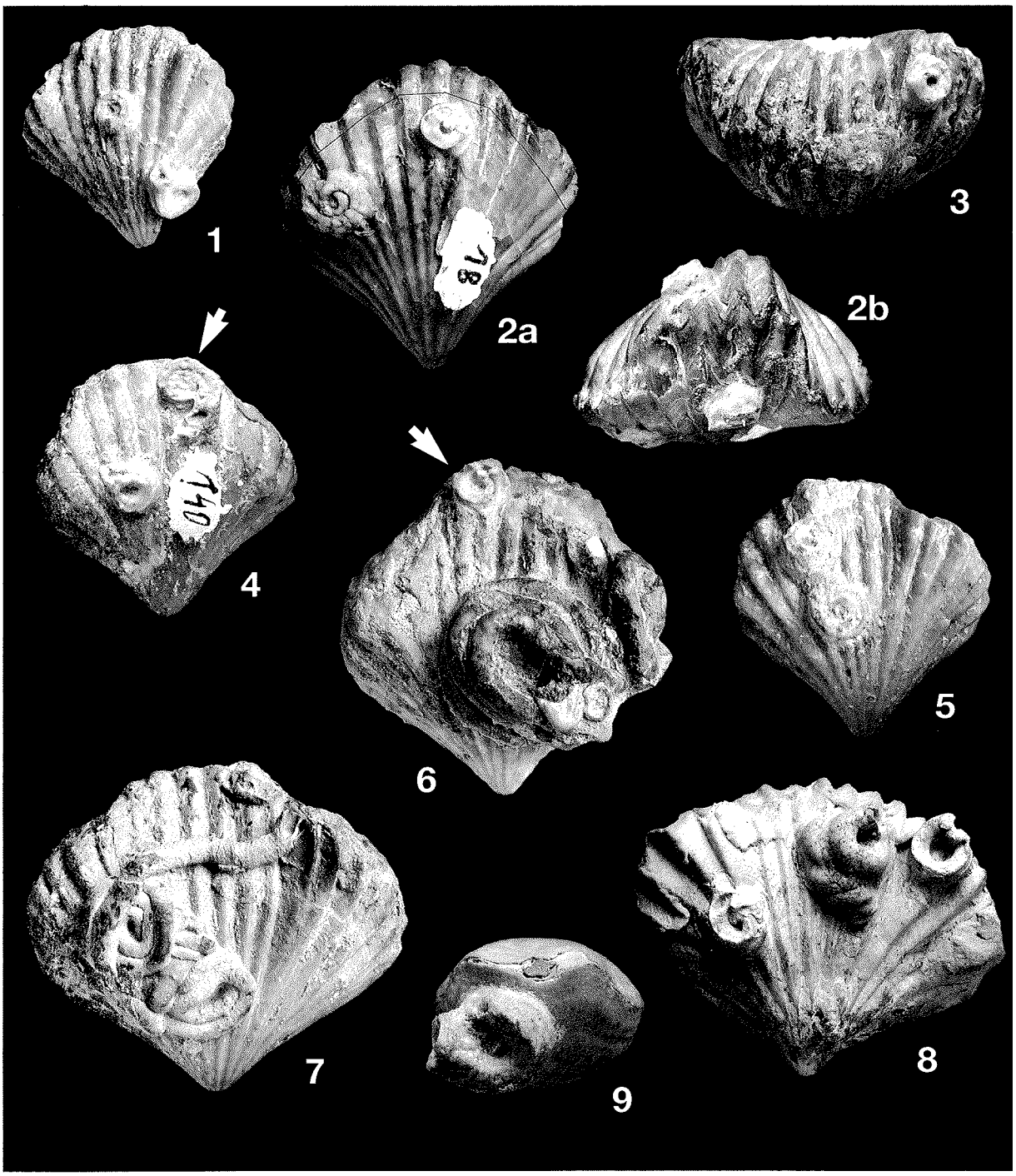

Fig. 4. 'Serpulid gardens' on brachiopod shells from the Wapienno/Bielawy succession: **1-8** – On the rhynchonellid *Lacunosella cracoviensis* (QUENSTEDT, 1871), **9** – On a terabratulid; all photos × 2, taken by the Author; in Fig. 2a a growth band reached by two serpulids is indicated; in Figs 4 and 6 the arrow indicates a serpulid that grew as far as the commissure

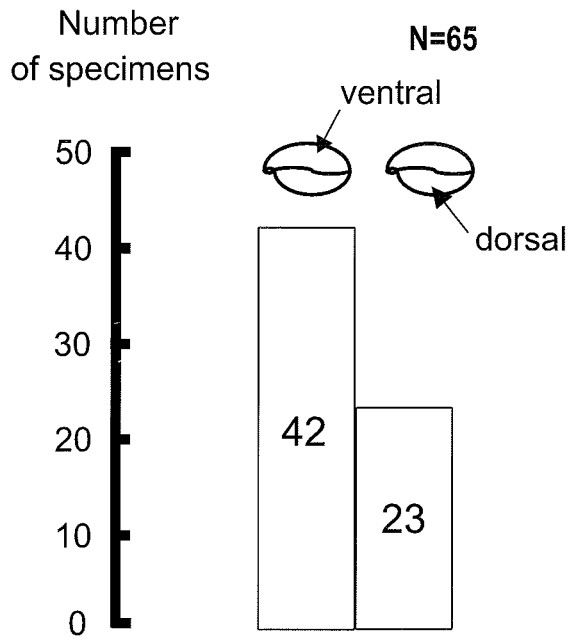

Fig. 5. Frequency of serpulids (N=65) epizoic on shells of the brachiopod *Lacunosella cracoviensis* (QUENSTEDT, 1871), to evaluate their location on each of the two valves: according to STUDENT's *t*-test the difference is significant at $p < 0.01$

were found loose in the sediment. This species occurs exclusively in a marly interbed in the highest part of the Bielawy section (see Text-fig. 2). Although the initial part of the tube bears a very small shell fragment, on which the larva settled, the remainder of the tube was unattached, up to the largest specimens studied. This small initial part is thus completely overlapped by the barrel-shaped portion, the function of which was to act as a stabilizing anchor. Various types of ecophenotypic response have formerly been suggested for other, similarly shaped tube-dwelling polychaetes, both serpulids and spirorbids (see KNIGHT-JONES & *al.* 1973, BAILEY-BROCK & KNIGHT-JONES 1977, KNIGHT-JONES 1978, MACELLARI 1984, KNIGHT-JONES & KNIGHT-JONES 1994, SAVAZZI 1995), but none matches such a case. The final (posterior, adult) corkscrew-like part of the tube evidently grew upwards, to keep pace with sedimentation of the marly ooze (see Text-fig. 6).

THE COMMENSAL HYDROID

Some specimens of *Ditrupula quadrisulcata* (PARSCH, 1956) were infested (see Pl. 6, Figs 4a, 4c) by the hydroid *Protulophila gestroi* ROVERETO, 1901, which grew simultaneously with the serpulid, whose tube progressively embedded the live hydroid. The polyp chambers, distributed throughout a reticulate stolonal network, are manifested by their apertures, which are observable as tiny openings scattered regularly along the tube exterior (see Pl. 6, Figs 4a, 4c). The ecological relationship of the hydroid symbiont to the polychaete should thus be classified as commensal, or even mutualistic (see SCRUTTON 1975, pp. 269 and 271; POHOWSKY 1978, p. 42; RADWAŃSKA 1996, p. 75).

The historical background to the discovery of this symbiont, *Protulophila gestroi* ROVERETO, 1901, a species ranging from the Upper Jurassic to the Pliocene (ROVERETO 1901, SCRUTTON 1975), and a review of its Jurassic occurrences, were presented in an earlier paper by the author (RADWAŃSKA 1996, pp. 75-76).

JÄGER & *al.* (2001, pp. 9-10 and fig. 3) recently reported the occurrence of this hydroid in tubes of *Pannoserpula spiralis* (MÜNSTER *in* GOLDFUSS, 1831) from the Middle Oxfordian of the Swiss Jura.

TAPHONOMIC PATHWAY

The taphonomic pathway of the tube-dwelling polychaetes is quite simple. All the specimens were redeposited by storm agitation and/or mass movements from their original biotopes and violently introduced into the talus facies of the biohermal buildup (Text-fig. 2, and RADWAŃSKA & RADWAŃSKI 2003a). Many have been found in lenses or blocks (olistholiths) replete with brachiopods *Lacunosella cracoviensis* (QUENSTEDT, 1871), predominantly (KRAWCZYŃSKI 2003). In such instances, it may be inferred that the brachiopod shells were favoured for settlement by the larvae of the tube-dwelling polychaetes, and that some of the polychaetes became commensals to particular brachiopod species. The others became epibionts on sponges (? living or dead), or on the shell hash (e.g., of oysters) scattered over the muddy bottom.

The relatively good preservation of the brachiopods bearing symbiont polychaetes suggests that they did not remain long on the bottom but, while they and their symbionts were still alive, were violently transported and buried, to be transformed into the fossil record.

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Fig. 6. Hypothetical growth of *Pannoserpula couiaviana* sp.nov. on an oyster shell fragment on the muddy bottom, to form erect tubes keeping pace with sedimentation of the marly ooze; heavy lines denote the successively higher positions of the (*arrowed*) sediment/water interface; drawn approx. × 2 (*compare* Pl. 4, Figs 1-8)

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PLATES 1 – 6

PLATE 1

Glomerula gordialis (SCHLOTHEIM, 1820)

1 – POx/W-001: 1a – top view, 1b – lateral view, 1c – basal view; **2** – POx/W-002, top view; **3** – POx/W-003, top view; **4** – POx/W-004, top view; **5** – POx/W-005, top view; **6** – POx/W-006, top view; **7** – POx/W-007: 7 – general view (natural size) of the brachiopod *Lacunosella cracoviensis* (QUENSTEDT, 1871), to show location of the tube, 7a – close-up view of the tube, taken × 2; **8** – POx/W-008, top view; **9** – POx/W-010, top view; **10** – POx/W-011, top view.

Except for Fig. 7, all figures are × 2

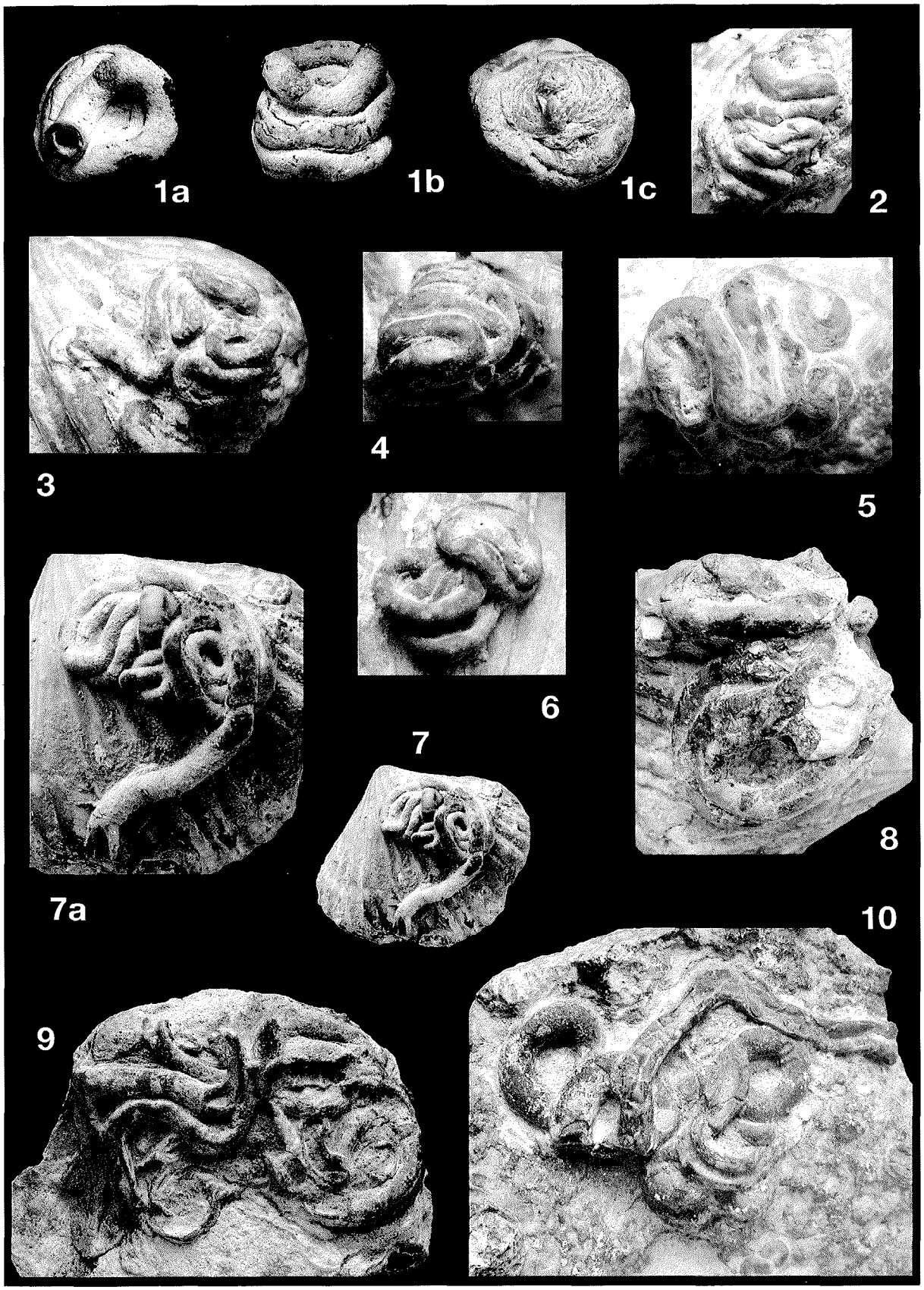
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PLATE 2

1 – *Cementula*? sp.; POx/W-012, top view; × 3.

2-5 – *Metavermilia*? *tricarinata* (GOLDFUSS, 1831); 2 – POx/W-013, top view, to show the overall shape, × 5; 3 – POx/W-014: 3a – close-up view, to show details of the sculpture, × 8, 3b – top view, to show the overall shape, × 5; 4 – POx/W-015, top view, to show the overall shape, × 5; 5 – POx/W-016: 5a – apertural view, × 5, 5b – top view, to show the overall shape, × 5.

6-8 – *Cementula spirolinites* (MÜNSTER *in* GOLDFUSS, 1831); 6 – POx/W-017, top view, to show the spirally coiled part, × 5; 7 – POx/W-018, 7a – close-up view, to show details of the sculpture, × 5; 7b – fragment of sponge wall with two specimens attached, × 4; 8 – POx/W-019, top view, to show the overall shape, × 5.

9-10 – *Mucroserpula jaegeri* sp.nov.; 9 – POx/W-020, paratype, top view, to show the overall shape, × 3; 10 – POx/W-021, holotype, top view, to show the overall shape with arcuate terminal part, × 3.

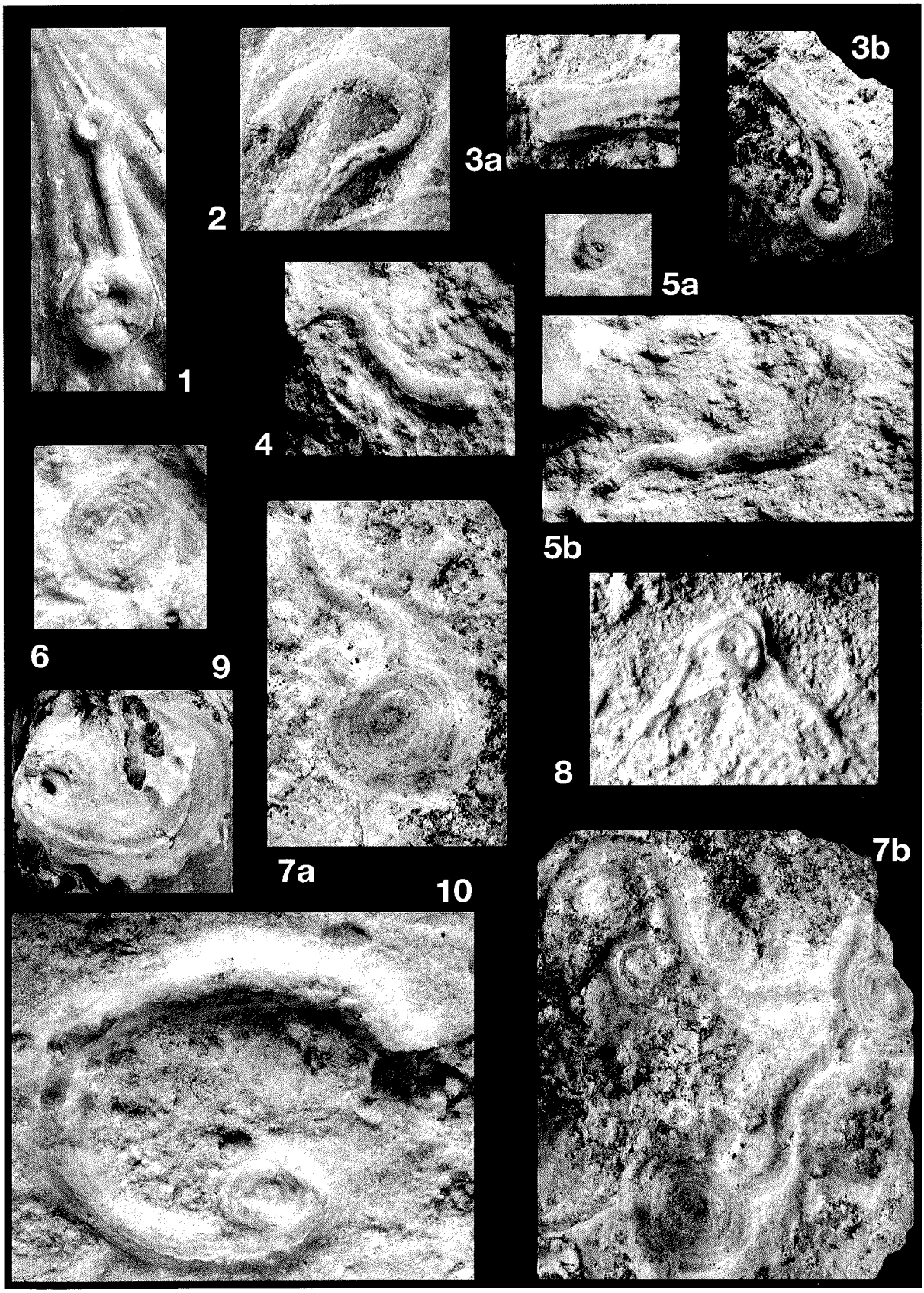
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PLATE 3

Placostegus conchophilus sp.nov.

1-8 – Paratypes, all × 5: 1 – POx/W-0221a – top view, 1b – lateral view, to show the trochospiral mode of coiling; 2 – POx/W-023, top view, to show the planispiral mode of coiling; 3 – POx/W-024, top view; 4 – POx/W-025: 4a – lateral view, 4b – top view; 5 – POx/W-026: 5a – top view, 5b – lateral view; 6 – POx/W-027, top view, to show the strongly developed marginal keel; 7 – POx/W-028, top view; 8 – POx/W-029, top view, to show the erect part.

9 – POx/W-030, holotype: 9a – top view to show the three-toothed peristome and marginal keel, 9 × 4, the holotype indicated by an arrow, 9a × 5.

Laqueoserpula intumescens sp.nov.

10-13 – paratypes, all × 5: 10 – POx/W-031, top view of the spirally coiled part; 11 – POx/W-032, top view of the spirally coiled part; 12 – POx/W-033: 12a – lateral view, to show the trochospirally coiled part and intumescent peristome, 12b – lateral view, to show ornamentation of the tube; 13 – POx/W-034, top view of the spirally coiled part, to show ornamentation.

14 – POx/W-035, holotype: 14a – lateral view, 14b – top view, to show the trochospirally coiled part and intumescent peristome, × 5.

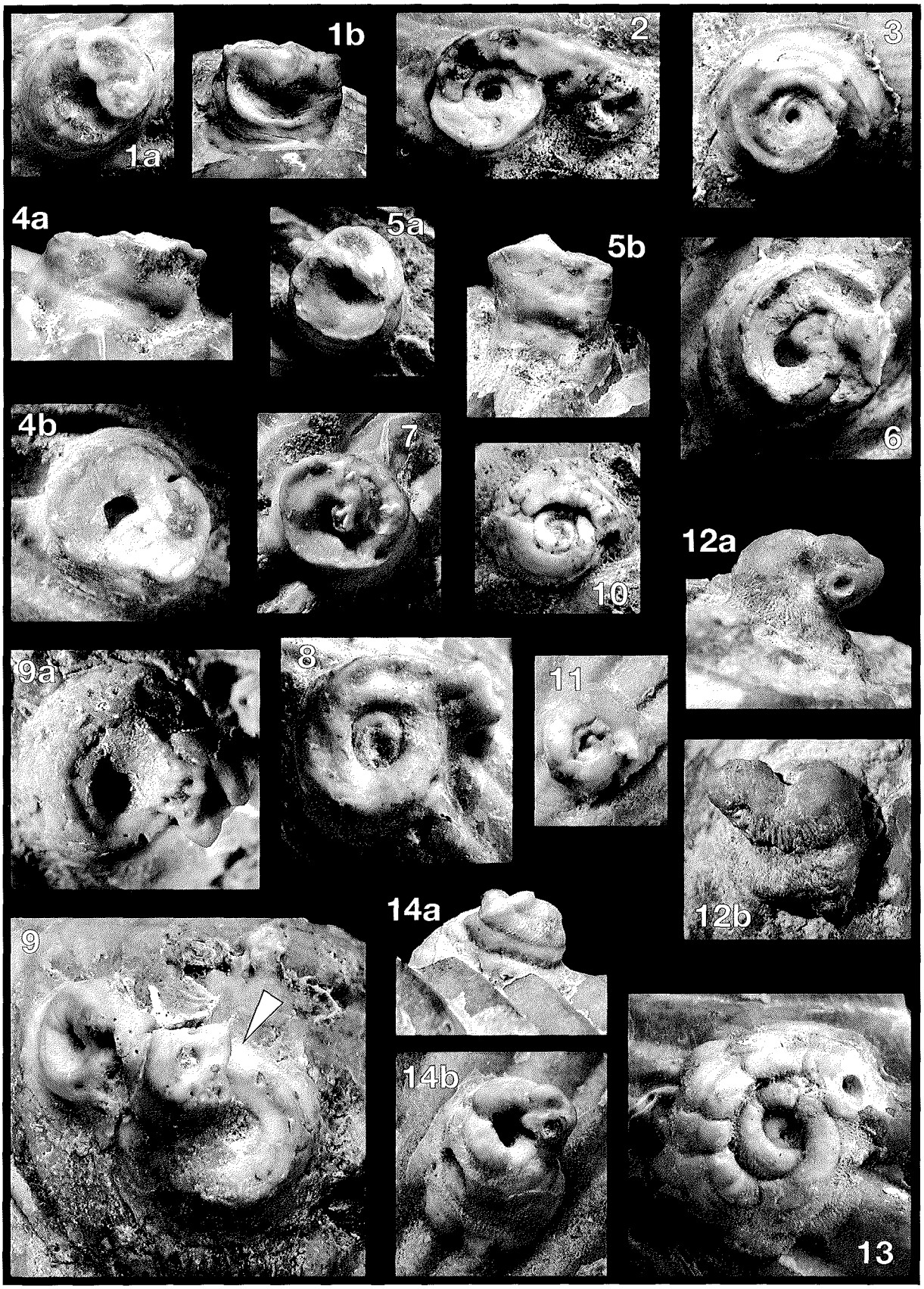
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PLATE 4

Pannoserpula couiaviana sp.nov.

1-7 – Paratypes, all × 2: 1 – POx/W-036, 1a-1b – lateral views of a specimen with a distinct barrel-like coiled part and a short erect part; 2 – POx/W-037, fragment of the erect part with distinct corrugations and a median furrow; 3 – POx/W-038, lateral view of tube with long, erect corkscrew-like part; 4 – POx/W-039: 4a – lateral view, 4b – lateral view, to show the basal part attached to an oyster shell; 5 – POx/W-040: 5a – lateral view with the erect part broken, 5b – basal part, to show the straight initial part; 6 – POx/W-041, lateral view with the erect part broken; 7 – POx/W-042: 7a-7b – lateral views, to show the distinctly barrel-like coiled part, 7c – basal part.

8 – POx/W-043, holotype: 8a-8b – lateral views, to show the distinctly barrel-like coiled part and long, erect corkscrew-like part, × 2.

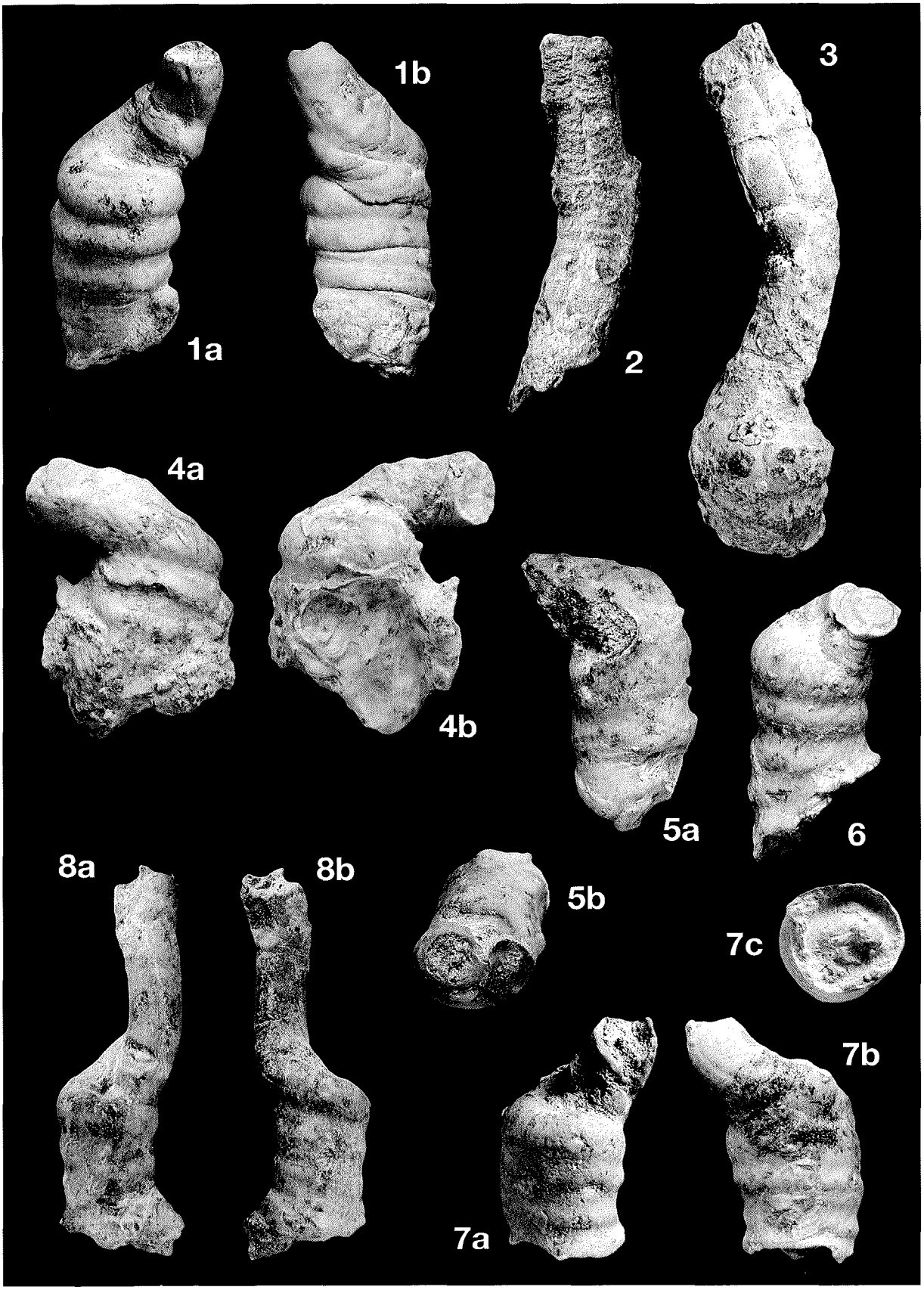
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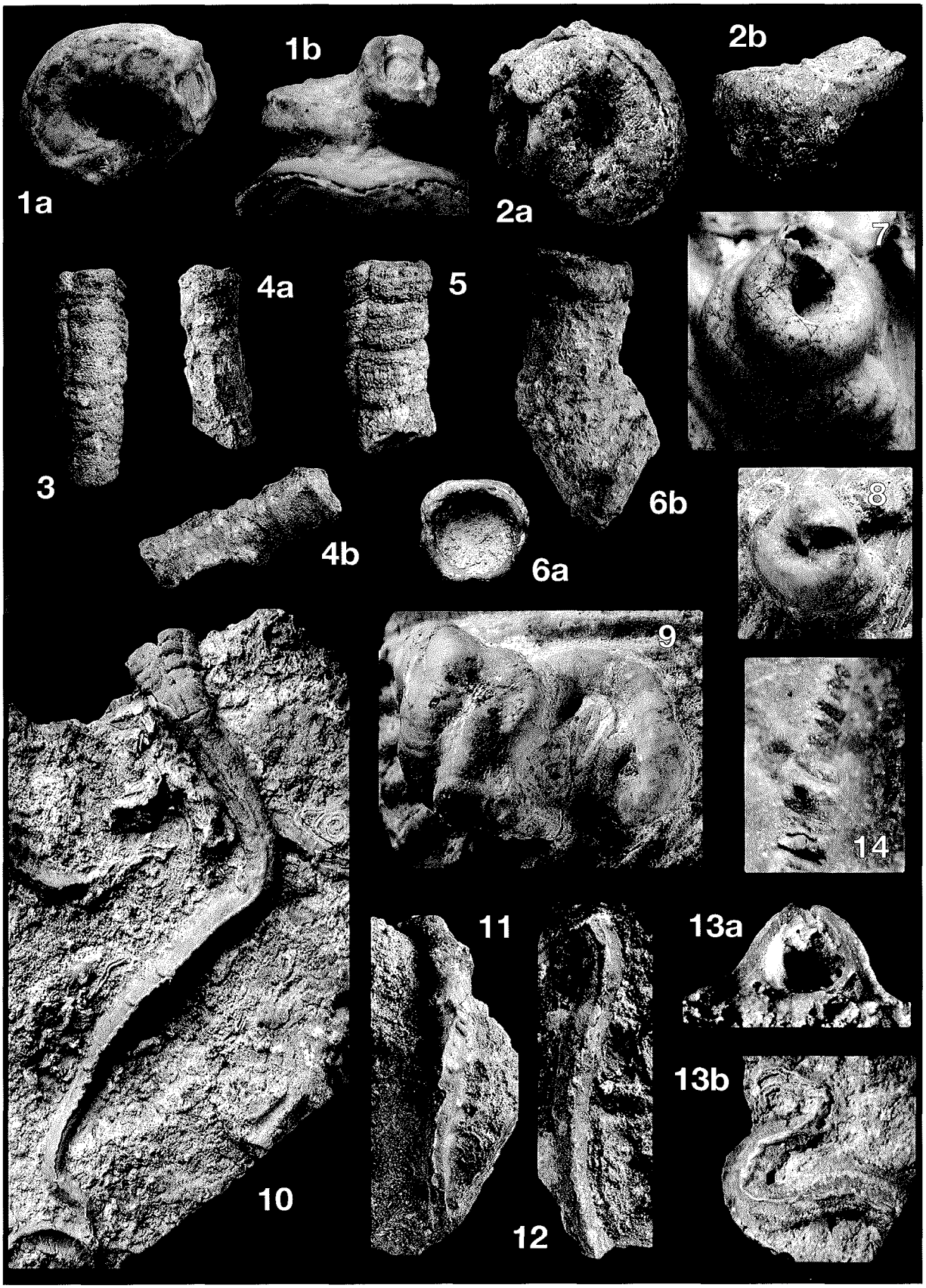
PLATE 5

1-6 – *Parsimonia deshayesi* (MÜNSTER *in* GOLDFUSS, 1831); 1 – POx/W-044: 1a – top view, to show the median keel, 1b – lateral view, to show its attachment to the substrate, × 3; 2 – POx/W-045: 2a – top view, to show the median keel, 2b – lateral view, × 3; 3 – POx/W-046, erect part, to show the longitudinal furrows, × 1.5; 4 – POx/W-047: 4a – top view, to show the median keel, 4b – lateral view, to show the ring-like peristomes, × 1.5; 5 – POx/W-048, erect part, to show the distinct corrugations and longitudinal furrows, × 1.5; 6 – POx/W-049: 6a – apertural part, to show the subquadrangular cross-section, 6b – top view; both × 1.5.

7-9 – ? *Serpula* sp.; 7 – POx/W-050, top view, × 3; 8 – POx/W-051, top view, × 3; 9 – POx/W-052, lateral view, to show the mode of coiling, × 3.

10-14 – *Neovermilia limata* (MÜNSTER *in* GOLDFUSS, 1831); 10 – POx/W-053, top view, to show the ornamentation and peristomes, × 1.5; 11 – POx/W-054, top view, × 1.5; 12 – POx/W-055, top view, × 1.5; 13 – POx/W-056: 13a – apertural view, × 10, 13b – top view, × 3; 14 – POx/W-057, fragment of the basal part, to show the densely spaced cells, × 15.


1a
1b
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13a
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14

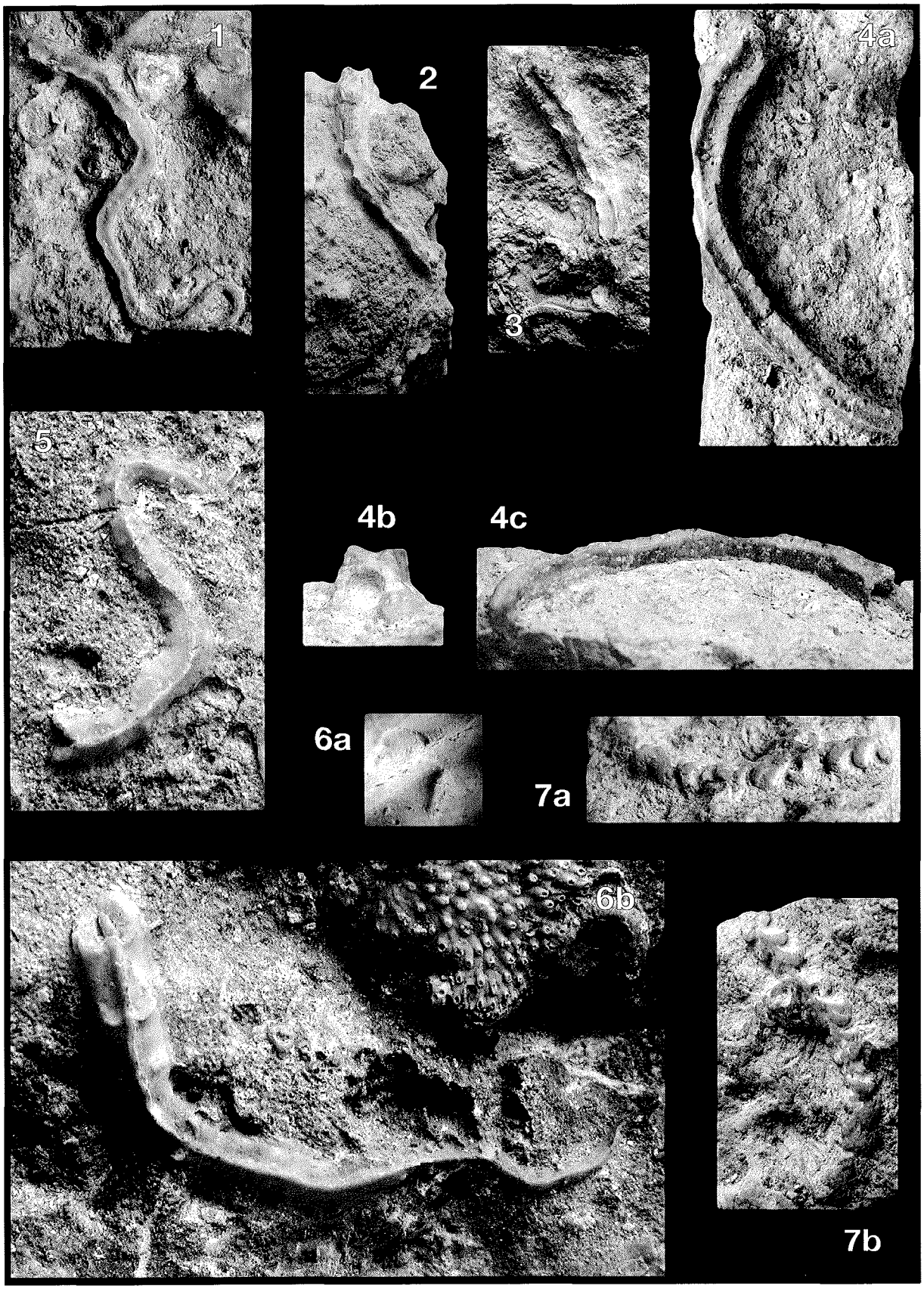
PLATE 6

1-3 – *Ditrupula meandrica* sp.nov.; 1 – POx/W-058, holotype, top view, × 3; 2-3 – paratypes: 2 – POx/W-059, top view, × 3; 3 – POx/W-060, top view, × 3.

4 – *Ditrupula quadrisulcata* (PARSCH, 1956), POx/W-061; 4a – top view, × 3, 4b – apertural view, × 5, 4c – lateral view, × 3; in Figs 4a and 4c the apertures of the commensal hydroid *Protulophila gestroi* ROVERETO, 1901, are visible.

5-6 – *Neovermilia limata* (MÜNSTER *in* GOLDFUSS, 1831); 5 – POx/W-062, top view, juvenile, × 5; 6 – POx/W-063: 6a – fragment of the tube, to show its alate peristome, × 10, 6b – top view, juvenile, × 5.

7 – *Filogranula gibbosa* (GOLDFUSS, 1831), POx/W-064; 7a – lateral view, 7b – top view, both × 5.


1
2
3
4a
5
4b
4c
6a
7a
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7b