

Contribution to the Revision of Some Late Callovian Serpulids (Annelida, Polychaeta) of Central Russia: Part 1

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Abstract—Representatives of the families Serpulidae and Sabellidae from the Upper Callovian of the locality Peski (Moscow Region) are described in accordance with the current state of supraspecific systematics. Species of the genera *Cycloserpula*, *Filogranula*, *Tetraserpula*, and *Metavermilina* are revised. One of the genera, *Cycloserpula*, which was previously assigned to the family Serpulidae, is transferred to the family Sabellidae. A new replacement name, *Metavermilina goldfussi* nom. nov., is proposed for the species that was previously described as *Serpula tricarinata* Goldfuss, 1831.

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INTRODUCTION

Calcareous tubes of polychaete worms of the families Serpulidae and Sabellidae (Annelida, Polychaeta) are common in Mesozoic and Cenozoic deposits; however, their taxonomy, ecology, and stratigraphy have been poorly studied. The reason is the widespread opinion that this group is of minor stratigraphic significance and that it is impossible to develop a natural supraspecific classification that would be based on structural features of tubes and yet consistent with the classification of recent forms, which is based on the soft body structures. The potential of this group for paleoclimatic and paleoecological reconstructions still remains unrealized.

In the Jurassic time this group showed a high degree of speciation as well as taxonomic and ecological radiation; however, the remains of serpulids of this age have not received as much study as those of the Cretaceous and Tertiary. A total of about 100 species have been described from Jurassic deposits (80 as early as the 19th century).

The only review of fossil serpulids of the Jurassic of Central Russia was done by Gerasimov (1955). The classification scheme developed by Parsch (1956) in the mid-20th century remains in common usage (Gerasimov et al., 1996).

A supraspecific classification applied to Mesozoic serpulids that closely matches the classification of recent forms was only developed during the last 40 years based on Upper Cretaceous material (Regenhardt, 1961; Lommerzheim, 1979; Jäger, 1983, 1993), and only Castell (1964) and Radwanska (2004) applied this classification to Jurassic forms.

MATERIAL

The author's collection comes from the Upper Callovian deposits of the locality Peski I (Kolomna district of the Moscow Region), which has been described many times by different authors (Smirnova et al., 1999; Tesakova, 2000; Rogov, 2001), and includes more than 1000 specimens, which have been collected directly from the section of the *Q. lamberti* Zone and in waste piles from the surface of the marl nodules that come from the condensation horizon at the top of the same zone. In addition, material collected by P.A. Gerasimov and E.Yu. Baraboshkin and housed in the Paleontological Institute of the Russian Academy of Sciences has been studied.

SYSTEMATIC PALEONTOLOGY

CLASS POLYCHAETA

Order Sabellida

Family Sabellidae Johnston, 1846

Subfamily Sabellinae Johnston, 1846

Genus *Cycloserpula* Parsch, 1956

Glomerula: Nielsen, 1931, p. 85; Pasternak, 1955, p. 24 (both unavailable according to ICZN 13.3); Regenhardt, 1961, pp. 24–25; Hecker and Ushakov, 1962, p. 452; Howell, 1962, p. W157; Lommerzheim, 1979, pp. 129–130; Jäger, 1983, pp. 24–25.

Serpula (*Cycloserpula*): (pars) Parsch, 1956, p. 213.

Cycloserpula: Jäger, 1993, pp. 74–76.

Omasaria: Regenhardt, 1961, p. 45.

Calcisabella: Perkins, 1991, p. 262.

Type species. *Serpula flaccida* Goldfuss, 1831; Germany, Upper Bajocian.

Diagnosis. Tubes solitary or pseudocolonial. Tubes up to 20 cm long or longer (full length is impossible to determine because of complexity of coiling

forms), as long as several hundred times the maximum diameter of a tube. Tubes highly convoluted and form, along their entire length numerous meanders, kneelike bends, irregular plane spirals and knots of chaotic coiling, occasionally alternating with straight segments. Bends usually characterized by swellings. Cross section circular or subcircular. Sculpture absent. Peristomes absent, uneven lines of breakage quite characteristic. Longitudinal sutures absent.

Species composition. *C. plexus* (Sowerby, 1829) (Europe, worldwide; Upper Jurassic–Upper Campanian, ?Maastrichtian); *C. lombricus* (Defrance, 1827) (Europe, worldwide, India, North America; Middle Aptian–Lutetian); *C. gordialis* (Schlotheim, 1820) (Europe, worldwide; Middle Oxfordian–Hauterivian); *C. intercepta* (Goldfuss, 1831) (Germany; ?Oxfordian); *C. ilium* (Goldfuss, 1831) (Germany; ?Oxfordian, ?Kimmeridgian); *C. vibicata* (Muenster in Goldfuss, 1831) (Germany; Upper Cretaceous); *C. piloseta* (Perkins, 1991) (the Great Barrier Reef; Recent); and the species described below.

Comparison. This genus differs from all known genera of the family Sabellidae in the presence of a calcareous tube (the other genera either have an organic tube or are boring forms).

Remarks. The genus *Cycloserpula* has been traditionally placed in the family Serpulidae (subfamily Filograninae), based on the absence of tube sculpture and sutures, circular section, and the presence of pseudocolonial forms. At the same time representatives of the genus have a tube with a number of characters that clearly distinguish them from representatives of the Serpulidae:

(1) a characteristic coiling of tubes in irregular 3D balls (in all species, except for *C. plexus* and *C. flaccida*);

(2) the presence of lines of transverse breakage, and the absence of peristomes;

(3) the presence of swellings on bends;

(4) a laminar structure of walls (Pasternak, 1955; Jäger, 1983, 1993), and the absence of a “parabolic” layer (Jäger, 1993);

(5) the great length of the tube (as long as several hundred times the maximum diameter); and

(6) no evidence of the rheotropism of the animal.

These features of *Cycloserpula* are characteristic of the modern genus *Calcisabella* Perkins, 1991 from the family Sabellidae, the tubes of which (Perkins, 1991, p. 265, text-figs. 3a, 3b) are almost indistinguishable from the tubes of the Cretaceous *Cycloserpula gordialis*.

Cycloserpula flaccida (Goldfuss, 1831)

Plate 7, figs. 1–6

Serpula deplexa: Phillips, 1829, p. 169, pl. XI, fig. 26.

Serpula flaccida: Goldfuss, 1831, p. 218, pl. LXIX, figs. 7a, 7b; Deshayes in Lamarck, 1838, p. 626; Quenstedt, 1867, p. 321, pl. 24, figs. 19–21; Eichwald, 1868, pp. 269–270, pl. XVIII, fig. 13;

Schmidt, 1969, p. 23; non Quenstedt, 1858, p. 393, pl. 53, fig. 16 [= *Spiraserpula subfilaria* (Eudes-Deslongchamps, 1877)].

Serpula (*Cycloserpula*) *flaccida*: Parsch (pars), 1956, p. 214, pl. 20, fig. 19; non Stoyanova-Vergilova, 1970, pp. 122–123, pl. III, fig. 1 [= *Cycloserpula gordialis* (Schlotheim, 1820)]; non Gerasimov et al., 1996, pl. 6, fig. 17 [= *Cycloserpula gordialis* (Schlotheim, 1820)].

Serpula gordialis: Quenstedt (pars), 1858, pl. 40, fig. 1 non p. 776, pl. 95, fig. 33 [= *Cycloserpula gordialis* (Schlotheim, 1820)]; Dumortier, 1874, pp. 218–219, pl. XLVII, fig. 2.

Lectotype. Paleontological Institute of the University of Bonn, no. 484 A, [designated by Schmidt (1969): specimen, figured by Goldfuss (1831) in pl. LXIX, fig. 7b]; southwestern Germany, Bajocian.

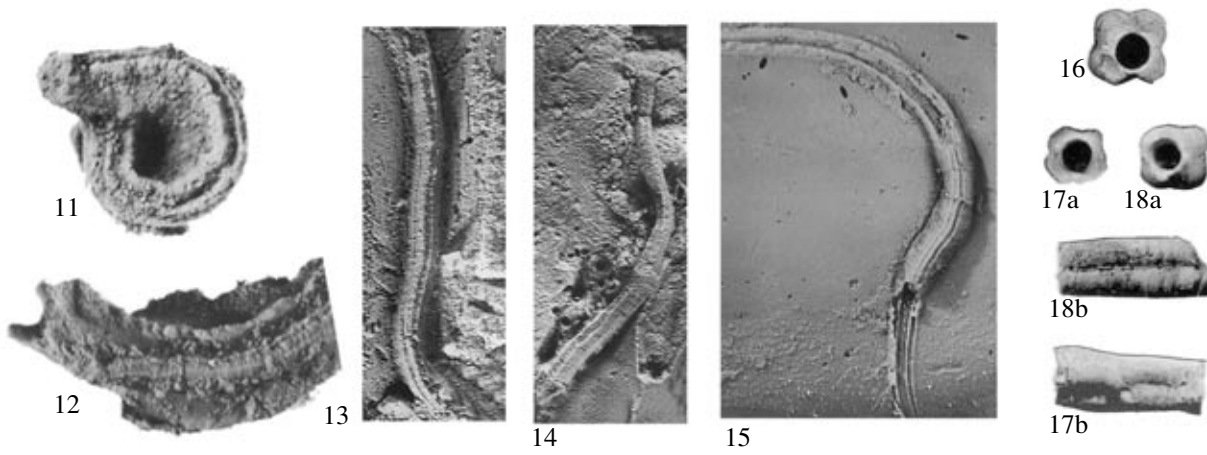
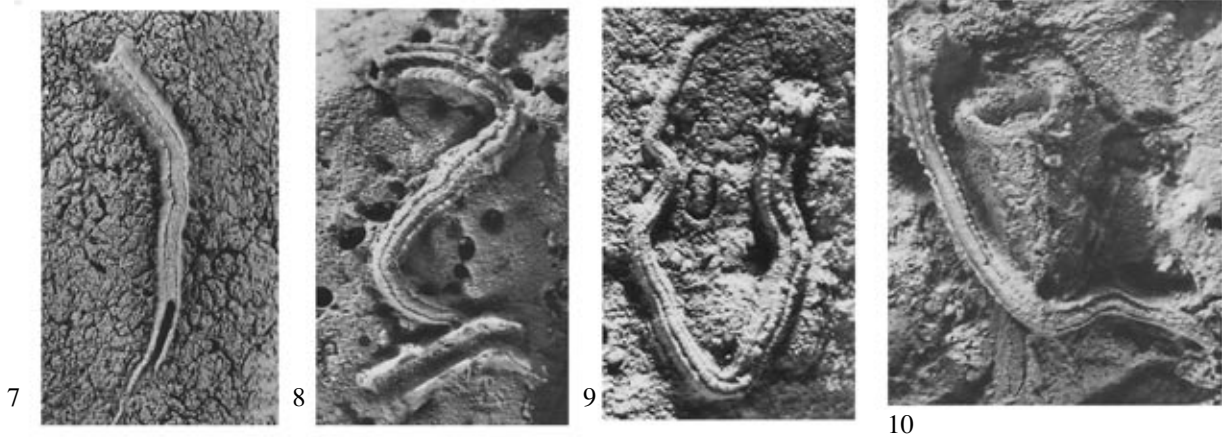
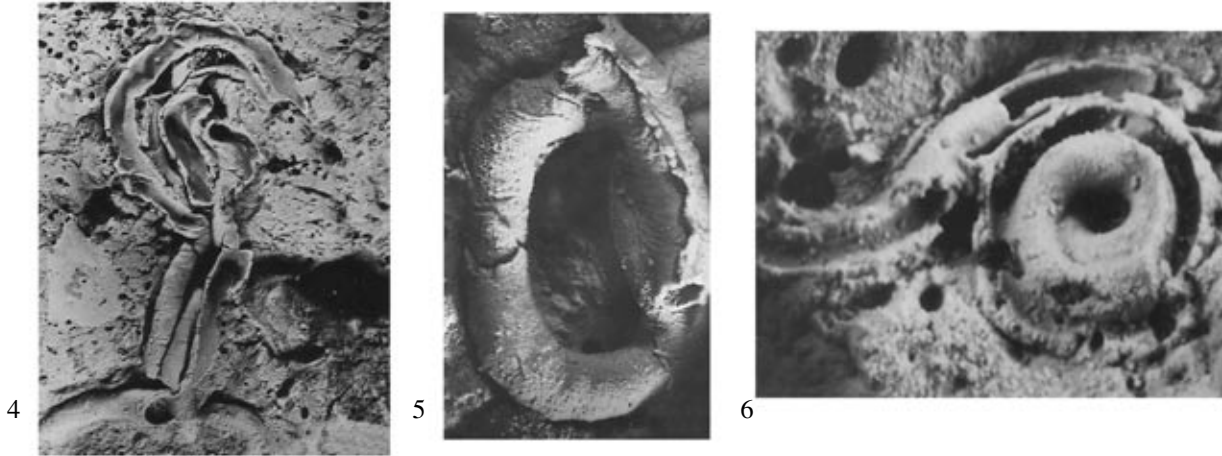
Description. The tubes are solitary, tending to creep in straight lines, with a rounded cross section and slightly flattened lower side. The tubes form long straight segments that are slightly bent with respect to each other, alternating with segments consisting of knots of chaotic coiling with characteristic kneelike bends. During the early growth stages irregular spirals may occasionally appear, the later growth stages are dominated by straight sections separated by a series of bends. There is a tendency for straight sections to duplicate: the subsequent section of the tube runs parallel to the previous section, adjoining its lateral side and following its bends. The surface is smooth, the later growth stages may occasionally show poorly defined straight transverse growth lines. The breakage lines are irregular and are spaced at intervals of 1 cm or more. The internal surface of the tube is smooth. The thickness of walls during the later growth stages is about one-third to one-fifth of the tube diameter (0.6–0.8 mm at a diameter of 2 mm), during the early growth stages this ratio is reduced.

Measurements in mm. Specimen no. 5071/5: tube diameter 2; specimen no. 5071/4: tube diameter 2.7; the full length of both specimens cannot be determined.

Comparison. *C. flaccida* differs from *C. gordialis* in the predominance of long straight sections without meanders and loops and in the more frequent kneelike bends, whereas in *C. gordialis* tubes are gently curved. It differs from *C. lombricus* in the same characters and in the absence of sections with a triangular cross section of the inner cavity; from *C. plexus*, in having solitary tubes; from *C. implicata*, in the absence of a regular alternation of straight sections and sections with chaotic ball-shaped coiling; from *C. ilium* and *C. vibicata*, in the absence of distinct growth lines and sections with chaotic 3D ball-shaped coiling.

Remarks. Jäger (1993) believed *C. flaccida* to be an ecological morph (but gave it subspecific rank) of *C. gordialis*. In his opinion, *C. flaccida* and *C. gordialis* may constitute a continuous phyletic line. However, Parsch (1956) pointed out the joint occurrence of *C. gordialis* and *C. flaccida*; thus, their separation at the rank of subspecies seems to be unjustified, and in this paper they are treated as separate species.

Plate 7



The tubes from the Middle Jurassic of Great Britain identified by Phillips (1829) as *Serpula deplexa* Bean belong to *C. flaccida*, Phillips's identification is incorrect since *S. deplexa* is another (Cenozoic) form (Bronn, 1849).

Occurrence. Bajocian–Callovian–?Tithonian; Germany, Austria, France, Switzerland. On the Russian Platform it occurs in Upper Callovian deposits.

Material. About 20 specimens, 10 of which are almost completely preserved.

Family Serpulidae Rafinesque, 1815

Subfamily Serpulinae Rafinesque, 1815

Genus *Filogranula* Langerhans, 1884

Filogranula: Langerhans, 1884, p. 282; Lommerzheim, 1979, p. 155; Jäger, 1983, pp. 67–68.

Serpentula: Nielsen (pars), 1931, p. 85.

Flucticularia: Regenhardt, 1961, pp. 56–57.

Type species. *Filogranula gracilis* Langerhans, 1884; Atlantic, Recent.

Diagnosis. Tubes of small size, with pentagonal or subangular cross section. In attached posterior part of tube, denticulate or undulate median keel and paired supralateral keels of similar structure usually developed. In free anterior part (and also occasionally in attached part), aperture petaloid, with denticles projecting both forward and away from aperture. Two lower denticles in position corresponding in position to that of inferolateral border (attachment lines) in attached part, upper denticle continues median keel, one or two pairs of lateral denticles represent extension of lateral keels or folds. Differentiated attachment structures absent, tube cemented to substrate by entire lower surface.

Species composition. *F. cincta* (Goldfuss, 1831) (Europe, worldwide; Lower Cretaceous–Upper Maastrichtian); *F. alata* (Nielsen, 1931) (Danian, Lower Danian); *F. tricristata* (Goldfuss, 1831) (Germany; Toarcian); the species described below; and four modern species.

Comparison. This genus differs from the genera *Janita* Saint-Joseph 1896, *Vermiliopsis* Saint-Joseph, 1896, and *Metavermlia* Buch, 1904 in the presence of a well-defined petaloid aperture. It differs from *Cementula*, in addition, in the usually denticulate median keel. It differs from the *Placostegus* with a petaloid aperture in the number of denticles per aperture (five or more instead of three in *Placostegus*), not triangular cross section, and in the nonspiral initial stage.

Remarks. “*Serpula*” *gibbosa* Goldfuss, 1831, which was tentatively assigned by Radwanska (2004) to the genus *Filogranula*, is most probably a member of *Propomatoceros* Ware, 1975 and bears no relation to the genus *Filogranula* (the figure of the type specimen clearly shows tubules at the base of the tube; the development of such structures is impossible within single-layered tubes).

Filogranula runcinata (Sowerby, 1829)

Plate 7, figs. 7–12

Serpula runcinata: Sowerby, 1829, p. 227, pl. DCVIII, fig. 6; Sowerby, 1837, p. 643, pl. 608, figs. 7, 8.

Serpula prolifera: Goldfuss (pars), 1831, pp. 215–216, pl. LXVIII, fig. 11a (non figs. 11b–11e).

Serpula tricarinata: Gerasimov, 1955, pp. 29–30, pl. IX, figs. 1–14.

Serpula tricristata (?) Quenstedt, 1858, pl. 40, fig. 1.

Serpula quinqueangularis: Gallinek, 1895, pp. 405–406, pl. I, fig. 9.

Serpula (Tetraserpula) quinqueangularis: Sazonova and Sazonov, 1967, pl. LII, fig. 2 [only the specimen at the center], pl. LIV, fig. 1.

Serpula (Tetraserpula) tricarinata: Gerasimov et al., 1996, pl. 6, figs. 12–15.

Holotype. Not designated. The specimens of the type series come from the Kimmeridgian of Great Britain.

Description. The tubes are small, gently curved, often rising above the substrate in the anterior part. The passage to the free stage is accompanied by angular folding in the vertical plane. The cross section is pentagonal to rounded-pentagonal (during the early growth stages). In the free part the cross section

Explanation of Plate 7

All specimens come from the Upper Callovian of the locality Peski (Moscow Region) and all (unless otherwise indicated) are attached to concretions from the condensation horizon. The originals are housed in the Paleontological Institute of the Russian Academy of Sciences, coll. no. 5071.

Figs. 1–6. *Cycloserpula flaccida* (Goldfuss, 1831): (1) specimen no. 5071/1, showing a small tube of *Filogranula runcinata* (Sowerby, 1829) (top right), $\times 1$; (2) specimen no. 5071/2, $\times 1.3$; (3) specimen no. 5071/3, $\times 1.2$; (4) specimen no. 5071/4, partly broken tube, $\times 2$; (5) specimen no. 5071/5, showing characteristic lines of the breakage and an attached tube of *Propomatoceros lumbricalis* (Schlotheim, 1820) at the top, $\times 5$; and (6) specimen no. 5071/6, juvenile, $\times 12$.

Figs. 7–12. *Filogranula runcinata* (Sowerby, 1829): (7) specimen no. 5071/7, on the rostrum of a belemnite, $\times 2.9$; (8) specimen no. 5071/8, $\times 4.8$; (9) specimen no. 5071/9, juvenile, $\times 8$; (10) specimen no. 5071/10, $\times 6$; (11) specimen no. 5071/11, spiral specimen attached to an oolite, $\times 10$; and (12) specimen no. 5071/12, showing a large tube with clearly visible lower denticles of a petaloid aperture and partly broken upper denticles, $\times 9$.

Figs. 13–15. *Metavermlia (?) goldfussi* nom. nov.: (13) specimen no. 5071/13, on the rostrum of a belemnite, $\times 4.5$; (14) specimen no. 5071/14, $\times 2.5$; and (15) specimen no. 5071/15, on the rostrum of a belemnite, hollow tubules and a peristome are clearly visible, $\times 3$.

Figs. 16–18. *Tetraserpula tetragona* (Sowerby, 1829), $\times 4.5$; (16) specimen no. 5071/30, apertural view; (17) specimen no. 5071/31, (17a) apertural view, (17b) lateral view clearly showing a lateral constriction; and (18) specimen no. 5071/32, (18a) apertural view, (18b) lateral view.

becomes regular pentagonal. The supralateral folds have well-defined keels, which are regular denticulate or slightly undulate during the early stages and irregular denticulate to nodular in the later stages. The median keel is similar to the lateral keels in structure but is less well-defined and may be absent in the middle part of the tube. The long axes of the denticles in all keels are arranged in centrifugal pattern. The wall of the tube does not break or become noticeably thinner on the lower side. The rising tubes have an aperture with five long well-defined denticles (petaloid aperture). Peristomes are quite uncommon, shaped like thickenings of the tube with well-developed denticles. The sutures are visible on the lateral faces, during the free stage they are also present on the lower face. The tube is single layered, the thickness of the wall is one-third to one-quarter of the tube diameter.

Measurements in mm. Specimen no. 5071/7: aperture diameter 1.8, estimated length 22.5; specimen no. 5071/9: aperture diameter 0.7, length 13.7.

Comparison. This species differs from *F. alata* in the denticulate median keel and separate supralateral and inferolateral denticles; from *F.(?) tricristata*, in the almost parallel walls, infrequent peristomes in the attached part of the tube, and in the slowly increasing diameter. It differs from the Cretaceous *F. cincta* in the infrequent peristomes during the sessile stage and in the absence of regular ornamentation in the free stage. It differs from the tubes of modern species in the irregularly denticulate keels.

Remarks. Evidence that the tubes of this species are single-layered supports its placement in the genus *Filogramula* (Sanfilippo, 1998).

The specimens from the Jurassic of the Moscow Region that were previously identified by Gerasimov (1955) as *Serpula tricarinata* Sowerby, 1826 are assigned to this species. However, the figures show that Sowerby's *S. tricarinata* is considerably larger than Goldfuss's species of the same name and has keels with weak denticles, the most developed of which is the median. One of the specimens of *S. tricarinata* (Sowerby, 1829, pl. DCVIII, fig. 3) has a pentagonal tube wound like a loop with nondenticulate keels and a rounded cross section during the free stage. In our opinion, Sowerby's material belongs to the genus *Mucroserpula* Regenhardt, 1961. In 1996 Gerasimov identified the same specimens as "*Serpula tricarinata* Goldfuss, 1833–1840." Goldfuss's specimens of *S. tricarinata* differ sharply both from Gerasimov's material and from *F. runcinata* (Sowerby, 1829) in the smooth keels. "*Serpula tricarinata*" Sowerby, 1829 and "*S. tricarinata*" Goldfuss, 1831 are primary homonyms.

One of Goldfuss's specimens assigned to the species *Serpula prolifera* (Goldfuss, 1831, pl. LXVIII, fig. 11a non figs. b–d) differs sharply from the others and may belong to *F. runcinata*.

Occurrence. Lower Callovian–Middle Oxfordian; European Russia, Great Britain, Poland, ?Germany.

Material. About 30 specimens.

Genus *Metavermia* Buch, 1904

Metavermia: Buch, 1904; Lommerzheim, 1979, p. 158; Jäger, 1993, p. 94.

Type species. *Vermilia multicristata* Philippi, 1844; Mediterranean Sea; Recent.

Diagnosis. Tubes solitary, of small and medium size, usually considerable in length, increasing in diameter uniformly and slowly or with distinct growth retardation after reaching one-third to one-half of full length. Cross section rounded or, more frequently, rounded polygonal, well-developed longitudinal ornamentation usually represented by three to seven longitudinal keels, occasionally quite complex in structure. Transverse growth lines well-defined. Peristomes uncommon or completely absent. Attachment area with wide basal margins usually well developed.

Species composition. Twelve modern species (Zhirkov and Kuprijanova, 2001). The fossil species, except for *M. goldfussi* Ippolitov, nom. nov. (see below), have been incompletely defined; i.e., without species names. This genus may include the Jurassic species described as *Serpula triangulata* Sowerby, 1829 etc.

Occurrence. ?Jurassic–Recent. All fossil forms are questionable, distributed in Europe; at present the genus is cosmopolitan.

Comparison. This genus differs from *Pseudo-vermia* Buch, 1904 in the transverse ornamentation being usually absent and the cross section of the tube being frequently triangular. It differs from *Vermiliopsis* Saint-Joseph, 1896 in the slowly expanding tube and in the absence of apertural flares. It differs from *Janita* Saint-Joseph, 1896 in the keels devoid of nodes.

Metavermia (?) *goldfussi* Ippolitov, nom. nov.

Plate 7, figs. 13–15

Serpula tricarinata: Goldfuss, 1831, p. 230, pl. LXVIII, fig. 6; Quenstedt, 1867, p. 321, pl. 24, fig. 10; non Sowerby, 1829 [primary senior homonym]; non Deshayes in Lamarck, 1838, pp. 629–630.

Serpula (Tetraserpula) quadrilatera: (pars) Parsch, 1956, pl. 19, fig. 11b (non pl. 19, fig. 11a; pl. 21, fig. 13).

Serpula (Tetraserpula) tricarinata: (pars) Parsch, 1956, p. 224, pl. 21, fig. 21 (non pl. 19, fig. 12).

Etymology. In honor of A. Goldfuss.

Lectotype. The current depository is unknown. The specimen figured by Goldfuss (1831, pl. LXVIII, fig. 6) is designated here. Germany, Middle Jurassic.

Description. The tube is attached to the substrate along its entire length, its diameter first relatively rapidly increases over a length of 15 mm and then remains nearly constant. The cross section is pentagonal with the widest part on the lower side; the median

fold has a costa and only slightly rises above the lateral folds. Three smooth straight costae run along the entire length of the upper side: the median costa and a pair of supralateral costae that are less developed and coincide with the folds. The peristomes (not necessarily present) are irregular and have the form of thin transversely straight ring-shaped thickenings. The growth lines are regular and well-defined on all faces of the tube. The attachment to the substrate is achieved by using irregularly alveolar or hollow tubules.

Measurements in mm. Specimen no. 5071/14: aperture diameter 1.5, estimated length 28–35; specimen no. 5071/13: aperture diameter 0.7, estimated length 16.

Comparison. This species differs from *M. (?) pentagona* (Goldfuss, 1831), which presumably belongs to this genus, in the absence of a denticle on the aperture and additional keels on either side of the median keel.

Remarks. Goldfuss's name (1831) is a junior homonym of *Serpula tricarinata* Sowerby, 1829, despite the fact that Sowerby's species and Goldfuss's species may at present be placed in different genera (*Mucroserpula* and *Metavermilia*, respectively). The species described here was first placed in the genus *Metavermilia* by Radwanska (2004); however, her own material from the Upper Oxfordian of Poland does not belong to "*Serpula tricarinata* Goldfuss, 1831 or even to *Metavermilia* at all. The specimens described have a massive base and undulate poorly defined keels and are apparently close to *Filogranula runcinata*.

Parsch (1956, pl. 19) reproduced Goldfuss's illustrations and confused figs. 11b and 12; thus, the species in fig. 11b is erroneously referred to as *S. (Tetraserpula) quadrilatera* Goldfuss, and that in fig. 12, *S. (T.) tricarinata* Goldfuss.

Metavermilia (?) goldfussi and *Filogranula runcinata* show a convergent resemblance in ornamentation and may occur in the same localities; however, the former differs from the latter in the thinner tube and tubular structures, tube wall that can break on the lower side, and in the less developed median fold.

Occurrence. Middle–Upper Jurassic, Germany, Russian Platform.

Material. About eight specimens.

Genus *Tetraserpula* Parsch, 1956

Tetralysis (?) Eudes-Deslongchamps, 1877, pp. 13–14.

Ditrupula: (pars) Nielsen, 1931, p. 85; (pars) Pasternak, 1955, p. 24 (both are unavailable according to ICZN Art. 13.3); Howell, 1962, p. W156; (pars) Hecker and Ushakov, 1962, p. 452; Lommerzheim, 1979, p. 147.

Serpula (Tetraserpula): (pars) Parsch, 1956, p. 223.

Ditrupa (Tetraditrupa): Regenhardt, 1961, p. 73.

Tetraserpula: Jäger, 1983, pp. 58–59.

Type species. *Serpula tetragona* J.D.C. Sowerby, 1829; Great Britain, Upper Jurassic (?Kimmeridgian).

Diagnosis. Tubes usually unattached or, occasionally, attached during very early stages; almost straight or irregularly curved, tusk- or occasionally fishhook-shaped. Tubes of largest species attain 4–5 mm in diameter and full length of more than 5 cm full. Cross section quadrangular, quadrate, usually with concave or, more rarely, flat lateral sides. No swellings on faces. Lateral sides bear sutures, but not necessarily well-defined.

Species composition. *T. trochleata* (Muenster in Goldfuss, 1831) (Germany, Upper Jurassic); *T. corticea* (Regenhardt, 1961) (Germany, Upper Valanginian), *T. canteriata* (Hagenov, 1840) (Europe, Maastriichtian), *T. dollfussi* (Loriol, 1873) (France, Tithonian), *T. superiora* Jäger, 1983 (northern Germany, Upper Maastriichtian), *T. quadrisulcata* Parsch, 1956 (Europe, worldwide; Toarcian–Upper Jurassic–?Lower Cretaceous), *T. quadricristata* Parsch, 1956 (Germany; Toarcian–Callovian), and the species described below.

Comparison. This genus differs from the genera *Ditrupa* Berkeley, 1835 (? = *Sinoditrupa* Yu et Wang, 1981), *Triditrupa* Regenhardt, 1961, and *Pentaditrupa* Regenhardt, 1961 in the quadrangular cross section of the tube. It differs from some members of the genus *Genicularia* Quenstedt, 1858 with a quadrangular tube in the absence of typical regular rounded swellings on the faces.

Remarks. The name *Ditrupula*, which was published earlier and used by Nielsen (1931) and Pasternak (1955), is not available for lack of type species fixation (International Code of Zoological Nomenclature, 4th ed., 1999, Art. 13.3).

There is a marked evolutionary trend in this genus from the Early–Middle Jurassic attached, irregularly curved forms to the Upper Jurassic–Cretaceous unattached, gently curved forms.

The genus *Tetraserpula* resembles in appearance the genus *Tetralysis* Eudes-Deslongchamps, 1877 with a single species, *T. quadratus* Eudes-Deslongchamps; however, the latter has a quadrangular cross section of the inner cavity of the tube, unknown in other serpulids, which always have a round cavity.

The modern genus *Bathyditrupa* Kuprijanova, 1993 with a single species, *B. hovei* (Kuprijanova, 1993), resembles *Tetraserpula* in the morphology of the tube. The lack of data on the microstructure of tubes prevents us from synonymizing the genera *Bathyditrupa* and *Tetraserpula* and considering *B. hovei* a "living fossil."

Tetraserpula tetragona (Sowerby, 1829)

Plate 7, figs. 16–18

Serpula tetragona: Sowerby, 1829, p. 203, pl. DXCIX, figs. 1, 2; 1837, p. 631, pl. 599, figs. 1, 2; Deshayes in Lamarck, 1838, p. 623; Quenstedt, 1858, p. 393, pl. 53, figs. 17–19; (pars) 1867, p. 321, pl. 24, fig. 12 (non fig. 13); Eichwald, 1868, p. 278; (pars?) Gerasimov, 1955, p. 29, pl. XI, figs. 1, 2, 4, 5, 3?; Oschmann, 1994, figs. 41, 42, pl. 15, figs. 1–3; non Roemer, 1839, p. 19, pl. XX, fig. 17 [primary homonym]; non Makowski, 1952, p. 3, pl. 2, fig. 1 [= *Tetraserpula* sp. nov.].

Serpula (Tetraserpula) tetragona: Parsch, 1956, p. 223, pl. 21, fig. 14; 1961, p. 6, pl. 1, fig. 6; Gerasimov et al., 1995, pl. 5, figs. 1–3; Gerasimov et al., 1996, pl. 6, fig. 16.

Serpula quadrilatera: Eudes-Deslongchamps, 1877, pl. II, figs. 18–21.

Holotype. Not designated. Type series comes from the Kimmeridgian deposits of Great Britain.

Description. The tubes are unattached, with concave lateral sides, slightly and gently curved or straight, frequently with sharp bends forming small angles and slight constrictions at the bends. The tube is frequently curved like a hook or may be irregularly curved, occasionally it is shaped like two or three successive flares, with the diameter of the tube reduced by a factor of 1.5 at the junctions. Within the flares coiling around the longitudinal axis may be possible. The tube diameter grows rapidly during the early stages, then the rate of growth decreases, and the diameter increases only slightly (if at all). The surface is smooth in the posterior part and slightly rugose in the anterior part. The apertural margin has lateral faces that are beveled posteriorly. The tube is two-layered, its wall varies in thickness from one-sixth of the diameter on the faces to one-third of the diameter at the rounded corners.

Measurements in mm. Specimen no. 5071/99: aperture diameter 1.7, length is indeterminable, exceeding 7.

Comparison. This species differs from all known species of the genus in the tube shaped like flares in combination with a rounded-square cross section, walls that gradually flatten in ontogeny, and in the presence of transverse plicae.

Remarks. Variability in the tubes of this species is largely observed in the variations in their shape and coiling and in the concavity of the walls during the later growth stages. Gerasimov's collection contains specimens of this species from various localities, each of which shows its own array of the ranges of variability in the characters, suggesting that the ecological variability of this species is extremely high.

The specimens included into the hypodigm may be divided into two groups. The first group includes the specimens figured by Sowerby (1829, pl. DXCIX, fig. 1) and Oschmann's specimens (Oschmann, 1994). They are characterized by their tube walls being strongly concave along their entire length and by the absence of constrictions. The second group consists of tubes curved like a hook (Gerasimov, 1955, pl. XI, fig. 4; Quenstedt, 1867, pl. 24, fig. 12), in which the concavity of walls gradually decreases in ontogeny to reach a circular cross section at the anterior end. The lack of material and data on ecological variability prevents separation of these groups at the rank of species with certainty.

Occurrence. Middle Jurassic (?Upper Bathonian, Callovian)–Upper Jurassic (Lower Volgian) (outside the Russian Plate up to the Upper Kimmeridgian), Europe. Widespread in the boreal realm.

Material. About ten specimens.

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