

Serpulid tubeworms (Annelida, Polychaeta) and a vermetid gastropod from the Late Oligocene of Denmark

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The serpulid palaeocommunity of the Late Oligocene Brejning Formation in Jylland (Jutland) is described and discussed based on specimens collected at Vilsund, Mogenstrup, Hinge, Aarhus, and Nørre Vissing localities. The serpulid species are: *Protula* cf. *septaria* (Giebel, 1858), *Filogranula mogenstrupensis* sp. nov., *Placostegus vilsundensis* sp. nov., *Placostegus* cf. *erectus* (Nielsen, 1931), and *Placostegus* cf. *bilobatus* (von Koenen, 1891). The semi-ordered irregularly oriented prismatic microstructure (SOIOP) of the tube wall of *Protula* cf. *septaria* (Giebel, 1858) is examined and discussed for the first time. These serpulids lived in a calm, normal marine palaeoenvironment below storm wave base. Furthermore, the first known vermetid gastropod from the Late Oligocene of Jylland, *Vermetus jyllandensis* sp. nov., is introduced, and its shell microstructure is discussed.

Keywords: Serpulidae, Vermetidae, Brejning Formation, Upper Oligocene, Jutland, Denmark, skeletal microstructure

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Serpulidae Rafinesque, 1815, a species-rich family of the order Sabellida Levinsen, 1883, are tube-dwelling polychaetes living in a self-built calcareous tube for their entire life (Bianchi 1981; ten Hove & Kupriyanova 2009; Kupriyanova *et al.* 2020, 2023; Capa *et al.* 2021). They inhabit all marine environments, from nearshore shallow water down to the bathyal and hadal zones (Zibrowius 1968; Sanfilippo 1998; ten Hove & Kupriyanova 2009; Kupriyanova *et al.* 2011, 2014). A few species, *e.g.*, *Ficopomatus enigmaticus* (Fauvel, 1923), occur in marginal marine hypo- or hypersaline waters or in waters of unstable salinity or temperature. Only a single species, *Marifugia cavatica* Absolon

& Hrabě, 1930, lives in freshwater habitats within karst caves in Slovenia and Croatia (Bosák *et al.* 2004; Kupriyanova *et al.* 2009; ten Hove & Kupriyanova 2009; Lukić *et al.* 2023). Serpulids have existed since the Permian (Sanfilippo *et al.* 2017b, 2018; Ramsdale 2021; Słowiński *et al.* 2024a).

Serpulid tubes consist of calcite, aragonite or a combination of both minerals (Vinn *et al.* 2008; Ippolito *et al.* 2014; Kupriyanova *et al.* 2020; Vinn 2020, 2021). In the vast majority of serpulid species, the tube, or at least its posterior tube portion, is attached to various kinds of hard substrates, such as rock, a pebble, a shell or other hard part of a dead or living

marine organism; such serpulids belong to the ecological group of sclerobionts (Schmidt 1955b; Taylor & Wilson 2002, 2023; Jäger 2005; Vinn *et al.* 2023). Mass-occurrence of attached serpulids may result in serpulid reefs, bioconstructions and pseudocolonies (ten Hove 1979; Schuhmacher & Zibrowius 1985; ten Hove & van den Hurk 1993; Bianchi & Morri 1996, 2000, 2001; Antonioli *et al.* 2001; Sanfilippo *et al.* 2015, 2017a; Rosso *et al.* 2015, 2020; Guido *et al.* 2017; Georgieva *et al.* 2019). The tubes can also be attached to soft and/or slightly flexible substrates, such as large algae or sponges (Catra *et al.* 2019; Rosssbach *et al.* 2021).

Only a few serpulid taxa are free-living, such as the genus *Ditrupa* Berkeley, 1835 (Cosentino & Giacobbe 2006; Morton & Salvador 2009; Hartley 2014), a few species of the genus *Nogrobs* de Montfort, 1808 (Jäger 2005), the genus *Spirodiscus* Fauvel, 1909 (Kupriyanova & Ippolitov 2015; Kupriyanova & Flaxmann 2023), and the species *Serpula crenata* Ehlers, 1908. However, the very first tube portion of recent *Ditrupa arietina* (O. F. Müller, 1776) is „organic, transparent and anchored by a mucous thread (3–4 times longer than the tube length) to numerous (i.e. more than 30) sediment grains” (Charles *et al.* 2003), before forming a free calcareous tube, and it remains unknown whether other species known only from unattached tubes exhibited the same behaviour. In several other free-living serpulid taxa, tube calcification starts somewhat earlier in ontogeny, before detachment of the anterior, animal-bearing tube portion. Therefore, under favourable conditions, small fragments of the attached tube portion remain preserved at the posterior end of the large anterior tube, for example, in some Eocene tubes of the genus *Rotularia* Defrance, 1827 or, very rarely, in Maastrichtian tubes of *Nogrobs* (*Tetraditrupa*) *canteriata* (von Hagenow, 1840).

Although Cenozoic serpulids have been reported from many parts of the world, detailed publications dealing with Oligocene serpulids are less common than those dealing with Eocene or Miocene serpulids. This may partly reflect the relatively short duration of the Oligocene in absolute geological time, though climate and sediment types also played a considerable role, as discussed in more detail below.

Spirally coiled serpulid tubes such as those occurring, for example, in the genera *Protula* Risso, 1826, *Serpula* Linnaeus, 1758 and *Rotularia* Defrance, 1827, have frequently been confused with shells of vermetid gastropods, *e.g.*, by von Koenen (1891), and vice versa. In principle, clear diagnostic features allow for reliable distinguishing between serpulid tubes and vermetid shells (*e.g.*, Schmidt 1951, 1955b; ten Hove & van den Hurk 1993). Despite all these distinguishing features, in practice, such determination may remain difficult in poorly preserved fossil material, in spite of the comprehensive and scientifically

valuable monograph by Bieler & Petit (2011), which, however, still leaves some open questions.

Geological setting

The Danish land area is situated in the eastern part of the Cenozoic North Sea Basin (*e.g.*, Knox *et al.* 2010). Oligocene sediments from Denmark crop out in cliffs and claypits in rather limited areas of Jutland (Fig. 1), but it can be assumed that they originally had a much wider distribution to the east, where they have been removed as a result of Late Oligocene and Quaternary erosion. To the west, the Oligocene sediments are covered by younger deposits and continue under the North Sea. Recent stratigraphic overviews of the Oligocene in Denmark are given in Ulleberg (1987), Rasmussen & Dybkjær (2005), Rasmussen *et al.* (2010) and Śliwińska *et al.* (2012, 2014).

In the Limfjorden area, Oligocene sediments have been found at several localities (Figs 1, 2). Ravn (1907) recognized the Branden Clay, which he considered to be middle Oligocene, at Branden, Lambjerg and Gjørup. The clay at the localities Norden-toft, Silstrup, Agger in Thy and Sundby on Mors was considered to be Upper Oligocene. The Branden Clay is now referred to the lower Upper Oligocene (Schnetler & Palm 2008; Śliwińska *et al.* 2012), and Agger (Lodbjerg) to the Lower Miocene (Rasmussen

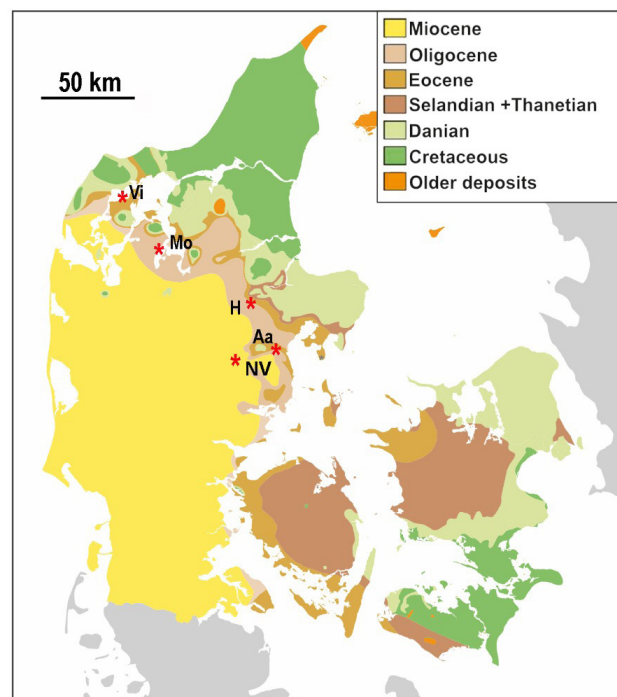


Fig. 1. Map of the pre-Quaternary subsurface in Denmark. The red asterisks indicate five Late Oligocene localities: **Vi:** Vilsund, **Mo:** Mogenstrup, **H:** Hinge, **Aa:** Aarhus, **NV:** Nørre Vissing.

et al. 2010). The non-glaucanitic Skive Clay occurs at Hesselbjerg near Skive and is considered to be a facies of the Branden Clay (Heilmann-Clausen 2006; Śliwińska *et al.* 2012).

Ravn (1909) described the claypit of Vilsund Brickworks on the island of Mors, where two different sedimentary facies were exposed: black micaceous clay with numerous spherical calcitic concretions that contain crab fossils, and greenish glauconitic clay with sideritic concretions. Based on the molluscs, Ravn (1909) considered both facies to be of Late Oligocene age. Schnetler & Beyer (1990) studied the coastal cliff at Mogenstrup, north of Skive, and recorded 197 mollusc species in the same greenish glauconitic clay with sideritic concretions. They assigned this clay to the Brejning Clay Member of the Vejle Fjord Formation (now the Brejning Formation) of Late Oligocene (Chattian B) age, based on molluscs and foraminifer zonation (*pers. comm.* Ulleberg 1987). Schnetler & Palm (2008) assigned greenish glauconitic clay in the claypit of the former Vilsund Brickworks to the Branden Clay. The greenish glauconitic clay at Mogenstrup is either Unit X or the lowermost Brejning Formation (Fig. 2), and the glauconitic clay in the former claypit of Vilsund Brickworks is probably of the same age.

At Nørre Vissing, the Brejning Formation overlies the Søvind Marl Formation (Schnetler & Beyer 1987). At Aarhus (Harder 1913) and at Hinge (unpublished), the Brejning Formation overlies the Lower Oligocene Viborg Formation.

Vilsund

The locality is a low coastal cliff on the western coast of Mors. The cliff exposes outcrops of the Viborg Formation, the Branden Clay and the Brejning Formation. Fish otoliths have been collected from a part of the low coastal cliff at locality 4 of the section studied and described by Schnetler *et al.* (2024). The pectinids *Palliolium venosum* (Speyer, 1864) and *Hilberia bifida* (Münster, 1835 in Goldfuss, 1826–1844) suggest an assignment to the Chattian A, whereas the dinocysts indicate zone DO7b and an assignment to either Unit X (Śliwińska 2012) or the Brejning Formation.

Mogenstrup

The fossils were collected from a coastal cliff, more than 1.5 km long, situated north of Skive. The Brejning Formation is exposed there, but the chances of finding fossils vary considerably, because landslides may completely cover the fossil-bearing layers. In the northern part of the outcrop, there are crab nodules in a type of clay very similar to the clay from Lyby Strand, whereas gastropods, bivalves and scaphopods can be found in both parts of the cliff. The rich mollusc fauna was described by Schnetler & Beyer (1990). In addition to molluscs, fossils of other

animal groups have been found, *e.g.*, brachiopods, shark teeth, serpulids, corals, bryozoans, marginal plates of starfish, and otoliths of bony fish. The fossils described in the present article come from a rarely exposed glauconitic clay, which is a centimeter-thick layer associated with three horizons of siderite.

Hinge (near Randers)

The large claypit near Hinge exposes Eocene and Oligocene strata, and until 2025, the Brejning Formation had not been recognized. Large samples of this formation have resulted in much material, especially molluscs, but also otoliths have been found. The limited material of fragments of *Palliolium hausmanni* (Goldfuss, 1835 in 1826–1844) suggests a Chattian B age. A description of the locality was given by Larsen & Kronborg (1994).

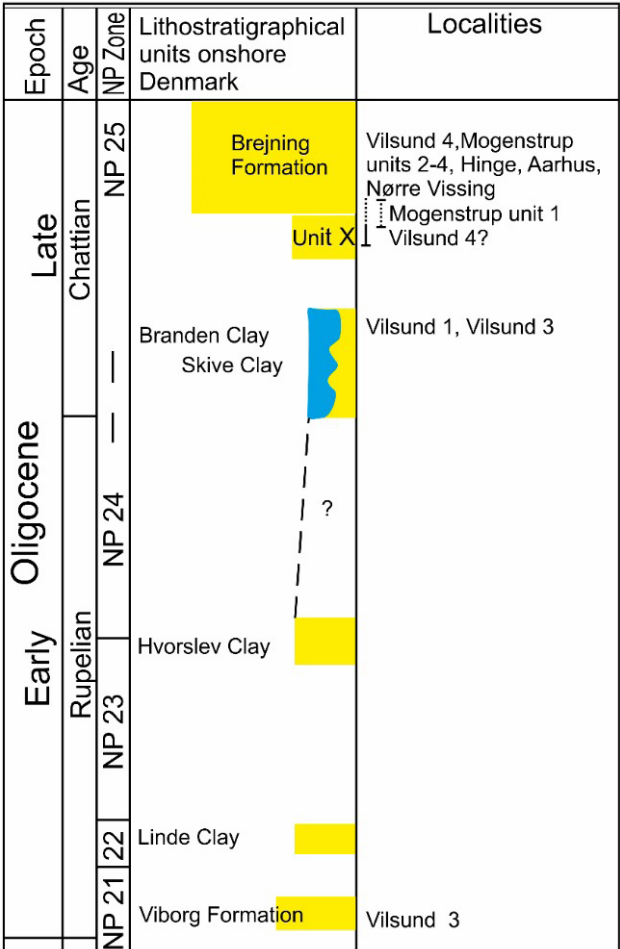


Fig. 2. Stratigraphical column of the Upper Oligocene deposits in NW Jylland. The stratigraphical positions of the five localities are indicated. Vilsund 1–3 are coastal outcrops, Vilsund 4 corresponds to the former Vilsund Brickworks. Modified and simplified after Schnetler *et al.* (2024).

Aarhus

The outcrop for the railway west of Aarhus is the classical locality of the Danish Oligocene. Material has been collected since 1860, and Harder (1913) published his results in a fundamental study. The pectinids *Palliolium hausmanni* and *Palliolium limatum ambignum* (H.-J. Anderson, 1958) suggest a Chattian B age. A single fragment of *Hilberia bifida* was found in the Harder collection by Kai Ingemann Schnetler (KIS). The presence of the pteropod *Ireneia tenuistriata* (Semper, 1861) suggests pteropod zone 16b, equivalent to upper Chattian A.

Nørre Vissing

The locality is a former claypit north of the village of Nørre Vissing. The clay was excavated until 1989 by the now-demolished Galten Brickworks. Now the claypit is totally overgrown. The Søvind Marl at the base is separated from the overlying Brejning Formation by an unconformity. The lower part of the Brejning Formation consists of greenish glauconitic clay with many fossils and phosphorites. The pectinids are represented by *Palliolium hausmanni* (most common), *Palliolium venosum*, *Parvamussium pygmaeum* (Münster, 1835 in Goldfuss, 1826–1844) and *Pseudoentolium corneum* (J. Sowerby, 1818 in 1818–1822). *Palliolium hausmanni* indicates the Chattian age. The specimen of *Aporrhais bicarinata* Koch & Boll in Koch, 1861, encrusted by the serpulid *Protula* cf. *septaria* (Giebel, 1858) (Fig. 5A), was found *in situ* c. 1.5 meters above the Søvind Marl. The locality and its molluscan fauna were described by Schnetler & Beyer (1987).

Material and methods

Vilsund

The vermetid *Vermetus jyllandensis* sp. nov. and parts of the material of the serpulid genera *Protula*, *Filigranula* and *Placostegus* (Table 1) were collected in 2022–2023 from the Vilsund 2 outcrop. The main part of the collected material was obtained by washing and sieving of 900 kg of glauconitic clay from Unit X using 2.0 mm and 0.5 mm meshes, and the residue was sorted out under a binocular microscope (10 × magnification).

Mogenstrup

Other parts of the material of the serpulid genera *Protula*, *Filigranula* and *Placostegus* (Table 1) were collected in 1987 and 1988 from the Mogenstrup cliff. The main part of the collected material was obtained by washing and sieving of several hundred kilograms of the aforementioned glauconitic clay using a 0.5 mm mesh, and the residue was sorted out under a binocular microscope (10 × magnification).

Hinge

In the claypit containing sediments ranging from Eocene to Oligocene, a profile with the Late Oligocene Brejning Formation was found in the spring of 2025. Since then, hundreds of kilograms have been washed and sieved by Kent Albin Nielsen (KAN), but only three serpulid tubes of *Placostegus* cf. *septaria* were found (Table 1).

Aarhus

Harder (1913) studied material collected by him in 1906, as well as material collected in 1860 by Kristian Erslev. His fundamental study of the Danish Oligocene gave no information on the processing of the material, so we may assume that his material was collected by hand picking.

Nørre Vissing

Fossils were collected between 1978 and 1990. Larger fossils were collected by hand picking, but several hundred kilograms of clay from the Brejning Formation were processed to collect small fossils. The specimen of *Aporrhais bicoronata* encrusted by the serpulid (Fig. 5A) was found *in situ*, c. 1.5 m above the Søvind Marl.

Material was photographed under a light binocular microscope Olympus SZX12. SEM images were taken using a Scanning Electron Microscope Hitachi S-3700 N. All figures of tubes were prepared using CorelDRAW 2018, and a few of them were improved using Adobe Photoshop CS6. The tube fragments of *Protula* cf. *septaria* shown in Figs 8–11 were cut, polished by means of 320, 400, 600, 800, 1000, 1500, 2000 carborundum, plus Microlite, and treated with 1% acetic acid for c. 3 minutes.

All holotypes and paratypes figured in the present article are kept in the collection of the Museum Mors, The Fossil and Mo-clay Museum (FMM).

Systematic palaeontology

Phylum Mollusca J. Jonstonus, 1650 (pre-Linnaean)

Class Gastropoda Cuvier, 1795

Subclass Caenogastropoda L.R. Cox, 1960

Order Littorinimorpha A.N. Golikov & Starobogatov, 1975

Superfamily Vermetoidea Rafinesque, 1815

Family Vermetidae Rafinesque, 1815

Table 1. List of the examined vermetid and serpulid species from the Late Oligocene Brejning Formation in Jylland (Jutland)

Species	Inventory number	Locality	Numbers	Figures	Collector
<i>Vermetus jyllandensis</i> sp. nov.	Holotype FMM 14951a Paratype FMM 14951b	Vilsund	2 shells	Figs 3A-B, 4A	HM
<i>Protula</i> cf. <i>septaria</i> (Giebel, 1858)	FMM 14949	Vilsund	7 tubes, 3 steinkerns with tube fragments	Fig. 6A-G	HM
<i>Protula</i> cf. <i>septaria</i> (Giebel, 1858)	KIS 1987.363	Mogenstrup	1 spiral tube	Fig. 5B	KIS
<i>Protula</i> cf. <i>septaria</i> (Giebel, 1858)	KIS 1987.363	Mogenstrup	8 tubes, 1 steinkern with tube fragments, 3 fragments	not figured	KIS
<i>Protula</i> cf. <i>septaria</i> (Giebel, 1858)	KIS 1988.589	Mogenstrup	7 tubes	Figs 7A-G, 8A-C, 9A-B, 10A-B, 11A-B	KIS
<i>Protula</i> cf. <i>septaria</i> (Giebel, 1858)	KIS 1988.589	Mogenstrup	5 tubes, 1 fragment	not figured	KIS
<i>Protula</i> cf. <i>septaria</i> (Giebel, 1858)	KIS 1988.325, 15L	Mogenstrup	2 tubes	not figured	KIS
<i>Protula</i> cf. <i>septaria</i> (Giebel, 1858)	KIS 1988.317	Mogenstrup	4 tubes, 2 steinkerns with tube fragments	not figured	KIS
<i>Protula</i> cf. <i>septaria</i> (Giebel, 1858)	KAN 2025	Hinge	3 tubes	not figured	KAN
<i>Protula</i> cf. <i>septaria</i> (Giebel, 1858)	KIS 1985	Nørre Vissing	2 tubes attached to an <i>Aporrhais bicarinata</i> Koch & Boll in Koch, 1861	Fig. 5A	KIS
<i>Filogranula mogenstrupensis</i> sp. nov.	Paratype FMM 14952	Vilsund	1 tube	Fig. 12E	HM
<i>Filogranula mogenstrupensis</i> sp. nov.	Holotype FMM 14977; Paratypes FMM 14978, 14979, 14980	Mogenstrup	4 tubes (holotype, 3 paratypes)	Fig. 12A-D	KIS
<i>Filogranula mogenstrupensis</i> sp. nov.	KIS 1987.363	Mogenstrup	1 tube	not figured	KIS
<i>Placostegus vilsundensis</i> sp. nov.	Holotype FMM 14950	Vilsund	1 tube attached to a brachiopod valve	Fig. 13A	HM
<i>Placostegus vilsundensis</i> sp. nov.	Paratype FMM 14954	Vilsund	1 tube	Fig. 13C	HM
<i>Placostegus</i> cf. <i>erectus</i> (Nielsen, 1931)	FMM 14953	Vilsund	1 tube	Fig. 13B	HM
<i>Placostegus</i> cf. <i>bilobatus</i> (von Koenen, 1891)	KIS 1988.317	Mogenstrup	1 tube	Fig. 14A	KIS
<i>Placostegus</i> cf. <i>bilobatus</i> (von Koenen, 1891)	KIS 1988.325	Mogenstrup	1 tube attached to echinoid spine	Fig. 14B	KIS

FMM: Museum Mors, The Fossil and Mo-clay Museum; HM: Henrik Madsen; specimens collected by HM are kept in Museum Mors, The Fossil and Mo-clay Museum; KAN: Kent Albin Nielsen; KIS: Kai Ingemann Schnetler.

Genus *Vermetus* Daudin, 1800

Type species: *Vermetus adansonii* Daudin, 1800 (based on “Le Vermet” of Adanson, 1757: 160; see Keen 1961: 186–188). Early authors incorrectly listed *Serpula lumbricalis* as type species (Bieler & Petit 2011).

Diagnosis. „Mainly solitary or in small clusters, coiling usually irregular; columellar wall smooth, without laminae; nuclear whorls two, globose to elongate; operculum thin, spiral, one-half or less the diameter of the aperture.” (Keen 1961). For ‘The Vermetid Shell’ in general, the same author states: „The shell is three-layered, with an inner layer that is glossy and porcellaneous...”

Vermetus jyllandensis sp. nov.

Figs 3, 4

Derivation of name. Jylland (Jutland), the mainland of Denmark (excluding the islands).

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Holotype. Fig. 3A, 4, Museum Mors, The Fossil and Mo-clay Museum, FMM 14951a.

Paratype. Fig. 3B, Museum Mors, The Fossil and Mo-clay Museum, FMM 14951b.

Type locality. Vilsund, Jylland, Denmark.

Type horizon. Brejning Formation, Late Oligocene.

Material. From Vilsund, 2 specimens (holotype and paratype), collected by Henrik Madsen, Museum Mors, FMM 14591a, b.

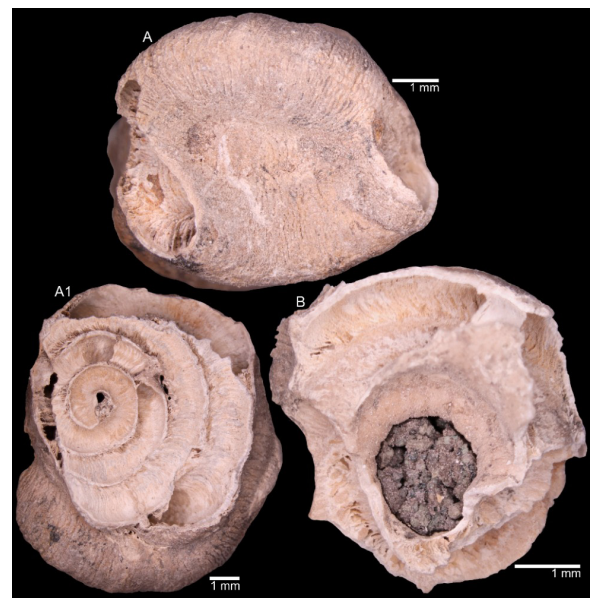


Fig. 3. *Vermetus jyllandensis* sp. nov., more or less damaged spiral tubes, showing the conspicuous densely spaced striation not only on the exterior surface, but also on the interior surface, Late Oligocene, Vilsund, collected by HM. **A, A1:** Holotype, no. 14951a. **B:** Paratype, no. 14951b. **A, B:** Upper sides. **A1:** Underside, showing imperforate septa.

Diagnosis. Shell forms a spiral measuring c. 5–10 mm in total diameter, consisting of five whorls reaching up to c. 2 mm. The entire exterior surface is covered by small but distinct, very densely and regularly spaced transverse striae.

Description. Shell tubular in shape, from 1 mm (first whorls) up to 3 mm (outer whorl) in outer diameter. Shell spirally coiled, with an external diameter over 10 mm. The inner $3\frac{3}{4}$ whorls are planispiral, the outer $1\frac{1}{4}$ whorls partly cover the previous whorls, forming a wide umbilicus. Shell wall approximately 100–150 micron thick. Broken open shells show that small but distinct, very densely and regularly spaced transverse striae, which are very similar to the striae on the exterior surface but slightly higher, also cover the interior surface, together with similar marginal rests of numerous damaged hemispherical septa.

Discussion. Due to their tubular shape, fossil shells of some vermetid gastropods and serpulid polychaetes are quite similar, causing confusion already to von

Koenen (1891) and many others, including the present authors. It was not until Bieler & Petit (2011) that many but not all species were more safely assigned to either vermetids or serpulids.

At localities where aragonitic fossils are dissolved and only their external or internal casts are preserved, gastropod shells (including vermetids) are also dissolved, whereas the tubes of many though not all serpulid species are composed entirely or partly of calcite and are therefore more likely to be well preserved. As a result, they are easily distinguishable from vermetid remains simply by different kinds of preservation. However, in sediments with well-preserved gastropod shells, such as those yielding the fossils studied here, this simple differentiation is not applicable.

Fortunately, undamaged shells of many vermetid specimens can be distinguished from serpulid tubes by a characteristic reticulate ornamentation composed of numerous thin and only slightly elevated longitudinal and transverse striae. In contrast, the tubes of most serpulid species have less than 10 elements

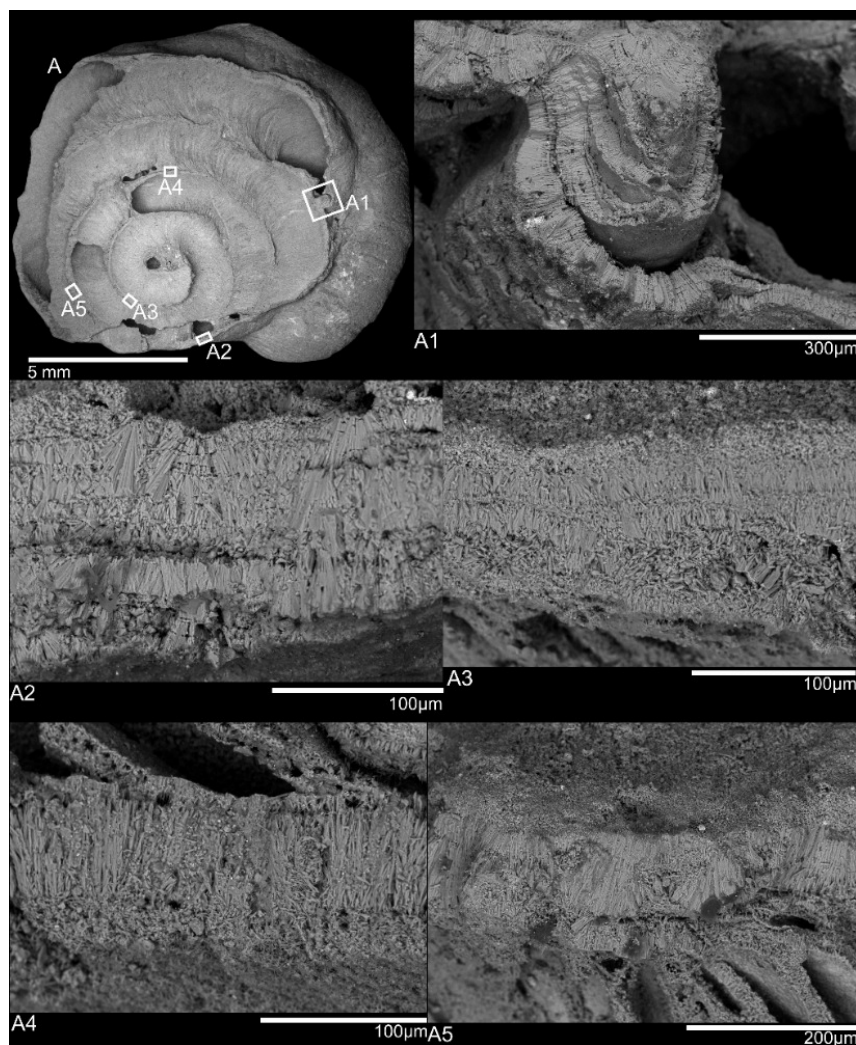


Fig. 4. *Vermetus jyllandensis* sp. nov., SEM images. The tube-wall consists of tall prismatic aragonite crystals. Same specimen as shown in Fig. 3A–A1. A: Overview indicating positions of subfigures A1–A5. Details showing vertical orientation of crystals characteristic for the outer layer and, in some species, also for the inner layer of vermetid gastropods, as well as fan-shaped arrangement of crystals formed later during diagenesis. In the lower parts of A3 and A5 and in the upper part of A4, obliquely oriented marginal remains of hemispherical internal septa are visible.

of longitudinal ornamentations, or, if there are more, they are usually not combined with similar densely spaced transverse striae. By their reticulate ornamentation, many of the Miocene and younger vermetid shells can be distinguished from serpulid tubes easily at first sight. However, *Vermetus jyllandensis* sp. nov. shows only a densely spaced transverse striation, but neither longitudinal striae nor a reticulate ornamentation. Thus, it is not clearly distinguishable from the very similarly ornamented coiled posterior tube portion of *Protula* cf. *septaria* (Fig. 5B), based on the exterior surface alone.

Other distinguishing features are internal and can be recognized only in sections, thin sections, or damaged specimens. Vermetid shells start with a posteriorly closed, more or less spherical protoconch, whereas the posterior end of serpulid tubes is open and not swollen. Unfortunately, in the studied shells of *Vermetus jyllandensis* sp. nov., the protoconch is not preserved.

Moreover, the lumen of vermetid shells is subdivided by several or numerous hemispherical imperforate septa, for example, in *Thylocodes devriesi* Sanfilippo *et al.*, 2021 (see their fig. 4F–I). In contrast, in only a few serpulid taxa, especially in the subgenus *Pyrgopolon* (*Septenaria*) Regenhardt, 1961, more or less plain, somewhat obliquely oriented, perforate septa may occur. In *Vermetus jyllandensis* sp. nov., hemispheric septa are developed but badly damaged in the studied specimens. Remains of the marginal parts of damaged septa are not clearly visible in Fig. 3A1, but are obvious in the SEM images Fig. 4A3–4A5.

Apart from the septa, vermetid shells, just like the shells of other gastropods, usually have an aragonitic inner shell layer, which results in a smooth, nacreous, sometimes shiny interior surface, whereas the interior surface of serpulid tubes is also smooth, but more or less dull, not shiny. However, in fossil specimens, this distinguishing feature is not always reliable due to diagenetic alteration or weathering. Unexpectedly,

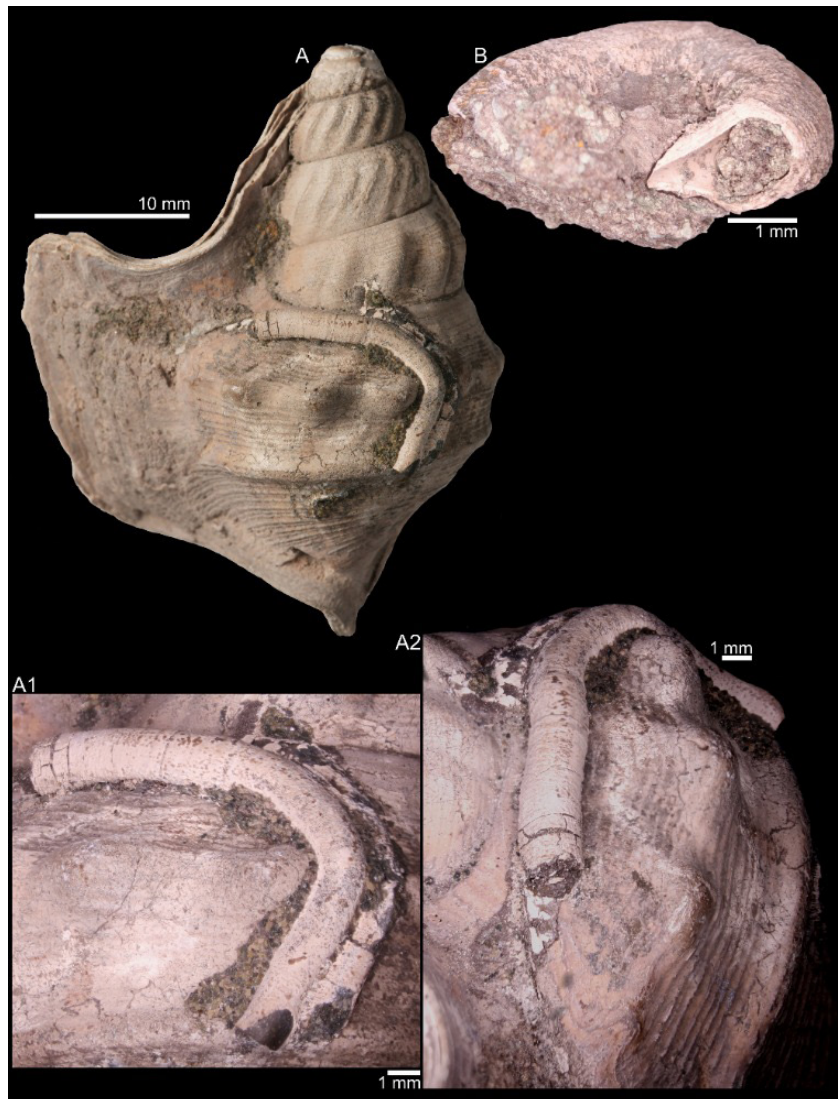


Fig. 5. *Protula* cf. *septaria* (Giebel, 1858), Late Oligocene, collected by KIS. A, A1, A2: An incomplete tube and a badly damaged fragment attached parallel to each other to a gastropod *Aporrhais bicarinata* Koch & Boll in Koch, 1861, Nørre Vissing, no. 1985. A: Overview. A1, A2: Slightly oblique detailed views to the upper side, A1 showing the serpulid tube's posterior cross-section, A2 showing its anterior end. B: A sinistrally coiled posterior tube portion presumably belonging to *Protula* cf. *septaria*, due to its smooth interior surface, Mogenstrup, no. 1987: 363; unfortunately, this specimen was lost.

the interior shell surface of *Vermetus jyllandensis* sp. nov. and the above mentioned *Thylocodes devriesi* (see Sanfilippo *et al.* 2021, Fig. 4F–I) show densely spaced transverse striae, presumably due to the absence of the endostracum, the layer that dissolves first and most easily with fossilization, whereas the interior surface of the coiled posterior tube portion of *Protula* cf. *septaria* (Fig. 5B) is smooth. It is a paradoxical situation, as this combination of characters is contrary to the common diagnostic criteria for vermetids and serpulids.

Vermetid shells and serpulid tubes show different microstructures (Schmidt 1951, 1955b; Keen 1961; Morton 1965; Burchette & Riding 1977; Barash & Zenziper 1985; ten Hove & van den Hurk 1993; Savazzi 1996; Vescogni *et al.* 2008). Vermetids have a typical molluscan shell structure, consisting of one layer or several layers (Fig. 4A1, A3), with a strictly vertically oriented microstructure of the outer shell layer, in contrast to the obliquely horizontal microstructure caused by the growth increments in serpulid tubes. Vermetids, at least when well preserved, show an aragonitic nacreous inner shell layer. – SEM images of *Vermetus jyllandensis* sp. nov. (Fig. 4A1–4A5)

show well-developed layers composed of long crystals oriented more or less vertically relative to the shell's longitudinal axis. These layers are indicative of vermetid gastropods (Schmidt 1951, 1955b), even though some of the original vertical crystals were elongated and arranged in a fan-shaped pattern during diagenesis. Conversely, serpulid tubes of *Protula* show smaller crystals arranged in the criss-cross pattern of the SOIOP or IOP microstructures (Vinn *et al.* 2008; Vinn & Kupriyanova 2011; Vinn 2013, 2020, 2021); see below.

In summary, *Vermetus jyllandensis* sp. nov., despite the distinct transverse striation of its interior surface (presumably due to the absence of the endostracum), is considered a vermetid, not a serpulid, due to the fragments of hemispherical septa and the vertically oriented crystals seen in sections, even though some of these crystals are diagenetic in origin.

Phylum Annelida Lamarck, 1802

Class Polychaeta Grube, 1850

Subclass Sedentaria Lamarck, 1818



Fig. 6. *Protula* cf. *septaria* (Giebel, 1858), Late Oligocene, Vil-sund, collected by HM, no. 14949. A–C, C1, C2, D–G: Lateral views. A1, B1, C3, D1–G1: Cross-sections. Note the smooth interior surface, which is in contrast to *Vermetus jyllandensis* sp. nov.



Fig. 7. *Protula* cf. *septaria* (Giebel, 1858), Late Oligocene, Mogenstrup, collected by KIS, no. KIS 1988.589. A–G: Lateral views. A1–G1: Cross-sections. A1, C1, E1, F show the smooth interior surface.

Infraclass Canalipalpata Rouse & Fauchald, 1997

Order Sabellida Levinsen, 1883

Family Serpulidae Rafinesque, 1815

Subfamily Filograninae Rioja, 1923

Genus *Protula* Risso, 1826

Type species: *Serpula tubularia* Montagu, 1803.

Diagnosis. Tube medium-sized to very large, white, opaque, consisting of an irregularly curved or coiled attached posterior portion and a long straight or slightly curved free anterior tube portion. Cross-section circular. No well-developed longitudinal keels, apart from occasional fine striae. Peristomes un conspicuous or lacking, not flaring. No operculum.

***Protula* cf. *septaria* (Giebel, 1858)**

Figs 5A–B, 6A–G, 7A–G, 8A–C, 9A–B, 10A–B, 11A–B

Synonymy list of *Protula septaria* sensu stricto, except for *Protula* cf. *septaria* in Madsen & Schnetler (2023).

non 1855 *Serpula*? *crassa* Bell. – Bellardi, p. 5.

1858 *Serpula septaria* – Giebel, p. 445.

1861 *Serpula septaria* Gieb. – Giebel, p. 46.

1864 *Serpula septaria* Giebel. – Bosquet, p. 796.

1864 *Serpula septaria* – Giebel, p. 268 (fide Albrecht & Valk 1943).

1868 *Serpula septaria*, Gieb. – Bosquet in Dewalque, p. 416.

1881 *Serpula septaria* Giebel. – Bosquet in Mourlon, p. 202.

1891 *Vermetus crassus* v. Koenen. – von Koenen, pp. 728, 742–743, pl. 51, fig. 11a–b.

1891 *Vermetus crinitus* v. Koenen. – von Koenen, p. 734, pl. 52, fig. 10a–c.

1899 *Protula oligocenica* n. mut. – Rovereto, p. 85.

1904 *Protula septaria* Giebel – Rovereto, p. 47, pl. 2, figs 4a–c, 5.

1905 *Protula septaria* Giebel – Fabiani, p. 1828.

1908 *Protula septaria* Giebel – Fabiani, p. 60.

1913 *Vermetus crassus* v. Koenen. – Harder, p. 72, pl. 5, fig. 25.

?1914 *Vermetus crassus* v. K. – Gripp, p. 13.

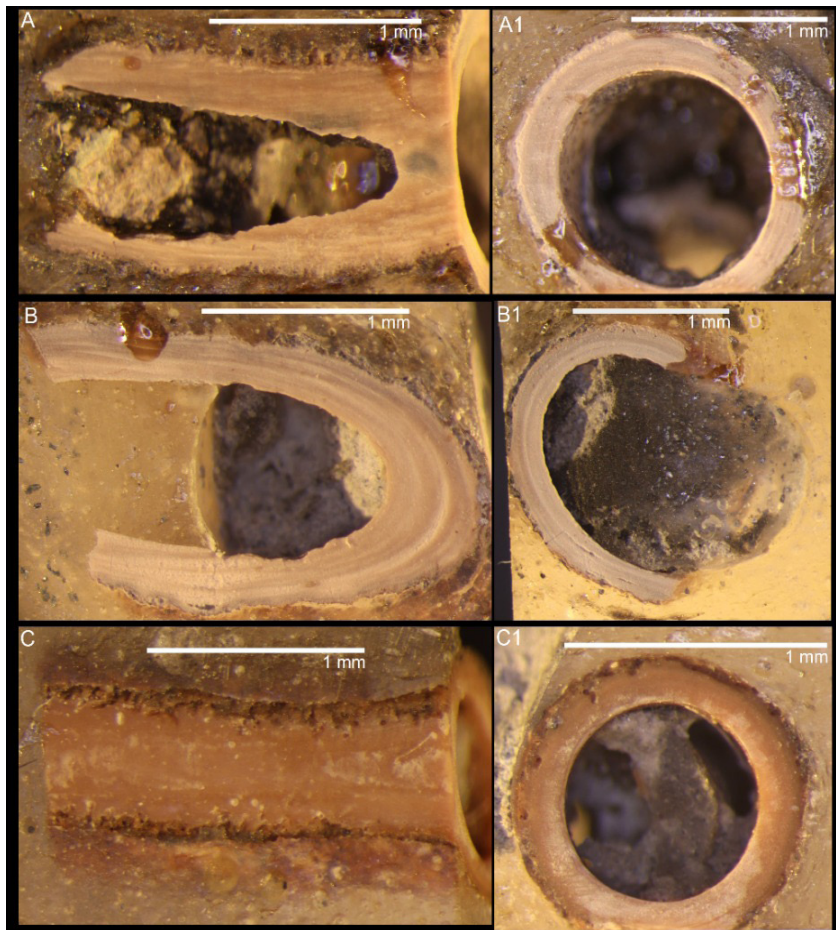


Fig. 8. *Protula* cf. *septaria* (Giebel, 1858), Late Oligocene, Mogenstrup, collected by KIS, no. KIS 1988.589, polished sections. A, A1: Same specimen as Fig. 7E. B, B1: Same specimen as Fig. 7F. C, C1: Same specimen as Fig. 7G. A, B: Oblique longitudinal sections. C: Horizontal section. A1, B1, C1: Transverse sections. The tube wall consists of a single layer composed of numerous distinct increments (sublayers). The longitudinal sections are comparable with recent *Protula* sp. from Sanremo, Italy (Malaroda 1987, Fig. 14). The transverse sections are comparable with *Protula isseli* Rovereto, 1899 from the Pliocene of Candelo, Italy (Malaroda 1987, Fig. 15).

1925 *Protula septaria* Giebel – Vincent, p. 23.
 1943 *Serpula septaria* Giebel – Albrecht & Valk, p. 14, pl. 26, fig. 1000.
 1950 *Protula septaria* Giebel – Malaroda, p. 160, pl. 3, figs 1–4.
 1952 *Vermetus* cf. *crassus* – Görges, p. 68.
 1975 *Serpula septaria* Giebel, 1864 [sic!] – van den Bosch, Cadée & Janssen, pp. 58, 66, 68, 69, 70, fig. 22.
 pars 1984 *Protula extensa* (Brander [sic!], 1766) – Liebau, p. 85, pl. 10, Fig. 11; non p. 40, pl. 2, fig. 10.
 1987 *Protula septaria* (Giebel, 1858) – Malaroda, p. 14–18, figs 4–13.
 ? 2009 ?*Lemintina* sp. – Welle, pp. 115–116, pl. 5, fig. 8.
 2011 *Protula* sp. – Müller, pp. 14–15, 44–46, fig. 17, pl. 3, fig. 15a–c.
 2023 Elongated round worm tube – Madsen & Schnetler, p. 108, left figure.

Material. From Vilsund, 7 tubes (Fig. 6A–G), and 3

fragments on steinkerns (not figured), collected by HM, no. 14949.

From Mogenstrup, all collected by KIS, 1 spiral tube (Fig. 5B), no. KIS 1987.363; 8 tubes, 1 fragment on steinkern, 3 fragments (not figured), no. KIS 1987.363; 7 tubes (Figs 7A–G, some of them cut and polished for study of microstructure and shown in Figs 8A–C, 9A–B, 10A–B, 11A–B), no. KIS 1988.589; 5 tubes, 1 fragment (not figured), no. KIS 1988.589; 2 tubes (not figured), no. KIS 1988.325, 15L; 4 tubes, 2 fragments on steinkern (not figured), no. KIS 1988.317.

From Hinge, 3 tubes (not figured), collected by KAN, no. KAN 2025.

From Nørre Vissing, 1 tube and 1 fragment attached to gastropod *Aporrhais bicarinata* (Fig. 5A), collected by KIS, no. KIS 1985.

Stratigraphic range. Early to Late Oligocene. In the eastern Netherlands, this species is an index fossil

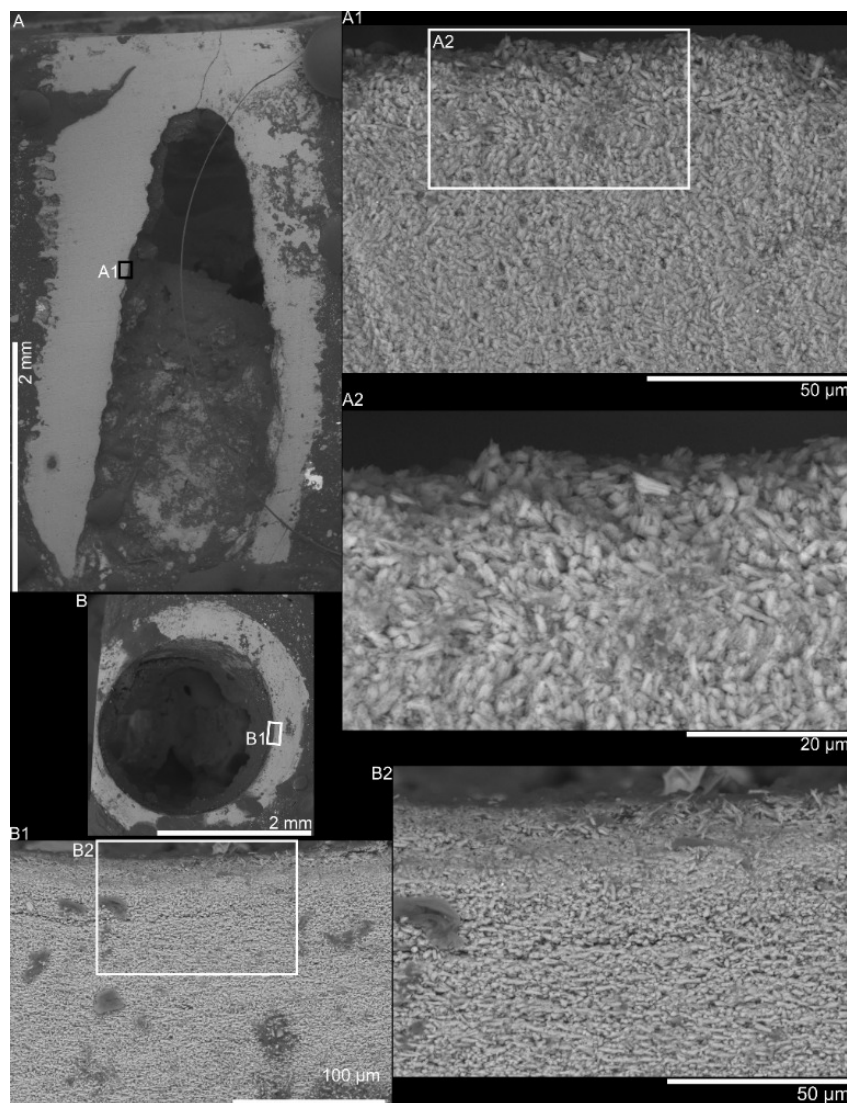


Fig. 9. *Protula* cf. *septaria* (Giebel, 1858), Late Oligocene, Mogenstrup, collected by KIS, no. KIS 1988.589, polished sections. Same specimen as Fig. 7E. **A, A1, A2:** Overall view and details of oblique longitudinal section. **B, B1, B2:** Overall view and details of transverse section. **A1, A2, B1, B2:** Semi-ordered irregularly oriented prismatic microstructure (SOIOP) sensu Vinn *et al.* (2008) and Vinn (2013).

of the *Serpula* [sic!] *septaria* – *Ancistrosyrinx volgeri* – Assemblage Zone in the Rupelian Brinkheurne Member (van den Bosch, Cadée & Janssen 1975).

Diagnosis. A medium-sized to large-sized species of the genus *Protula*. The attached tube portion may form a spiral in a few specimens, but generally, non-spiral tubes are much more common. Transverse ornamentation consists of densely or irregularly spaced fine striation, which may be well developed, weakly developed, or lacking.

Description. The attached posterior tube portion increases slowly to moderately in diameter (in one specimen from 2 to 2.4 mm) and is subcircular or tunnel-shaped in cross-section. It forms a curve, a loop or a spiral. Its surface bears fine but conspicuous densely spaced transverse striation. The tube wall is thin. The free anterior tube portion increases rather slowly in diameter, reaching 2 mm in small specimens and commonly 3–5 mm in adult specimens. The tube is

straight, less often slightly curved or slightly serpentine. Its surface may bear very fine transverse striation. The cross-section is circular.

The thickness of the tube wall varies between moderately thin and moderately thick. Already under a binocular light microscope at low magnification, the relatively simple construction of the tube wall of *Protula* cf. *septaria* is visible. As is typical for the genus *Protula*, it consists of a single layer composed of numerous successive increments forming sub-layers sticking inside each other. The boundaries between neighbouring increments run slightly obliquely to the tube's longitudinal axis, causing an almost constant outer tube diameter and an increasing lumen diameter close to the aperture, but a diminishing outer tube diameter (Figs 6A, 6D, 6F, 6G, 7D) and an almost constant lumen diameter toward the posterior end of many fragments. The tube wall construction of genus *Protula* is comparable to a stack of high and slender one-way water or coffee drinking cups or yogurt cups, but lacking their base plates.

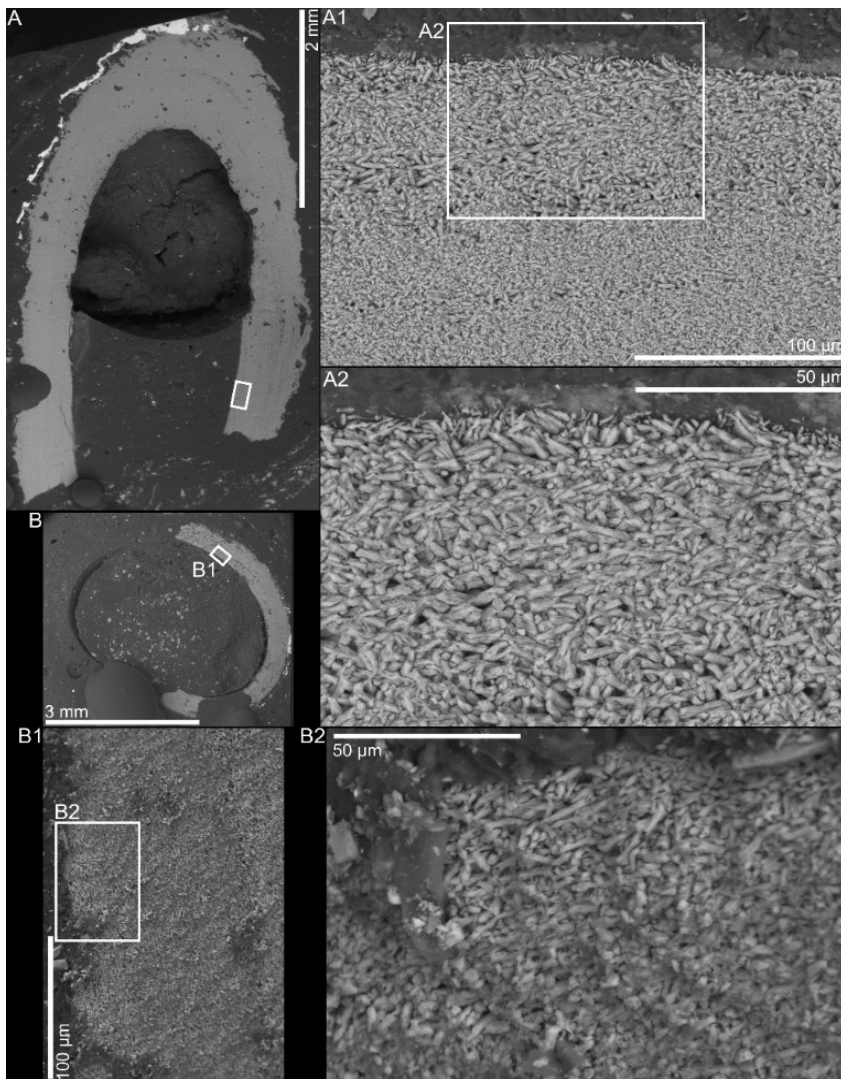


Fig. 10. *Protula* cf. *septaria* (Giebel, 1858), Late Oligocene, Mogenstrup, collected by KIS, no. KIS 1988.589, polished sections. Same specimen as Fig. 7F. **A, A1, A2:** Overall view and details of oblique longitudinal/transverse section. **B, B1, B2:** Overall view and details of transverse section. **A1, A2, B1, B2:** Semi-ordered irregularly oriented prismatic microstructure (SOIOP) sensu Vinn *et al.* (2008) and Vinn (2013).

Microstructure. *Protula* cf. *septaria* possesses a semi-ordered irregularly oriented prismatic microstructure (SOIOP) sensu Vinn *et al.* (2008) and Vinn (2013). The SOIOP microstructure is composed of short prismatic crystals. These crystals have an oriented substructure, being composed of thin, long crystallites, oriented parallel to the longitudinal axes of the SOIOP crystals. In the SOIOP microstructure as well as in the Ordered Fibrillar (OF) microstructure, most of the crystals and crystallites orient their long axes perpendicular to the tube's longitudinal axis and parallel to the tube's transverse section. But in contrast to the OF microstructure, in the SOIOP microstructure a minor number of the crystals together with their crystallites orient their long axes more or less parallel to the tube's longitudinal axis and more or less perpendicular to the tube's transverse section, as most obvious in the transverse sections shown by Vinn (2013, figs 2, 8b) and in the schematic drawings in Vinn *et al.* (2008) and Ippolitov *et al.* (2014), but also

in our Figs 9–11.

The tube wall microstructure of *Protula* cf. *septaria* from Mogenstrup is comparable to the SOIOP microstructure of *Protula protensa* (not Gmelin, 1791) sensu Philippi, 1844, figured by Vinn (2013, Fig. 3) and *Protula diomedea* Benedict, 1887, figured by Vinn *et al.* (2008, p. 640, Fig. 4A–B) and Vinn (2013, p. 454, Figs 1–2). However, the oriented prismatic crystals are less preserved and less visible.

Discussion. Jäger (unpublished) studied tubes of *P. septaria* from the Early Oligocene of Mammendorf and Latdorf in northeastern Germany. At Mammendorf, the tubes reach larger sizes up to 8 mm in diameter, and Müller (2011) has observed large tubes more than 150 mm long attached to vertical faces of Andesit blocks *in situ*. As in Denmark, non-spiral tube fragments are much more common than spiral tubes. While transverse striation is well-developed and densely spaced in Denmark, it is generally more

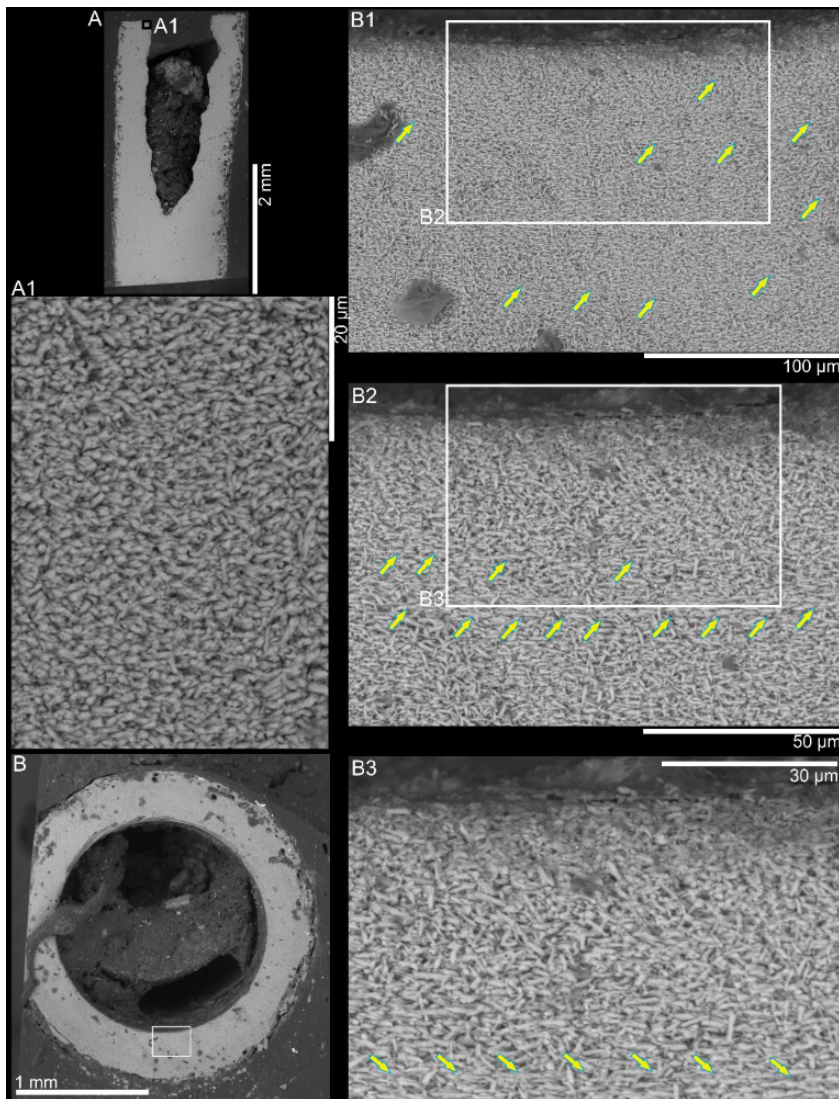


Fig. 11. *Protula* cf. *septaria* (Giebel, 1858), Late Oligocene, Mogenstrup, collected by KIS, no. KIS 1988.589, polished sections. Same specimen as Fig. 7G. **A, A1:** Overall view and details of oblique longitudinal section. **B, B1–B3:** Overall view and details of transverse section. The arrows point to crystals which are oriented parallel to the tube's surface and perpendicular to the tube's longitudinal axis, in accordance with the semi-ordered irregularly oriented prismatic microstructure (SOIOP) sensu Vinn *et al.* (2008) and Vinn (2013).

weakly developed, less densely and more irregularly spaced, and lacking in many specimens at Mammendorf. Due to these regional differences, the Danish specimens are referred to as *Protula* cf. *septaria*.

Genus *Filogranula* Langerhans, 1884 (non Nielsen, 1931)

Type species: *Filogranula gracilis* Langerhans, 1884.

Diagnosis. Tube opaque, increasing in diameter at a slow to moderate pace to reach a small to medium-sized final diameter, but especially the obliquely or steeply rising free anterior tube portion may grow very long. The tube bears one, three, or five keels and conspicuous peristomes, which often are annular, stellate, or spiny stellate, and may be rather common, especially in the free anterior tube portion. Operculum present in recent species (not yet found in fossils).

***Filogranula mogenstrupensis* sp. nov.**

Fig. 12A–E

2023 Pentagonal worm tube – Madsen & Schnetler, p.

109 (left figure).

Derivation of name. After the locality Mogenstrup, Jylland, Denmark.

Zoobank LSID.

<https://zoobank.org/urn:lsid:zoobank.org:act:A45CE7A9-8027-4A17-9C52-1BD74110D4BD>

Holotype. The specimen shown in Fig. 12A, collected by KIS, Museum Mors, The Fossil and Mo-clay Museum, FMM 14977.

Paratypes. The specimens shown in Fig. 12B, C, D, collected by KIS, Museum Mors, The Fossil and Mo-clay Museum, FMM 14978, 14979 and 14980, and in Fig. 12E, collected by HM, FMM 14952.

Type locality. Mogenstrup, Jylland, Denmark.

Type horizon. Brejning Formation, Late Oligocene.

Material. From Vilsund, 1 tube (Fig. 12E), collected by HM, FMM 14952.

From Mogenstrup, all collected by KIS, 4 tubes, including the holotype FMM 14977 and 3 paratypes

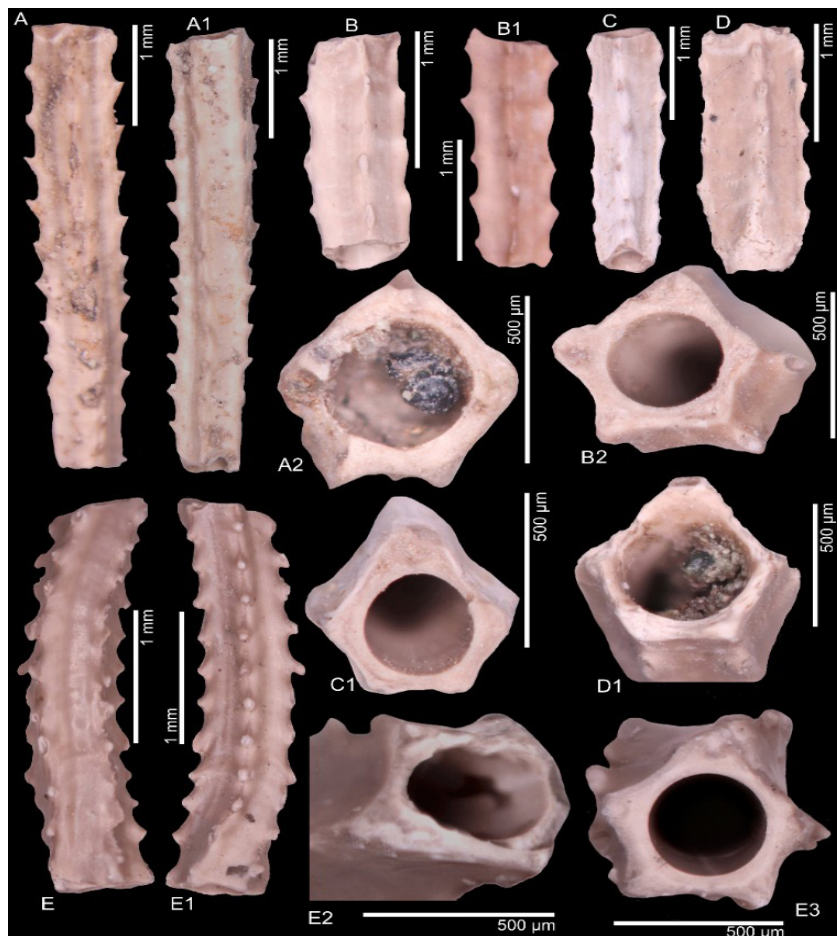


Fig. 12. *Filogranula mogenstrupensis* sp. nov., Late Oligocene. A–D: Mogenstrup, collected by KIS, A: Holotype, FMM 14977. B–D: Three Paratypes, FMM 14978, 14979 and 14980. E: Vilsund, collected by HM, Paratype, FMM 14952. A, B, B1, C, D, E1: Upper sides. A1, B1, E: Undersides. A2, B2, C1, D1, E1, E2: Cross-sections.

FMM 14978, 14979, 14980 (Fig. 12A–D); 1 tube, KIS 1987.363 (not figured).

Diagnosis. The almost straight free tube portion increases very slowly in diameter, reaching only up to 0.8 mm. Five longitudinal keels are almost equally spaced around the circumference, but the upper median keel is slightly more widely spaced, whereas the other four keels on the underside and the latera are slightly more densely spaced. The areas between the keels are plain or somewhat concave. Each keel is topped by a sawblade-like row of almost equally spaced denticles. Peristomes as well as any other transverse ornamentation is lacking. The cross-section is pentagonal.

Discussion. The attached posterior tube portion is unknown, as all or almost all specimens are fragments of the anterior free tube portion. At first sight, the straight, keeled and denticulated free tube por-

tions resemble spines of a regular echinoid.

Although small size and rows of spines or granules are also characteristic of the subgenus *Metavermilia* (*Vepreculina*) Regenhardt, 1961, assignment to the genus *Filogranula* is preferred, due to the presence of a long free tube portion.

Subfamily Serpulinae Rafinesque, 1815

Tribus Ficopomatini Pillai, 1960

Genus *Placostegus* Philippi, 1844

Type species: *Serpula tridentata* Fabricius, 1779.

Diagnosis. Tube small to medium-sized, increasing slowly to gradually in diameter. The attached tube portion may form inward-coiling loops in many but not all species, whereas the free anterior tube portion is usually straight and rises more or less steeply. There is one median keel in the attached portion and

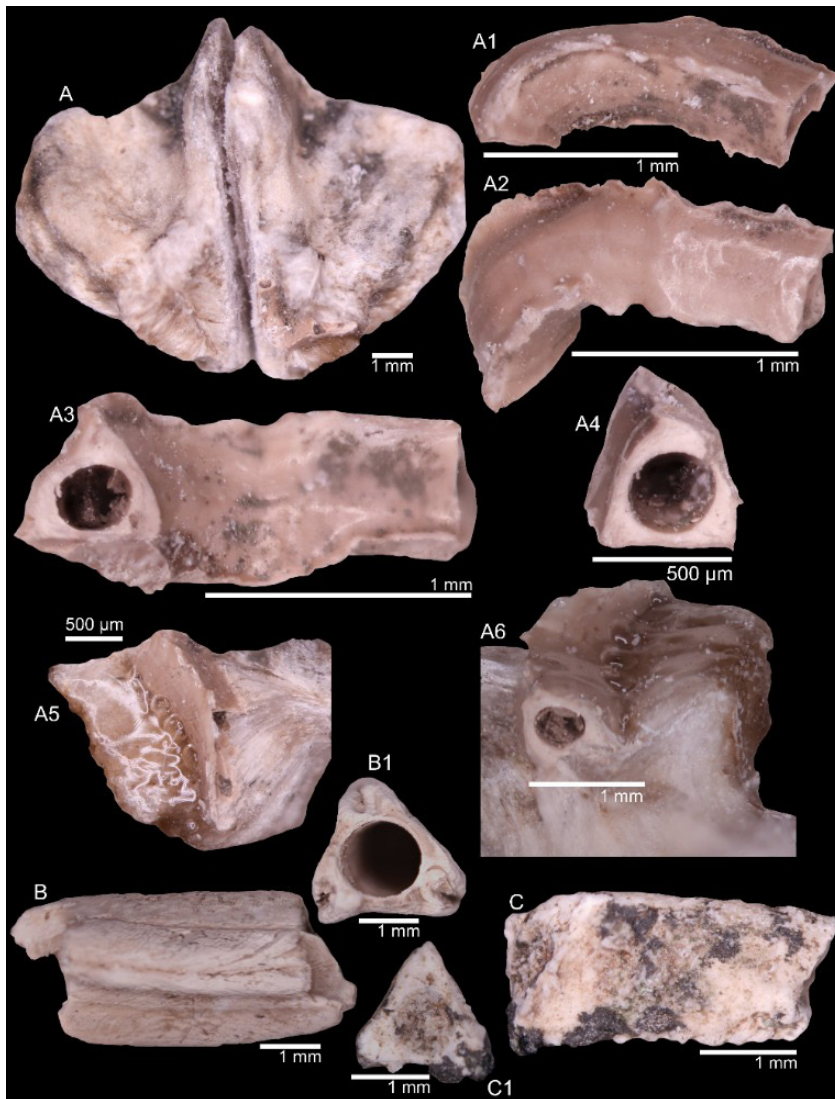


Fig. 13. Two *Placostegus* species, Late Oligocene, Vilsund, collected by HM. **A–A6, C, C1:** *Placostegus vilsundensis* sp. nov. **A–A6:** Holotype. Two tubes attached to a brachiopod, broken into pieces during the photography session, FMM 14950. **A:** Entire specimen. **A1:** Upper side. **A2:** Lateral view. **A3:** Anterior cross-section. **A4:** Oblique posterior cross-section. **A5:** Lateral view of, respectively upper side of, the two damaged tubes. **A6:** Oblique view of anterior cross-sections. **C, C1:** FMM 14954. **C:** Paratype. Lateral view. **C1:** Cross-section. **B, B1:** *Placostegus* cf. *erectus* (Nielsen, 1931), FMM 14953. **B:** Lateral view. **B1:** Cross-section showing tiny canals.

three equally spaced keels in the free portion, giving the tube a generally triangular cross-section in most species, but a few species have a circular cross-section in the free portion. The growth lines are curved forward towards the keel, causing a spine over the aperture in the attached tube portion, and three protruding spines at the aperture of the free tube portion. Alae (birdwing-shaped peristomes) are present in only a few species. Transverse riblets are present in a few species. Tubes of recent *Placostegus* specimens are usually translucent, which, however, is not directly observable in fossil tubes. However, in fossil specimens, former translucidity can be inferred from the presence of a single-layered tube wall composed of a simple prismatic (SP) microstructure, which is a characteristic feature of fossil (Słowiński *et al.* 2024b) as well as of extant *Placostegus* species (Vinn & Kupriyanova, 2011).

***Placostegus vilsundensis* sp. nov.**

Fig. 13A, C

Derivation of name. After the locality Vilsund, Jylland, Denmark.

Zoobank LSID.

<https://zoobank.org/https://zoobank.org/urn:lsid:zoobank.org:act:BCF47D32-8D72-4F01-ACD3-ADCFEFF123B>

Holotype. The specimen shown in Fig. 13A, collected by HM, Museum Mors, The Fossil and Mo-clay Museum, FMM 14950.

Paratype. The specimen shown in Fig. 13C, collected by HM, Museum Mors, The Fossil and Mo-clay Museum, FMM 14954.

Type locality. Vilsund, Jylland, Denmark.

Type horizon. Brejning Formation, Late Oligocene.

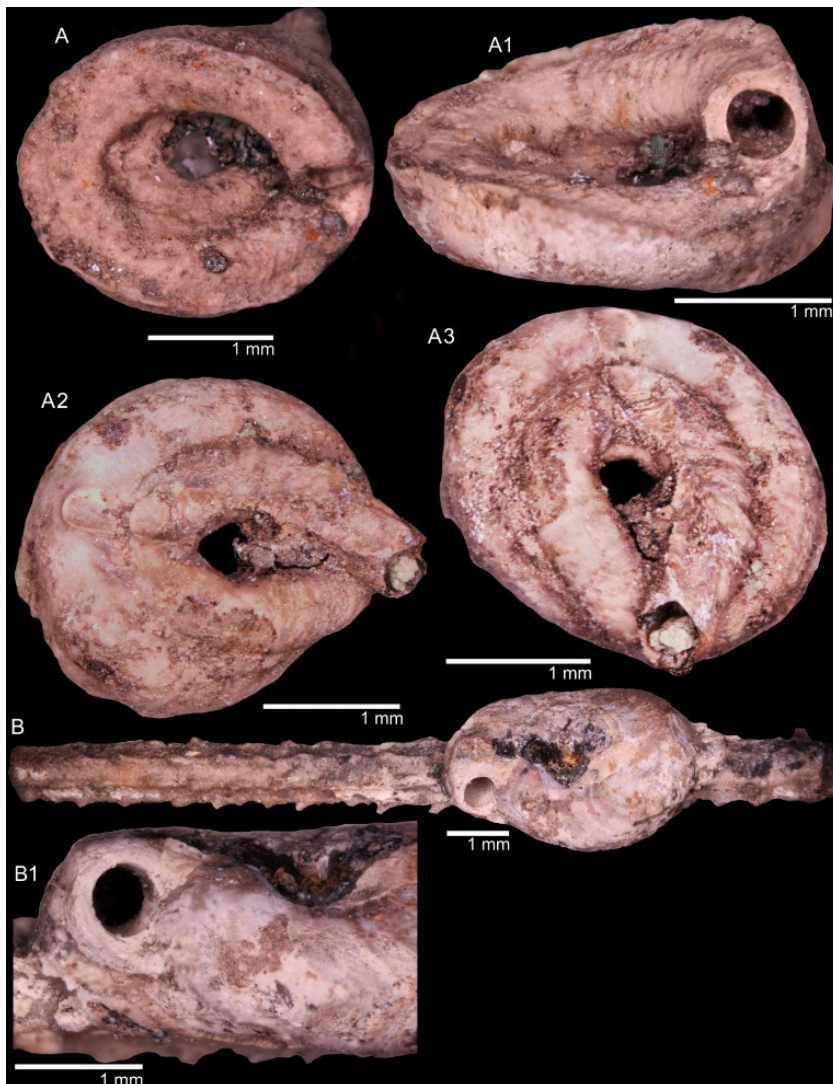


Fig. 14. *Placostegus* cf. *bilobatus* (von Koenen, 1891), Late Oligocene, Mogenstrup, collected by KIS. A, A1: no. KIS 1988.317. A: Upper side. A1: Anterior view. A2, A3: Underside. B, B1: no. KIS 1988.325. B: Entire specimen, attached to echinoid spine. B1: Detail showing tunnel-shaped aperture.

Material. From Vilsund, all collected by HM, 1 tiny tube (the holotype, broken to pieces during photography session) attached to a brachiopod valve (Fig. 13A), FMM 14950; 1 short fragment of somewhat larger tube (the paratype, Fig. 13C), FMM 14954.

Diagnosis. Tube small, attached tube portion irregularly curved, bearing one sharp, slightly undulating and locally frayed or denticulated keel in the attached portion and three such keels in the free tube portion. Areas between the keels are plain or only slightly convex, with a smooth surface, lacking any transverse ornamentation. Cross-section triangular with sharp edges and straight or only slightly convex sides. Tube wall moderately thick between the keels and thick at the keels. External surface is light brown.

Additional description. The two tubes measure between 0.6 and 1.8 mm in diameter. Due to the sparsity of material, it remains unknown whether or not other specimens of this species form loops and whether or not the incremental growth lines protrude at the keels and form spines at the aperture.

Discussion. The present species resembles three Danian *Placostegus* species by shape and size: *P. tridentiger* (Regenhardt, 1961) from Vincentown, New Jersey, U.S.A., differs by having three long spines at the aperture of the free tube portion. In *P. erectus* (Nielsen, 1931), the keels are straight rather than undulating or frayed, and are either smooth or, less often, topped by a regular row of granules or blunt spines, and the areas between the keels bear a narrow but distinct median furrow. Moreover, the cross-section of the free tube portion is often more rounded. *P. alatus* (Nielsen, 1931) from Faxø differs by the occasional presence of alae-type peristomes occurring in wide, irregular intervals and by a non-denticulated keel.

***Placostegus* cf. *erectus* (Nielsen, 1931)**

Fig. 13B

Synonymy list of *Placostegus erectus* sensu stricto:

non 1831 *Serpula erecta* nobis. – Goldfuss, p. 238, pl. 70, fig. 15.

non 1897 *Serpula erecta* n. spec. – Reis, pp. 77, 79, pl. 9, fig. 3.

1926 *Serpula* (*Pomatocerus*) [sic!] *erecta* Br. N. – Ødum, pp. 167, 202, 204, 207, 225, 263, 265, 282–289, 295, 298, 300–304, 306.

1928 *Pomatocerus* [sic!] *erectus* Br. N. – Ødum, p. 209.

1931 *Serpentula erecta* n. sp. – Brünnich Nielsen, pp. 95, 99, 100, pl. 2, figs 12–13.

1961 *Eoplacostegus* (*Eoplacostegus*) *erectus* (Nielsen). – Regenhardt, pp. 61, 70, 103.

1961 *Eoplacostegus* (*Concamerarius*) *inexpectatus* n. sp. – Regenhardt, pp. 61–63, 103, pl. 9, fig. 10.

1993 *Placostegus erectus* (Brünnich Nielsen, 1931). – Jäger, pp. 79, 94, 100–101, 110, tpls 1–3, pl. 7, figs 5–14.

2006 *Eoplacostegus inexpectatus* Regenhardt, 1961. – Ziegler, p. 19.

2006 *Proliserpula erecta* (Nielsen), 1931. – Ziegler, p. 31.

2018 *Placostegus erectus* (Brünnich Nielsen, 1931). – Jäger, Kočí, Schnetler, Andersen & Jakobsen, p. 33, pl. 1, fig. 15.

Material. From Vilsund, 1 short fragment of the free anterior tube portion (Fig. 13B), collected by HM, FMM 14953.

Description. The fragment of the free tube portion measures c. 2.5 mm in diameter. It bears three equally spaced, wide, rounded longitudinal edges. At least each of the two edges in basal lateral positions bears a very narrow median longitudinal furrow which, as visible in the cross-section Fig. 13B1, appears to widen within the tube wall and, perhaps, forms a tiny longitudinal canal. Transverse ornamentation is lacking, but the incremental growth lines are curved and strongly protrude toward the longitudinal edges, so that the not preserved aperture must have had three long protruding spines.

Discussion. The tube is similar to, but somewhat larger than *Placostegus erectus* (Nielsen, 1931) from the Danian of Faxø (Nielsen 1931; Jäger 1993, pl. 7, fig. 12b). For this reason, the specimen is provisionally assigned to *Placostegus* cf. *erectus*.

Similar longitudinal canals within a tube wall have also been observed by MJ in a yet undescribed species of *Placostegus* from the earliest Oligocene of Mammendorf in material collected by Frank Trostheide. In that material, the described canals are usually more or less well visible or at least traceable in cross-section and appear to be present along the entire length of the attached tube portion, where a pair of cross-sections of longitudinal canals is visible near each of the two lateral-basal edges and the median keel, making six canals in total. The lower four of the six canals are semi-circular in cross-section, whereas the two upper cross-sections are narrow. However, the morphology and degree of development of these canals appear to be variable. Usually, the canals terminate at, or just anterior to, the transition from the attached to the free portion; however, in some tubes, they are present in the free tube portion, too.

Placostegus cf. *bilobatus* (von Koenen, 1891)

Fig. 14A–B

Synonymy list of *Placostegus bilobatus* sensu stricto:

1891 *Vermetus bilobatus* v. Koenen – von Koenen, pp. 728, 735–736, pl. 41, fig. 12a, b.

1904 *Vermetus bilobatus* Koenen – Rovereto, p. 65, footnote 3. [Rovereto considered this species rather a *Spirorbis* than a juvenile *Vermetus*.]

2011 *Vermetus bilobatus* Koenen, 1891 [polychaete] – Bieler & Petit, p. 27.

Material. From Mogenstrup, all collected by KIS, 1 tube (Fig. 14A), KIS 1988.317; 1 tube attached to an echinoid spine (Fig. 14B), KIS 1988.325.

Description. Tube small, 0.6–1.2 mm in diameter. Following a formerly attached initial tube portion of which a straight, c. 1 mm long anteriormost fragment is preserved, the tube forms an outward coiling spiral c. 2–4 mm in diameter, consisting of two whorls. A straight free anterior tube portion is absent in the two studied specimens, but may have originally been present in at least one of them (Fig. 14A), which ends anteriorly at a transverse fracture. The tube bears a rounded but distinct median keel. The transverse ornamentation consists of densely spaced, blurred but discernible transverse ribs, which are curved and protrude toward the tube's base and toward the keel, on which they may form small granules. Except for the keel and the plain underside which may be narrow or moderately wide, the tube's cross-section is circular.

Discussion. Although originally von Koenen (1891) considered his new species *bilobatus* from the Early Oligocene of Latdorf to be a vermetid gastropod of the genus *Vermetus* Daudin, 1800, subsequent authors Rovereto (1904) and Bieler & Petit (2011) agree that this species may rather be, or is a serpulid, and MJ (unfinished manuscript) further assumes, although tentatively, that it could belong to the serpulid genus *Placostegus*, due to its small size, its non-spiral initial tube portion followed by a spiral, and its transverse ribs which protrude toward the base and the keel. However, it remains unknown whether or not the present species may have formed a free anterior tube portion and how this was ornamented. In the Early Oligocene of northern Germany, *Placostegus* occurs at Latdorf, but not at Mammendorf. For the Late Oligocene specimens from Denmark, a 'cf.' is designated due to the – although only small – stratigraphic distance, as well as to the presence at Latdorf of a vermetid gastropod, whose juvenile shell resembles *Placostegus bilobatus*, but later in ontogeny starts to form a reticulate ornamentation very characteristic of vermetid gastropods.

Discussion

Palaeoecological and taphonomic remarks

Although in only three serpulid specimens (Figs 5A, 13A, 14B) the original substrate to which they are attached is preserved, all the above-described serpulids from the Brejning Formation of Jylland belong to genera which are known to live as epibionts attached to hard substrates (e.g., Schmidt 1955b; Regenhardt 1961 (with species of *Filogranula* assigned to its junior subjective synonym *Flucticularia* Regenhardt, 1961 and with species of *Placostegus* assigned to its junior subjective synonym *Eoplacostegus* Regenhardt, 1961); Zibrowius 1968 (with species of the valid genus *Filogranula* Langerhans, 1884 assigned to their former genus name *Omphalopoma* Mörch, 1863 which, however, is considered a nomen dubium); Jäger 2005; Jäger *et al.* 2018; Kupriyanova *et al.* 2020).

In later ontogeny, all these genera raise their anterior tube portion for a more or less considerable length, growing freely away from the substrate. Extant relatives of the serpulid genera recorded from the Brejning Formation of Jylland are studied by, e.g., Zibrowius (1968), who described several species to occur in some hundred meters deep water as well as in sheltered submarine caves in a few tens of meters in the Mediterranean. The often long or very long free anterior tube portion of fossil and extant representatives of these genera are figured by, e.g., Schmidt (1955b); Rovereto (1899, 1904); Zibrowius (1968). Such tubes are mechanically less stable against being tilted, either along with their substrate or due to the breakage of the free anterior portion. This suggests that hydrodynamic energy from currents or storm waves must have been relatively low also at the seafloor where and when the sediments of the Brejning Formation were deposited.

This assumption is supported by ecology data of extant relatives of the Late Oligocene marine animals, especially of the diverse mollusc fauna co-occurring with the serpulids. For example, in the North Sea and in the Mediterranean Sea, the recent *Aporrhais pespelecani* (Linnaeus, 1758) lives on or in soft muddy, sandy or shelly substrates in relatively calm waters at depths from below tidal zone to c. 130 m (von Cosel 1977). The fossils found at Nørre Vissing, at least in unit 2, indicate "euhaline, open marine, most probably lower sublittoral conditions, with a water depth of about 70 to 100 m" (Schnetler & Beyer 1987). The assemblages found at Mogenstrup and Vilsund indicate a thanatocoenosis consisting of biota living in deeper water and shallow marine species transported down the delta or shelf slope to the basin floor (Schnetler & Beyer 1990; Schnetler *et al.* 2024). Otoliths found at Vilsund indicate c. 100–200 m deep water at that locality, deeper than at Mogenstrup

(Schwarzahns, pers. comm. 2022 cited in Schnetler *et al.* 2024; Schwarzahns *et al.* 2024).

Did the above mentioned serpulids settle on hard parts of an alive or a dead invertebrate animal? The larvae of the two *Protula* cf. *septaria* individuals attached to the *Aporrhais bicarinata* shell (Fig. 5A) settled on a shell lying oriented in the most stable position, and they chose the most favourable position at the highest position above the sediment surface, but both is true for shells of alive as well as dead *Aporrhais* and allows no decision. However, adult aporrhaisids are seasonal burrowers, sometimes occurring in large populations (Young, 1937). Only during part of the year do they live epifaunally, grazing on benthic diatoms and decaying macroalgae (Perron 1978), whereas during the rest of the year they burrow to a shallow depth below the surface of the soft seafloor. And according to Kupriyanova *et al.* (2001), juvenile serpulids increase faster in tube length than adults, serpulids of small and moderate size reach maturity already a few weeks after settling, and longevity varies from several months to 5–6 years in small to moderate serpulids and spirorbins to 35 years exceptionally in the largest serpulids. Considering these data, it remains questionable whether or not the *Aporrhais*' annual epifaunal period lasted long enough to enable the attached *Protula* to complete its full life circle to maturity and spawning, respectively to complete building its attached posterior tube portion and to increase its steeply rising anterior tube portion high enough, before the serpulid is smothered or starved by the *Aporrhais*' apertural edge burrowing into the sediment. Therefore, it seems more probable that the *Protula* larvae settled on a dead gastropod.

In the case of *Placostegus vilsundensis* (Fig. 13A, A5, A6), it remains uncertain whether the brachiopod was alive or already dead when the serpulid larva settled, but a *syn vivo* encrustation seems more probable, because the serpulid is located close to the brachiopod shell's edge, a position favourable for obtaining food particles suspended in the water currents propelled by the brachiopod's lophophore and the serpulid ciliary crown. However, given the significant size disparity between the two invertebrates, the small serpulid certainly profited more from the water action produced by the much larger brachiopod, suggesting a commensal relationship.

Similarly, for the spiral tube of *Placostegus* cf. *bilobatus* attached to an echinoid spine (Fig. 14B), a *syn vivo* encrustation seems more probable. Serpulids may encrust spines of living echinoids, although more frequently they attach to spines of dead echinoids, especially if the spines are large and thick, as in cidaroids. However, the spine shown in Fig. 14B is thin and had certainly been very light before diagenesis. A dead spine, detached from the corona and encrusted by the serpulid, usually lies horizontally on the

muddy seafloor and is prone to being swept away and redeposited with the serpulid turned underneath the spine and buried in the mud. Therefore, it would certainly be a more favourable strategy for the serpulid to encrust the spine of a living echinoid.

Serpulid evolution and fauna distribution in the Cenozoic, with focus on Europe and on Oligocene serpulid faunas

According to the International Chronostratigraphical Chart (International Commission on Stratigraphy 2024), the Oligocene, spanning from 33.9 to 23.04 Ma (million years ago; the age) before present, is a relatively short epoch (with a duration of only 10.86 Myr (million years, the timespan), bracketed by the longer Eocene (22.1 Myr) and Miocene (17.71 Myr). This is certainly one reason why the number of publications on Oligocene serpulids is considerably lower than that on Eocene and Miocene serpulids. Other reasons include the drastic decrease in atmospheric CO₂, temperature, and sea level around the Eocene/Oligocene boundary, and the relatively wide areas with marine Miocene sediments accessible at or near the surface.

The temperature curve of the Cenozoic reached its absolute maximum at 51 Ma in the Early Eocene (Ypresian). Following this, during the Eocene, the plate tectonic drift of the Indian Subcontinent toward Eurasia caused increased weathering of the silicates within the elevated Deccan Traps, leading to a considerable decrease in atmospheric CO₂ and consequent global cooling (Kent & Muttoni 2008). This cooling culminated near the Eocene/Oligocene boundary, and temperature reached a minimum at 33 Ma in the earliest Oligocene (earliest Rupelian). Already in the Middle Eocene, the ephemeral formation of the Antarctic ice sheet started (Ladant *et al.* 2014), becoming permanent by the Late Eocene. The opening of ocean gateways (Drake Passage and Tasmanian Gateway) enabled the development of the Antarctic Circumpolar Current (ACC), causing changes in oceanic currents, water masses, and global oceanic circulation systems. The main drop in global temperature occurred within c. 0.8 million Myr around the Eocene/Oligocene boundary (*e.g.*, Hutchinson *et al.* (2021), and references therein), peaking in the earliest Oligocene and marking the transition from a global warm 'greenhouse' climate to a cooler 'icehouse' climate.

Following the cooling event, global temperature rose again, albeit slowly, reaching a modest maximum at c. 15 Ma in the early Middle Miocene (Langhian). This generally cooler climate was in part responsible for the prevalence of siliciclastic (sandy, clayey) over calcareous sedimentation in the Oligocene and Miocene, particularly in Denmark, north-

ern Germany and other parts of central/northern Europe. However, it should be noted that in these regions, the most remarkable decrease of calcareous sedimentation in the entire Cenozoic occurred much earlier, during the Paleocene, despite the prevailing 'greenhouse' climate.

Paleocene – In Denmark (Nielsen 1931; Regenhardt 1961; Jäger 1983, 2005; Jäger *et al.* 2018 and unpublished) and in the region around the cities of Maastricht (the southeastern Netherlands) and Liège (northeastern Belgium) (Jäger 1993), many serpulid genera survived the Cretaceous/Paleocene extinction event remarkably well, although many changes occurred at species level. Serpulids reached a diversity peak in the middle Danian at Faxe, Denmark (Nielsen 1931; Milàn *et al.* 2022, 2023; Jäger *et al.* 2018, unpublished). In these parts of Europe, after the Cretaceous/Paleocene extinction event, sedimentation soon returned to deposit a similar kind of material as before in the respective region. In Denmark, the main extinction phase for serpulids (and other benthic marine invertebrates) occurred near the Danian/Selandian boundary, coinciding with a remarkable shift from predominantly calcareous to predominantly siliciclastic sedimentation. In the Gundstrup gravel pit in Denmark, hitherto in two of the numerous Cretaceous and Danian genera, *Neovermilia* Day, 1961 and *Pentaditrupe* Regenhardt, 1961, descendants of were found in early Selandian sediments (Kočí *et al.* 2023, 2025).

Following the early Selandian, serpulids became rare or absent across large parts of Europe for the rest of the Paleocene. Among the few serpulid-rich exceptions of Thanetian age are two localities in the Helvetic palaeorealm of the northernmost Alps (MJ, personal observations): In the glauconitic sandstone in the Kroisbach stream at the Haunsberg hill near Salzburg in Austria, tubes of the genera *Protula*, *Filograna* Berkeley, 1835 and undetermined Serpulidae were found together with *Glomerula* Nielsen, 1931, a genus assigned not to the family Serpulidae but to the closely related family Sabellidae Latreille, 1825, although it also secretes a serpulid-like calcareous tube, and an undetermined species of rotulariid serpulids is detected in the upper Thanetian of the Kressengraben creek near Siegsdorf in Bavaria, southern Germany. Moreover, Wrigley (1950) reported *Pyrgopolon* (*Turbinia*) *praecursor* Wrigley, 1950 from the Thanetian of several localities in France.

Outside Europe, some regions show a higher abundance and diversity of serpulids during the Selandian and Thanetian. From the Middle Paleocene of the Emperor Seamounts in the northwestern Pacific Ocean, Lommerzheim (1981) described fragmentary material tentatively assigned to *Protula*? sp. and *Hydroides*? sp., as well as tubes and opercula

of *Spirobranchus*? sp. (reported under the synonym '*Pomatoceros*? sp.'), and six different, morphologically advanced genera of the subfamily Spirorbinae Chamberlin, 1919.

Spirorbinae, characterized by their small spiral tubes, have existed since at least the Bajocian (MJ, personal observation) or Bathonian (Vinn *et al.* 2024a), but are recorded from only a few localities until the end of the Early Cretaceous. Some of the Cenomanian Spirorbinae described by Lommerzheim (1979) are now interpreted as Serpulinae instead (Jäger, unpublished). In the Late Cretaceous and in the Danian (Early Paleocene), the genus *Neomicrobis* Rovereto, 1903, a phylogenetically basal genus combining features of Spirorbinae and Serpulinae, was common and widespread. It was occasionally associated with the small *Bipygmaeus* Regenhardt, 1961 and, less often and mainly during the later half of the Late Cretaceous and in the Danian (Jäger 1983, 1993, 2005), with specimens of the genera *Spirorbis* Daudin, 1800, *Pileolaria* Claparède, 1868 in 1868–1870 and *Neodexiospira* Pillai, 1970. Given the slow diversification of Spirorbinae, the presence of the six above-mentioned Middle Paleocene genera in the Emperor Seamounts (Lommerzheim 1981) is surprising. Probably, an earlier rise in diversity of Spirorbinae is obscured by the simple morphology of their tubes. Furthermore, apart from the relatively large and conspicuous opercula of *Neomicrobis*, hitherto only very few of the tiny and therefore usually not recognized, but diagnostically important opercula of other Late Cretaceous and Paleocene Spirorbinae have been adequately described.

Rotulariid Serpulinae build larger spiral tubes than Spirorbinae and can be distinguished by not being permanently cemented to a substrate for their lifetime. 'Rotulariids' is not a tribe or genus in the sense of zoological nomenclature, but a polyphyletic group of non-spirorbin Serpulinae displaying a uniform morphogenetic countdown program (Seilacher *et al.* 2008) and forming a usually medium-sized to large, tightly coiled spiral. The juvenile initial tube portion is non-spiral and attached to a substrate, but soon the tube starts to form a tightly coiled spiral, which is only indirectly attached to the substrate in the small centre of the spiral's underside via the anterior end of the initial tube portion. Later, the spiral becomes free by breaking off and rests on, or partly embedded in, the soft seafloor. Finally, at least some rotulariids turn the entire spiral vertically and build a straight anteriormost tube portion standing upright like a chimney. Rotulariids have existed since the Jurassic, but in Europe they thrived predominantly from the Hauterivian to the Cenomanian (locally to Turonian). Although they subsequently disappeared from Europe, they continued to flourish elsewhere, for example, in the Santonian to the Maastrichtian of Western Australia (McNamara 2023), before re-colonizing Europe (southern

Sweden, Denmark, the Netherlands, Belgium) in the Danian. A non-European example of Paleocene rotulariids is *Tectorotularia tobar* (Gardner, 1935) from the Late Paleocene Midway Group of Texas.

Eocene – In general, the Eocene serpulid fauna of Europe is rich in specimens and diversity. From the Early Eocene temperature maximum to the minimum in the earliest Oligocene, surprisingly, serpulid diversity gradually increased throughout the Eocene and locally (Latdorf and Mammendorf, northeastern Germany) into the earliest Oligocene. Only close to the temperature minimum, partly at the Eocene/Oligocene boundary, partly during the Early Oligocene, some phylogenetic lineages of serpulids and closely related sabellids, which had been common and widespread during the Cretaceous, Paleocene and Eocene, became either extinct or disappeared from Europe (see below).

During the Eocene, two main regions with distinct serpulid faunas can be recognized in large parts of Europe:

(1) The southern European fauna occurs in calcareous, marly or sandy sediments and extends northward to the Helvetic palaeorealm of the northernmost Alps in northern Switzerland, Bavaria (southern Germany) and northern Austria, and to the Waschbergzone north of Vienna. The fauna is dominated by large benthic foraminifera (LBF) and often common or mass-occurring rotulariid serpulids, predominantly *Rotularia spirulaea* (Defrance, 1827). This species ranges from the Early to Late Eocene and is recorded from Spain, France, Switzerland, southern Germany, Austria, Hungary, Italy, Croatia, Romania, Turkey, and, outside Europe, in Egypt, Iran and India.

In addition to *R. spirulaea*, three other species of *Rotularia* and several other genera of Serpulinae occur, including *Filograna*, *Protula*, *Serpula*, *Ditrupa*, *Propomatoceros* Ware, 1975, *Spirobranchus* de Blainville, 1818, *Placostegus*, *Pyrgopolon* de Montfort, 1808 (e.g., Rovereto (1904); Schmidt (1955a, b); Gatto & Radwańska (2000); Jäger (personal observations). The sabellid genus *Glomerula* (e.g., '*Serpula maeandrica*' Schmidt 1955b) is also present, but very rare. A morphologically specialized species of the genus *Pyrgopolon*, *P. alata* (d'Archiac, 1850), found in France, Italy and Croatia, bears two very large lateral keels acting like a snowshoe on soft ground (Savazzi 1995, 1999). Spirorbinae stay moderately diverse in the Eocene, with *Neomicrorbis* occurring in the Late Eocene (Priabonian) of the Helvetic palaeorealm.

From western Washington State, U.S.A., Kočí *et al.* (2022a, b) introduced two new species of the genus *Neodexiospira* Pillai, 1970, one from the Early Eocene and one from the Late Eocene, as well as one new species of serpulid subgenus *Metavermilina* (*Veprecu-*

lina) from the Late Eocene.

(2) The central/northern European fauna occurs in predominantly clayey or sandy sediments in northern France, southern England, Belgium, the Netherlands, northern Germany and Denmark, and extends to eastern Europe as far as Samland, Russia (Noetling 1885, 1888). In claystones and sands, serpulids adapted to life on, or partly within, soft substrates dominate by far, at least in number of individuals, and at some localities also in number of species.

Rotularia spirulaea, despite being a soft substrate dweller, is absent from the central/northern European fauna. In contrast, *Rotularia bagnoriensis* (Mantell, 1822) is very common in the Early Eocene (Ypresian) London Clay at the coast at Bognor Regis, southern England, and also occurs, together with *Ditrupa plana* (J. Sowerby, 1815 in 1812–1815), at other London Clay localities in southern England. *R. bagnoriensis* is also recorded from the Plastic Clay of the latest Early Eocene (Ypresian) to early Middle Eocene (Lutetian) Lillebælt Formation in Denmark (Gravesen 1993; specimens from the coast at Trelde near Fredericia exist in the collection of the late Inga Krause, which is now added to MJ's collection) and extends northeastward to Samland, Russia (Noetling 1888). Mychko & Clachula (2025, Fig. 5 m, n) figured badly preserved tubes of *Rotularia* sp. indet. under the name '*Vermicularia bagnoriensis*' from the Sambia peninsula in Kaliningrad, Russia. However, these authors stated a Late Eocene age, so that the affiliation to the species *R. bagnoriensis* remains questionable. It appears that *R. bagnoriensis* benefited not only from the Ypresian temperature maximum but was also adapted to tolerate lower temperatures than *R. spirulaea* (Defrance, 1827), which is widespread throughout the Eocene, but restricted to the southern parts of Europe and a few regions outside Europe.

The most characteristic serpulid assemblage in central European Eocene claystones consists of other typical soft-bottom dwellers with a long free tube portion and a short or absent attached tube portion. Here, the most common and widespread species is *Ditrupa strangulata* (Deshayes, 1825), often accompanied by *Pyrgopolon* (*Pyrgopolon*) *mellevillei* (Nyst & Le Hon, 1862) and *Protula extensa* (Solander in Branden, 1766), but also other species of these three genera were described from the Eocene and Oligocene, mainly from England, France, Belgium, the Netherlands and northern Germany (e.g., Wrigley (1950, 1951) and references cited therein). Due to the lack of any characteristic ornamentation in tubes of *Ditrupa* and *Protula*, it is often difficult to properly distinguish between species, and some nominal species may prove to be synonyms. For example, Zibrowius & ten Hove (1987) detected very similar microstructure in tubes of Middle Eocene (Lutetian) *Ditrupa*

strangulata and extant *Ditrupa arietina* (O.F. Müller, 1776), and ten Hove & Smith (1990) likewise noted the close similarity of *Ditrupa strangulata* and *Ditrupa arietina*. Species of the subgenus *Pyrgopolon* (*Turbinia*) Michelin (1845 in 1840–1847) also occur at several localities.

In the genus *Ditrupa*, the calcareous tube is not attached to a substrate at all, and in adult *Protula* and *Pyrgopolon* the free anterior tube portion is longer than the attached posterior tube portion. Among these three genera, *Ditrupa* is the most specialized for life on soft, sandy or muddy substrate. While *Protula* and *Pyrgopolon* possess not only a long free tube portion, but also a well-developed attached posterior tube portion, *Ditrupa* initially attaches to some sand grains only by means of its primary, organic tube (Charles et al. 2003), which is not preserved in any fossil and normally also not in any recent adult specimen. Subsequent longitudinal tube growth continues in an unattached and calcified mode and only from this stage onward becomes well preservable.

The genus *Protula* has existed since at least the Paleocene (Thanetian) and is common from the Eocene to the present. A possible relationship of *Protula* to several species of the Cretaceous genus *Parsimonia* Regenhardt, 1961 may be debated; the youngest known specimen of *Parsimonia* comes from the Maastrichtian of Turkey (Vinn et al. 2024b).

Among the studies dealing more comprehensively with central/northern Eocene and Oligocene serpulids, a considerable proportion focuses on the relatively large and morphologically conspicuous opercula of the genus *Pyrgopolon* de Montfort, 1808 (syn. *Sclerostyla* Mörch, 1863), e.g., Nyst (1845), Schmitt (1927); Gerth (1941); Wrigley (1951); Cupedo (1980); Gatto & Radwańska (2000).

Species of the genera *Ditrupa*, *Protula*, and *Pyrgopolon* occur together at several localities, for example, in the late Middle Eocene (Bartonian) at the coast of Barton-on-Sea in southeastern England, and in the latest Eocene ‘Gehlbergsschichten’ at Handorf near Peine, northwestern Germany (MJ, personal observation). At least two of these three genera are present in many outcrops of siliciclastic sediments, ranging from the Ypresian (Early Eocene) London Clay at the Isle of Sheppey in southeastern England to the Early Oligocene of several central European localities. For example, MJ found *Ditrupa* and a few *Pyrgopolon* tubes, but no *Protula*, in Eocene sediments at the coast between Cadzand-Bad in the Netherlands and Knokke in Belgium. A similar assemblage occurs also in the Eocene of Samland (Noetling 1885, 1888).

Together with these serpulid genera adapted to life on soft seafloor, a few genera adapted to permanent attachment to solid substrate lived during the Eocene in central/northern Europe, but they are considerably less common at most localities. For example,

Noetling (1885) described and figured two species under the genus ‘*Serpula*’, which nowadays may be tentatively assigned to *Josephella* Caullery & Mesnil, 1896 and *Bipygmaeus* Regenhardt, 1961.

Eocene/Oligocene boundary – The Oligocene serpulid fauna is impoverished. For example, Şuraru & Şuraru (1966) reported five species in the Late Eocene, but only three species in the Early Oligocene of Romania. The relatively cool Oligocene climate, compared to the much warmer Eocene and the somewhat warmer Miocene, probably contributed to the relatively lower diversity of the Oligocene serpulid fauna.

At least three serpulid genera and one sabellid genus became almost extinct at the Eocene/Oligocene boundary or, respectively, during the Early Oligocene. Before, all four genera had very long and successful histories. In detail:

The genus *Rotularia* Defrance, 1827 and related rotulariids had existed since the Jurassic (Stevens 1967) and had been diverse, common and widespread from the Hauterivian until the Late Eocene (Priabonian).

Pyrgopolon is recorded by a single operculum of the subgenus *P.* (*Turbinia*) Michelin, 1845 in 1840–1847 from the Middle Permian (Sanfilippo et al. 2018), then disappeared from the fossil record until it re-occurred either in the Hauterivian, although more detailed studies are necessary to prove their possible affiliation to *Pyrgopolon*, or in the Barremian at the locality Serre de Bleyton, Drôme, southern France (Jäger 2011) and thrived in the Albian Washita Group in Texas, where *Pyrgopolon* (*Septenaria*) Regenhardt, 1961 is found in high numbers of tubes encrusting large coronas of the echinoid *Macraster* F. Roemer, 1888 (Jäger 2005 and personal observation). Since the Early Cenomanian (Lommerzheim 1979), during the entire Late Cretaceous (e.g., Jäger 2005; Kočí 2012; Kočí & Jäger 2016; Kočí et al. 2016), during the entire Late Cretaceous, and until the Eocene, (Wrigley, 1951), *Pyrgopolon*, its synonym *Sclerostyla*, and several subgenera thrived at many localities, until in the Early Oligocene (Rupelian) only few *Pyrgopolon* species existed, although locally tubes and opercula of *Pyrgopolon* (*Pyrgopolon*) *mellevillei* were still common in the Rupelian (‘Tongrian’) in the southeastern Netherlands and northeastern Belgium; see below. Only a few questionable *Pyrgopolon* specimens (reported under the synonym *Sclerostyla* Mörch, 1863) were recorded by Rovereto (1899, p. 90; 1904, p. 68) from the Pliocene of Savona, Italy.

Neomicrorbis has existed since at least the Bajocian (MJ, personal observation) or the Bathonian, but had been restricted to only a few localities until the end of the Early Cretaceous (Vinn et al. 2024a), before it became common and widespread from the Cenomanian to the Early Paleocene (Danian) (Nielsen

1931; Regenhardt 1961; Jäger 1983, 1993, 2005; Jäger *et al.* 2018), and persisted until the Late Eocene (Priabonian) at few localities, but with several species, in the alpine Helvetikum realm in Bavaria, southern Germany (Rovereto 1904; MJ personal observation).

The sabellid *Glomerula* exists since the Middle Permian (Sanfilippo *et al.* 2017b) and was common and widespread in the Jurassic (*e.g.*, Goldfuss 1831 in 1826–1844 (reported under *Serpula*); Ippolitov 2007 (reported under *Cycloserpula* Parsch, 1956); Jäger 2005; Słowiński *et al.* 2022; and many others), Cretaceous and Danian (*e.g.*, Nielsen 1931; Regenhardt 1961; Wiesemann 1966, Jäger 1983, 1993, 2005; Kočí *et al.* 2017; Jäger *et al.* 2018) and locally persisted until the Late Eocene (late Priabonian) (Jäger 2005).

In summary, *Rotularia* and some other closely related rotulariids and also *Neomicrorbis* and *Glomerula* disappeared from the fossil record at, or very close to, the Eocene/Oligocene boundary, at least in the northern hemisphere, whereas from New Zealand, Fleming (1971) provided a simple drawing of a tube of '*Glomerula* sp.' from the Oligocene and mentioned also occurrences in the Late Eocene, Early Miocene and recent tubes from dredgings. However, without more detailed illustrations and description it remains uncertain, whether or not all these tubes from New Zealand really belong to *Glomerula*. *Pyrigopolon* disappeared somewhat later, within or at the end of the Early Oligocene (Rupelian).

Unlike *Rotularia* and some other closely related rotulariids, which became extinct worldwide, the genera *Pyrigopolon*, *Neomicrorbis*, and *Glomerula* still have living representatives. However, they are separated from their fossil ancestors by a long gap in the fossil record lasting up to 33.9 Myr in the case of *Neomicrorbis* and somewhat less in *Pyrigopolon*, whereas in the case of *Glomerula* the gap may be shorter, depending on the interpretation of the Oligocene and Early Miocene specimens mentioned by Fleming (1971). However, extant species of most of these genera did not return to European seas, except for *Neomicrorbis* which lives in the Azores (Zibrowius 1972). *Pyrigopolon* is known by three Recent species occurring near Curaçao and other Caribbean Islands (ten Hove 1973). Perkins (1991) detected the Recent *Glomerula piloseta* (Perkins, 1991) in a lagoon near Lizard Island, Queensland, Australia, and introduced it under the synonym *Calcisabella* Perkins, 1991.

The situation is a bit different in two other serpulid taxa – the subgenus *Metavermilina* (*Vepreculina*) Regenhardt, 1961 and the genus *Neodexiospira* Pillai, 1970. In both taxa, Kočí *et al.* (2022a, b) introduced a new species from the Late Eocene (and in *Neodexiospira* also another new species from the Early Eocene) of western Washington State, U.S.A. While it is still uncertain whether the Miocene '*Serpula*' *granosa* Reuss, 1860 from the Czech Republic belongs to *Metavermil-*

ia (*Vepreculina*), it is obvious from Kočí *et al.* (2022a, Table 1) that *Neodexiospira* reappears with different species in the Middle and Late Miocene and in the Pleistocene, and approximately a dozen *Neodexiospira* species live in recent seas. Despite several differences, these two genera match the above-discussed four genera (except for the Early Oligocene occurrence of *Pyrigopolon*) by their gap in the fossil record covering the entire Oligocene and the Early Miocene. Although this worldwide gap is considerably shorter than in the other four genera, the gap in the European fossil record is also very long. In *Neodexiospira*, it begins already in the Middle Paleocene (Selandian), and in *Vepreculina* in the Early Paleocene (Danian), as several assignments of Danian species to *Vepreculina* are erroneous and will be revised.

Although the fossil histories of the above-discussed genera differ in detail, they share a long gap in the Oligocene and a more or less long timespan later. But except for *Rotularia* and related genera, they must have survived at unknown, presumably southern, localities for millions of years, until Neogene or/and living descendants were discovered.

Presumably, this long gap is partly caused by a sampling bias, as palaeontological research has historically focused more on higher latitudes with temperate (palaeo-)climate (Europe and North America) than on lower latitude regions with warm (palaeo-)climate, to which many marine species may have migrated at or soon after the Eocene-Oligocene cooling event. Another bias may be that, due to increasing competition in warm shallow shelf regions, several geologically old taxa shifted into deeper water habitats with reduced competition. Sediments of such environments are in many regions still buried beneath younger deposits, remaining poorly accessible.

Early Oligocene ('Latdorfian', *Rupelian*) – However, local exceptions to the general trend of low serpulid diversity at the Eocene/Oligocene boundary and in the Early Oligocene are recorded from eastern Germany. In the earliest Oligocene claystones at Latdorf and in the coastal Early Oligocene sediments at Mammendorf, the serpulids reached a maximum in diversity just at, respectively, shortly after the conspicuous minimum in the oceanic temperature curve. Von Koenen (1891) described part of this exceptional fauna from eastern Germany, mainly from Latdorf, but erroneously combined true serpulids and gastropods under the gastropod genus *Vermetus* Daudin, 1800. Recent revision (MJ, unpublished) shows the presence at Latdorf and Mammendorf of at least 16 different serpulid genera, 14 of which still exist today, albeit by different species. But the geologically youngest tubes of *Protectoconorca* Jäger, 1983 and the spirorbin *Bipygmaeus* tubes are known from the Early Oligocene of Mammendorf (MJ, personal

observations), before they became extinct. The six genera discussed in the previous chapter are absent even in these highly diverse communities.

The genus *Ditrupa* appeared in the Danian and rapidly became common or even mass-occurring in Denmark, the Netherlands and Belgium (Rosenkrantz 1920, Jäger 1993) and was again abundant during the Eocene. In contrast, it is rare or absent at several moderately to highly diverse Early Oligocene soft-bottom localities. Finally, during the Late Oligocene and especially since the Miocene, it became widespread and often abundant in soft-bottom communities until today.

Protula is common in the Eocene and even more frequent in the Early Oligocene, although its worn fragments are sometimes hardly distinguishable from similarly shaped shells of vermetid gastropods (see Bieler & Petit 2011), which became more common and diverse in the Oligocene and Miocene.

The small spirals of the subfamily Spirorbinae slowly but steadily increased their diversity and geographical occurrences in the entire Cenozoic until today.

Shortly before disappearing, *Pyrgopolon* had been common in the southeastern Netherlands and northeastern Belgium, from where Nyst (1845) named small fossils, which he erroneously interpreted as solitary corals, '*Cyclolites trochoides*'. Later, these small fossils were recognized to be opercula of serpulids, respectively the serpulid genus *Sclerostyla* Mörch, 1863, which, however, is a junior synonym of *Pyrgopolon* de Montfort, 1808, by Rovereto (1903, 1904), Gerth (1941), Albrecht & Valk (1943), Wrigley (1951) and others. From the 'Tongrien' (Early Oligocene) of Southern Limburg, Albrecht & Valk (1943) described *Protula septaria* and *Pyrgopolon* (*Pyrgopolon*) *mellevillei*, together with *Vermetus* (*Turbinella*) *tumidus* von Koenen, 1891 and *Vermetus* (*Turbinella*) *turbinatus* (Philippi, 1846), two species which Albrecht & Valk considered gastropods, but perhaps may be serpulids. Moreover, Kadolsky (2022) identified opercula of a new species, *Spirobranchus limburgicus*.

During the Early Oligocene, a narrow and only temporarily normal marine connection in the Rhine valley linked the North Sea Basin to the Molasse Basin along the northern border of the Alps. A less deeply sunken lateral widening of the Rhine valley is known as the Mainz Basin in western Germany. From the Mainz Basin, Grimm & Grimm (2003) documented *Serpula* sp. and *Spirobranchus* sp. (reported as '*Pomatoceros*') attached to nearshore rhyolite boulders from the Eckelsheim sandpit. Grimm et al. (1999) listed very common *Spirorbis* sp. attached to small pebbles and rare *Protula* sp. and Serpulidae indet. from a sandpit at Siefersheim.

Late Oligocene (Chattian) – During the Late Oligo-

cene, the southern margin of the North Sea Basin was characterized by several embayments extending southward to southeastward into northern Germany. From west to east, these bays were named: (1) The Köln (= Cologne) Bay extending into parts of the Netherlands, Belgium and westernmost regions of northwestern Germany, (2) the Kassel Bay in the central region of northwestern Germany including Astrup near Osnabrück, the Doberg hill near Bünde, Bodenburg south of Hildesheim, and the region around Kassel, (3) the Thuringian Basin and Subhercynian Basin in eastern Germany.

(1) Köln Bay: Görges (1940) reported *Serpula corrugata* Goldfuss (a junior homonym; the actual name is *Spiraserpula? subpacta* (Rovereto, 1904)), *Serpula flagelliformis* J. de C. Sowerby, 1844 in 1840–1846 and *Spirorbis* sp. from green-grey Late Oligocene sands at Rumeln in Lower Rhine lowland, northwestern Germany.

(2) Kassel Bay: Concerning Late Oligocene serpulids, the Kassel Bay and especially the localities Doberg hill near Bünde and Astrup near Osnabrück are the most diverse and most fossiliferous localities. From Astrup, Goldfuss (1831–1833 in 1826–1844), partly supported by Münster, described and figured six species, all introduced under the genus '*Serpula*'. Later, Diedrich (2012) provided additional details and small photographs of two of Goldfuss' species and documented a third taxon, *Josephella* sp. Rovereto (1904) and Schmidt (1955b) provided a few systematic and nomenclatural updates. The current, though still provisional names of the six Goldfuss species from Astrup are as follows:

Metavermilia? quadricanaliculata (Münster in Goldfuss, 1833).

Spiraserpula humulus (Münster in Goldfuss, 1833); this species includes '*Cementula angulata* (Münster)' sensu Diedrich (2012, pp. 167, 170, fig. 7.1) and one specimen of '*Rotularia corrugata* Goldfuss' sensu Diedrich (2012, pp. 167, 170, fig. 7.3).

Spiraserpula? subpacta (Rovereto, 1904), syn. *Serpula corrugata* Goldfuss, 1833 (non Link); this species includes a different specimen of '*Rotularia corrugata* (Goldfuss)' sensu Diedrich (2012, pp. 167, 170, fig. 7.2).

Spirobranchus angulata (Münster in Goldfuss, 1831), syn. *Spirobranchus triqueter* fide Schmidt (1955b).

Spirobranchus triqueter bicanaliculatus (Münster in Goldfuss, 1831).

Spirorbis umbiliciformis (Goldfuss, 1831).

Josephella sp. was not mentioned in Goldfuss' monograph, but described and figured by Diedrich (2012, p. 167, 170, fig. 7.4) as '*Janita dentalina* (Münster)' from Astrup. Before Diedrich (2012), this species, but named '*Serpula dentalina*', had been reported several times from the Doberg hill near Bünde. The first such record was by Hubach (1957, pp. 15, 31), who described fist-sized colonies of this species, occurring at Doberg hill in layer no. 10. Hubach noted these tubes to resemble small smooth *Dentalium* shells. This occurrence of '*Serpula dentalina*' was subsequently mentioned also by Pannkoke (1979) and Kaiser & Ebel (eds; 2014). However, a taxon of an Oligocene species '*Serpula dentalina* Münster' can not be traced in modern taxonomic databases. The only valid species, '*Serpula dentalina*', had been introduced by Leymerie (1851). This is a species occurring in Maastrichtian sediments in the Pyrenees; it is large-sized and has a long, horn-shaped, smooth free tube portion. Probably it belongs to the subgenus *Pyrgopolon* (*Pyrgopolon*) de Montfort, 1808, or, less probably, to the genus *Pentaditrupe* Regenhardt, 1961. However, the colonies from Doberg hill and from Astrup mentioned by Hubach and subsequent authors, respectively, figured by Diedrich, are much smaller in tube diameter and clearly belong to a different species and genus.

Two additional serpulid species already listed from Astrup also occur at Doberg hill: Hubach (1957) mentioned '*Serpula*' *corrugata*, Pannkoke (1979) '*Serpula*' *angulata* and *corrugata*.

From three localities – Diekholzen near Hildesheim, between Bodenburg and Evensen, and the Eichteiche lakes near Neuhoof/Lamspringe – Rust (1999) described and figured local mass occurrences of accumulated *Ditrupe* tubes, and from Diekholzen and the Eichteiche, he also reported occasional tubes of *Spiraserpula*? *subpacta* (Rovereto, 1904) (as '*Serpula corrugata* Goldfuss'). Much earlier, Philippi (1843) had already listed '*Serpula corrugata*' and an undeterminable '*Serpula conorta* n. sp.' from Diekholzen, although Rust (1999) states that many of Philippi's fossils had instead been collected at Freden. At Diekholzen, MJ collected *Ditrupe* tubes, a high-spiral tube of *Spiraserpula*? *subpacta*, and small spirorbins.

From Kassel-Wilhelmshöhe, Goldfuss (1831 in 1826–1844) described and figured a small '*Serpula corniculum* Goldfuss, which belongs to the subfamily Spirorbinae and possibly to the genus *Spirorbis* sensu stricto.

(3) In eastern Germany, the Late Oligocene serpulid fauna appears to be scarce, although only a few localities have been studied. Serpulids, if present, are mainly represented by the genera *Ditrupe* (common, for example, at Kabrow gravel pit near Sternberg)

and *Protula*.

Surprisingly, the Late Oligocene serpulid fauna in Denmark is very different from the approximately contemporary serpulid faunas in northern Germany. The only serpulid genus reported from both regions is *Protula*, which, however, is considerably more common in Denmark than in northern Germany. This striking difference can only partly be explained by the fact that the above mentioned classical fossil-rich Late Oligocene outcrops in northern Germany represent more or less sandy sediments deposited in relatively shallow, more or less nearshore waters, in contrast to the clayey sediments in deeper shelf offshore regions of the Oligocene North Sea basin in Denmark. Paradoxically, the Late Oligocene serpulid fauna in Denmark is somewhat more similar to the Early Oligocene serpulid fauna in eastern Germany, despite the differences in facies and geological age, because both faunas include the common occurrence of *Protula* and the occasional presence of *Filigranula* and *Placostegus* (at Mammendorf; MJ, unpublished) and vermetid gastropods.

Miocene – The serpulid fauna in Miocene micaceous claystones in the southeastern part of the North Sea basin is relatively low diverse, and most species are rather rare, except for locally common occurrences of *Ditrupe arietina* or *Spirorbis*? sp. In contrast, a highly diverse but generally small-sized mollusc fauna prevails during the Miocene. However, the presence of many small mollusc shells did not compensate for the disadvantage of a muddy sea-floor for fixosessile serpulid taxa. For example, at the classic localities Twistingingen claypit and Morsum cliff in north-western Germany, as well as the Gram claypit in Jylland, Denmark, *Ditrupe arietina* is the only common serpulid species, whereas other serpulids are rare. From Twistingingen, Janssen (1972) described tube fragments belonging to four more serpulid species: *Protula* cf. *canavarii* Rovereto, 1899, *Josephella* sp., *Serpula* sp., and a very small unidentified species, but the material is too sparse and fragmentary to allow reliable species-level determination. In the Middle Miocene Diest Sands at Ramsel, province of Antwerpen, Belgium, concretions yielded relatively common '*Spirorbis* sp.', very rare '*Serpula* sp.' and other unidentified annelids (Janssen & Müller 1985).

In contrast to the serpulid-poor clayey Miocene sediments of the North Sea basin, the often more sandy or/and more calcareous sediments in southern parts of central Europe and in southern Europe, at least locally, yield a higher diverse serpulid fauna, reported, for example, from southern Germany (Jäger & Schneider 2009), Austria (Schmidt 1955b, 1968), the Czech Republic (Reuss 1860); southern Poland (Radwańska 1994a, b), Romania (Zilch 1934), Spain (Zibrowius in Barrier 1991; Jäger in Hoffmann

et al. 2020), France (Philippe & Prieur 1984) and Italy (Seguenza 1880; Rovereto 1899, 1904; Zibrowius 1991). Jäger & Schneider (2009) concluded, “that considerable similarity in composition exists between the Miocene serpulid faunas from the Mediterranean (Southern Alpine Molasse Basin, N Italy) via the Rhone Graben (SE France) into the western (Northern Alpine Molasse Basin, SE Germany) and eastern Central Paratethys (Carpathian Basin, Romania)”.

As shown in the major historical monographs by Rovereto (1904), Schmidt (1955b) and Radwańska (1994a), the number of described serpulid species increased considerably during the Miocene. However, the number of serpulid genera distinguished by palaeontologists increased only moderately. When several of the most comprehensive works on European Miocene serpulids are considered together, the most frequently mentioned genera (in part updated to current nomenclature) are *Josephella*, *Filograna* (or *Salmacina* Claparède, 1870 in 1868–1870), *Vermiliopsis* de Saint-Joseph, 1894, *Serpula* sensu stricto (or ‘*Serpula*’ in the broad historical sense, encompassing several different genera), *Spiraserpula* Regenhardt, 1961, *Hydroides*, *Ditrupea*, *Spirobranchus*, *Placostegus*, *Spirorbis* sensu stricto (or ‘*Spirorbis*’ encompassing several different genera). Less frequently mentioned genera include *Filogranula*, *Metavermilium* Bush, 1905, *Metavermilium* (*Vepreculina*), *Semivermilium* ten Hove, 1975, *Pseudovermilium* Bush, 1907, *Janita* de Saint-Joseph, 1894, *Neovermilium*, *Ficopomatus* Southern, 1921, *Pomatostegus* Schmarda, 1861, the spirorbin genera *Neodexiospira* Pillai, 1970, *Leodora* de Saint-Joseph, 1894, *Pileolaria* and *Protolaespira* Pixell, 1912. Several additional genera that are rarely or not at all mentioned in European Miocene literature must nevertheless have existed during the Miocene elsewhere on Earth, as they are known both from pre- and post-Miocene strata. Examples include *Pyrgopolon* and *Neomicrobis*. Altogether, slightly more than 25 genera have been recorded from the Miocene. This number appears low, if compared to the 47 genera of only the non-spirorbin genera recognized worldwide in the extant fauna by ten Hove & Kupriyanova (2009), to which a considerable number of spirorbin genera must be added.

However, this discrepancy should not be interpreted as an ‘explosive’ diversification of serpulids within the geologically relatively short timespan of 5.333 Myr from the end of the Miocene to the present. Instead, it reflects preservational and methodological biases. In the fossil record, usually only calcareous serpulid tubes are preserved as fossils, which considerably diminishes the number of diagnostic features used for taxonomic differentiation, if compared to recent taxa, where soft parts morphology and often the non-calcified opercula are available for study and differentiation between taxa. In Miocene serpulids,

the sparsity of recognized fossilized opercula (but see Radwańska 1994b; ten Hove & Nishi 1996 and, for Oligocene opercula, Kadolsky 2022), as well as the total lack of preserved soft parts, hamper proper assignment of many fossil serpulid tubes to well-established recent genera.

For the determination of Miocene and geologically younger fossil serpulid tubes, it appears more promising to compare them with morphologically identical tubes of extant species than with geologically older species. This approach has been successfully applied by several zoologists specializing in recent serpulids, who revised Neogene fossils or improved previous paleontological identifications; e.g., Zibrowius & ten Hove (1987); Zibrowius (1979, 1988, 1991); ten Hove & van den Hurk (1993); ten Hove & Nishi (1996); Sanfilippo (1998, 2003).

Conclusions

The calcareous tubeworm palaeocommunity of the Late Oligocene Brejning Formation has yielded previously undescribed material from five localities in Jylland, Denmark, located along a west-northwest – east-southeast oriented line of subcrops/outcrops of Late Oligocene rocks running through northern Jylland. This palaeocommunity comprises the following serpulid species: *Protula* cf. *septaria* (Giebel, 1858), *Filogranula mogenstrupensis* sp. nov., *Placostegus vilsundensis* sp. nov., *Placostegus* cf. *erectus* (Nielsen, 1931) and *Placostegus* cf. *bilobatus* (von Koenen, 1891).

This is further complemented by the recognition of *Vermetus jyllandensis* sp. nov., which represents the first documented vermetid gastropod in the Danish Late Oligocene. In the external view, the vermetid shell appears remarkably similar to the posterior tube portion of the serpulid *Protula* cf. *septaria*. Despite this macromorphological similarity, these two zoologically unrelated marine invertebrates can be distinguished by their shell microstructures. *Vermetus* possesses a shell of tall prismatic aragonite crystals, whereas *Protula* cf. *septaria* displays a semi-ordered, irregularly oriented prismatic microstructure (SOIOP). The persistence of SOIOP in this lineage reinforces the diagnostic value of biocrystallography in serpulid taxonomy, especially where opercula and soft parts – essential for identifying extant genera – are absent from the fossil record.

The tube of the serpulid *Protula* cf. *septaria* has a semi-ordered irregularly oriented prismatic microstructure (SOIOP) sensu Vinn *et al.* (2008) and Vinn (2013), which consists of short prismatic crystals. While most of these crystals and crystallites align their long axes perpendicular to the tube’s longitudinal axis and parallel to the transverse section,

the defining feature of the SOIOP microstructure is that a minor portion of the crystals – and their constituent crystallites – orient their long axes roughly parallel to the tube's longitudinal axis and perpendicular to the tube's transverse section. This is most evident in the cross-sections illustrated by Vinn (2013, figs 2, 8b) and in our Figs 9–11.

In contrast, the shell wall of *Vermetus jyllandensis* sp. nov. consists of several layers; the most prominent layer is formed of tall prismatic aragonite crystals, all oriented perpendicular to the longitudinal axis of the shell. However, some similar layers in which the crystals are arranged in slightly fan-shaped aggregates may represent secondary diagenetic features. Moreover, the shell lumen of *Vermetus jyllandensis* sp. nov. was originally subdivided by hemispherical imperforate septa characteristic of vermetid gastropods, of which, however, only marginal remnants are preserved in the damaged shells.

The vast majority of the studied tube fragments, especially those belonging to the genera *Protula* and *Filogranula*, represent the long free anterior tube portion, which was originally attached only indirectly to a foreign substrate via a short posterior tube portion. In contrast, most of the few *Placostegus* and vermetid fragments belong to the attached posterior tube portion. Together with the associated marine fauna and the clayey sediment, this result indicates a community living on a soft seafloor in a shelf sea in relatively calm normal marine *c.* 70–200 m deep water.

On only three of the studied fossils, serpulid tubes are found still attached to the hard parts of other invertebrates used as substrates. Although in neither of these three cases a safe decision between *syn vivo* and *post-mortem* encrustation is possible, comparisons with the life habits respectively taphonomies of recent relatives of the invertebrates used as substrates provide hints. Presumably, *Protula* encrusted the shell of an already dead gastropod, whereas *Placostegus* encrusted the spine of a living echinoid, respectively, the shell of a living brachiopod. The association of *Placostegus vilsundensis* with brachiopod margins suggest opportunistic commensal strategies aimed at exploiting host-generated feeding currents.

The Late Oligocene serpulid palaeocommunity of Jylland is surprisingly different from other Late Oligocene serpulid faunas in the southeastern part of the North Sea basin in northern and eastern Germany and Belgium, and shows only moderate similarities to the considerably more diverse and somewhat older Early Oligocene serpulid community in eastern Germany.

A rough and certainly still incomplete overview is provided on the serpulid evolution and fauna distribution in the Cenozoic, with focus on Europe and on Oligocene serpulid faunas. Two major changes in serpulid communities occurred during the Cenozoic

– the first at the Early/Middle Paleocene (Danian/Selandian) boundary, the second at and shortly after the Eocene/Oligocene boundary. The first change is connected with a change from calcareous to siliciclastic sedimentation. Global cooling is the main reason for the second change.

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