

Neovermilia gundstrupensis sp. nov. (Polychaeta, Serpulidae) from the Selandian (middle Paleocene) of Fyn, Denmark

TOMÁŠ KOČÍ, JESPER MILÀN & MANFRED JÄGER



Geological Society of Denmark
<https://2dgd.dk>

Received 24 March 2023
Accepted in revised form
9 June 2023
Published online
21 June 2023

© 2023 the authors. Re-use of material is permitted, provided this work is cited.
Creative Commons License CC BY:
<https://creativecommons.org/licenses/by/4.0/>

Kočí, T., Milàn, J., & Jäger, M. 2023. *Neovermilia gundstrupensis* sp. nov. (Polychaeta, Serpulidae) from the Selandian (middle Paleocene) of Fyn, Denmark. Bulletin of the Geological Society of Denmark, Vol. 72, pp. 135–151. ISSN 2245-7070.
<https://doi.org/10.37570/bgsd-2023-72-05>

Tubes of a new serpulid species, *Neovermilia gundstrupensis* sp. nov., from the lower part of the Kerteminde Marl Formation (Selandian, middle Paleocene) of Gundstrup gravel pit, Fyn, Denmark, represent the first serpulids of this group from the Selandian of Denmark. Within the long-ranging genus *Neovermilia* (Oxfordian to Recent), the new finds extend the last recorded occurrence of an informal sub-group of closely related serpulids from the upper Danian to the lower Selandian. *Neovermilia gundstrupensis* is characterized by a tube increasing only slowly in diameter reaching up to approximately 5 mm and possessing small, often densely spaced annular striae occasionally merging into weakly but never strongly developed annular peristomes. Almost all specimens found so far are attached to siliceous sponges of the genus *Ventriculites*. The tube morphology of the new species and the microstructure of the tube wall, as well as its palaeoecology are discussed.

Keywords: Polychaeta, tube worm, *Neovermilia*, microstructure.

Tomáš Kočí [protula@seznam.cz], Ivančická 581, Prague 9 – Letňany, 19900, Czechia and Palaeontological Department, Natural History Museum, National Museum, Cirkusová 1740 193 00 Praha 20 - Horní Počernice, Czechia. Jesper Milàn [jesperm@oesm.dk], Geomuseum Faxel/Østsjælland Museum, Østervej 2, DK-4640 Faxel, Denmark. Manfred Jäger [langstein.jaeger@web.de], Lindenstrasse 53, 72348 Rosenfeld, Germany.

The family Serpulidae includes almost exclusively marine polychaete worms living in a self-built tube made of calcareous minerals (calcite or aragonite or both). Most species attach their tube to solid substrates, e. g., pebbles or shells or other hard parts of marine animals lying at the sea-floor, or to algae or sea-grass. The earliest serpulids are known from the Permian (Sanfilippo *et al.* 2017, 2018; Ramsdale 2021), and they diversified during the Jurassic, Cretaceous and Cenozoic (e.g., Ippolitov *et al.* 2014), up to nowadays with several hundred species of serpulids inhabiting the seas and oceans (e.g., ten Hove & Kupriyanova 2009; Kupriyanova *et al.* 2020; Rouse *et al.* 2022 and many references herein). Serpulids represent a considerable part of benthic (palaeo)communities in different marine habitats, where they play a more or less important (palaeo)ecological role interacting with other marine organisms (e.g., Taylor & Wilson 2003; Rosso & Sanfilippo 2005; Schlögl *et al.* 2008; Vinn & Wilson 2010; Garberoglio & Lazo 2011; Zatoń *et al.* 2011; Sklenář *et al.* 2013; Luci & Cichowolski 2014; Luci & Lazo 2014;

Kočí & Jäger 2015; Kočí *et al.* 2017; Kočová Veselská *et al.* 2021). They also contribute to form bioconstructions associated with other reef-building organisms or microbialites (Rosso & Sanfilippo 2005; Guido *et al.* 2017), and a few serpulid species aggregate their tubes to form small reefs (e. g. ten Hove & van den Hurk 1993; Sanfilippo *et al.* 2013).

In the Maastrichtian chalk and Danian limestone, which form the pre-Quaternary subsurface in the eastern and northern parts of Denmark and in commercial inland quarries (Fig. 1), serpulids are very common and have been extensively studied (e. g., Rosenkrantz 1920; Ødum 1926; Nielsen 1931; Regenhart 1961; Jäger 1983, 2005; Jäger *et al.* 2018 and in prep; Lauridsen & Surlyk 2008; Lauridsen *et al.* 2018, Lauridsen & Bjerager 2021; Milàn *et al.* 2022, 2023). In stark contrast, only very few serpulids have been reported from the Selandian and Thanetian sediments of Denmark. Harder (1922) collected serpulids from the basal Selandian, Lellinge Greensand, which was later revised by Schnetler (2021), who concluded it

contained “numerous tubes of *Ditrupa* and *Serpula* which seem to be reworked”.

Another record is from the basal conglomerate of the Selandian Lellinge Greensand Formation, the ‘Echinoderm conglomerate’. The conglomerate formally belongs to the basal Selandian (Stouge *et al.* 2000; Clemmensen & Thomsen 2005; Schmitz *et al.* 2011), its fossil content including many *Ditrupa schlotheimi* Rosenkrantz, 1920, *Rotularia hisingeri* (Lundgren, 1891) and other invertebrate specimens reworked from the upper Danian. Among the few literature data on serpulids which really lived during Selandian time in Denmark is the record from the lower Selandian Kerteminde Marl Formation in Gundstrup gravel pit (Schnetler & Nielsen 2018). Thanks to the successful

activities at this locality of several enthusiastic amateur collectors (see Acknowledgements), a considerable number of serpulid tubes were found here and provided for our study.

Many homoeomorphies impede studies on systematics of fossil serpulids of which only the tubes, and in some genera also the calcified opercula, are preserved. Another problem when separating fossil serpulid tubes into taxa is the small morphological difference between species and the high intraspecific variation. Since about three decades, microstructure or ultrastructure of the tube, in spite of including homoeomorphies, too, is a valuable additional tool for research on systematics of living and fossil serpulid. Modern studies on the microstructure of

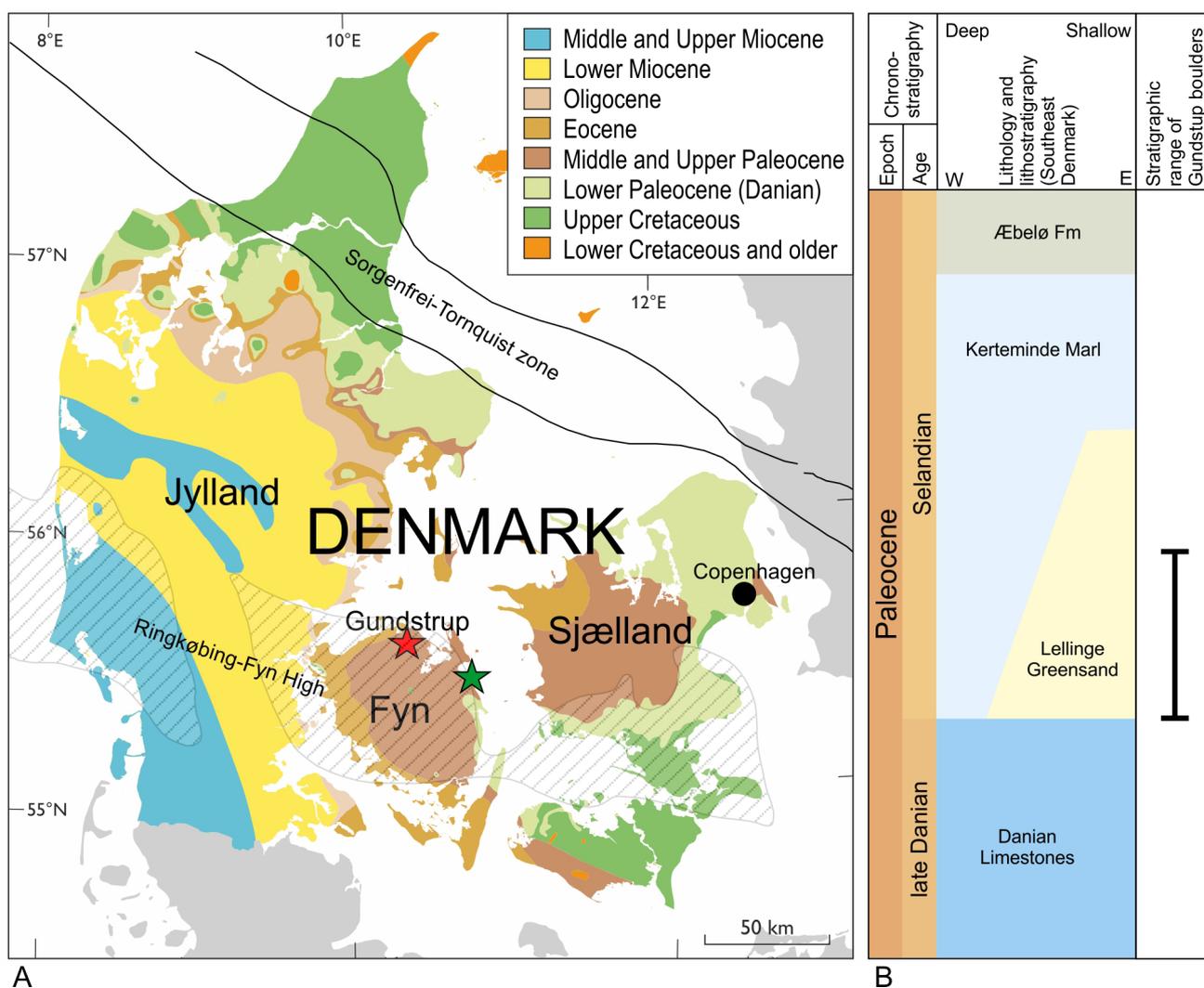


Fig. 1. **A**, Map of the pre-Quaternary subsurface in Denmark. The Gundstrup gravel pit is located at Fyn (55.56°N; 10.35°E), indicated by a **red** asterisk. Even though the pieces of Kerteminde marl found here had been transported by Pleistocene glaciers, they have been found within the subsurface area consisting of Selandian (middle Paleocene) sediments. The nearest other outcrop of the Kerteminde marls is at its type locality Lundsgårds Klint, situated south of the town of Kerteminde, indicated by a **green** asterisk. Modified after Håkansson & Pedersen (1992) and Schwarzzhans *et al.* (2021). **B**, Schematic section showing upper Danian and Selandian stratigraphy of southeast Denmark. Modified from Clemmensen & Thomsen (2005).

tube-dwelling polychaetes have been undertaken by Weedon (1994), Sanfilippo (2009a), Vinn (2005, 2007, 2008, 2020, 2021), Vinn and Furrer (2008), Vinn and Mutvei (2009), Vinn *et al.* (2008a, b, c) and references therein; for general summaries, see Ippolitov *et al.* (2014), Kupriyanova *et al.* (2020), and references therein.

The aim of the present publication is to describe these Selandian serpulids from Gundstrup gravel pit, including the microstructure of their tube wall, and to discuss their palaeoecology.

Geological setting and location

After the K-Pg boundary, the lower Paleocene sedimentation in the Danish basin was initially carbonatic, but carbonate sedimentation ceased by the end Danian due to a major regression that took place about 61.6 mya (Vandenberghe *et al.* 2012; Cohen *et al.* 2013 updated 2022), causing an erosional unconformity to the overlying Selandian deposits (e. g., Thomsen & Heilmann-Clausen 1985; Clemmensen & Thomsen 2005). The succeeding Selandian transgression gave rise to a different depositional regime dominated by siliciclastic sediments in the form of the Lellinge greensand in the eastern part of Denmark, and its lateral equivalent, the Kerteminde Marl Formation, in the deeper depositional setting towards Fyn (Clemmensen & Thomsen 2005). The Selandian Kerteminde Marl Formation is interpreted as being deposited in an outer shelf environment in the deep neritic zone at about 100 – 150 m depth with a high sedimentation rate due to a considerable input of reworked chalk, a well-oxygenated bottom water with low current activity, and a low planktonic production (Clemmensen & Thomsen 2005; Heilmann-Clausen 2010). The thickness of the Kerteminde Marl Formation is up to 150 metres, thinnest over the Ringkøbing-Fyn High and thickest northward towards the Sorgenfrei-Tornquist Zone (Sorgenfrei & Buch 1964; Clausen & Huuse 1999, 2002; Clemmensen & Thomsen 2005). The Selandian depocenter of the Kerteminde Marl Formation is interpreted to be located on the western part of Sjælland (Clemmensen & Thomsen 2005). The Kerteminde Marl Formation is overlain by the Selandian – Thanetian Æbelø Formation which is predominantly clay and represents a progressively deeper depositional environment (Clemmensen & Thomsen 2005).

The latest years have revealed a rather extensive fauna in the Kerteminde Marl Formation, especially in the glacially derived blocks at Gundstrup gravel pit. Schnetler & Nielsen (2018) described the mollusc fauna and found it to be a very diverse assemblage comprising 133 species. Vertebrates are recorded in the form of

abundant skeletal remains of teleost fishes (King 1994, Schwarzhans *et al.* 2021), and trace fossils are known in the form of *Lepidenteron mortenseni* (Schwarzhans *et al.*, 2021) a burrow interpreted to be made by the predatory Bobbit worms, which contained abundant prey remains from teleost fishes, especially the small *Bobbitichthys rosenkrantzi*, and peculiar sponge lined crustacean burrows, *Koptichnus rasmussenae*; see Vallon & Rindsberg (2022).

A large, hitherto undescribed assemblage of chondrichthyan teeth exists in the collection of the Natural History Museum of Denmark. Reptiles are known in the form of a partial turtle plastron which shows traces of predation by sharks and crocodylians (Myrvold *et al.* 2018). In addition, ostracods, sponges and fragments of echinoderms are also mentioned by King (1994), and several undescribed specimens exist in the collection the Natural History Museum of Denmark.

Material and methods

Studied material consists of 11 rock samples with serpulid tubes from the Selandian Kerteminde Marl Formation. Some pieces were cut into several smaller pieces and polished for study of microstructure, so that today the total number is more than 11. Many of the specimens are attached to ventricullid sponges; some are fragments of the free anterior tube portion. The specimens were found in Gundstrup gravel pit (Fig. 1) by the amateur collectors Peter Tang Mortensen, Mogens Nielsen and Mette Agersnap Grejsen Hofstedt (Fig. 2). The type material comprising three specimens are stored in the collection of the Natural History Museum of Denmark in Copenhagen, MGUH 34202 – 34204.

Seven additional specimens are stored in the collection of Østsjælland Museum, Faxe, OESM 11694 – 11700 and one unnumbered specimen is housed at Davinde Stenmuseum, Fyn. Although some of the tubes are fragmented and poorly preserved and their attribution to *N. gundstrupensis* is uncertain, we found no clues pointing to the presence of a second serpulid species in the studied material from Gundstrup gravel pit.

The specimens were prepared with an Air Scribe tool. Six of the marl pieces, including the second paratype, were selected for SEM analysis of microstructure. These specimens were embedded in epoxy resin 1200 and hand polished using 200, 400, 600, 800, 1000, and 1200 carborundum powder paper with water. Then they were finely polished by means of Microlite powder with water, after which they were treated with 1% acetic acid for 5 minutes. Light microscope



Fig. 2. A, Gundstrup pit, B, Peter Mortensen with large rock sample of Kerteminde marls in Gundstrup pit, C, Mette Hofstedt at Kerteminde marls locality, D, Gundstrup pit with Kerteminde marlstones. (photo P. Mortensen and Mette Hofstedt).

Olympus SZX12 images and SEM were made by using a Hitachi S-3700 N in the Palaeontological Department of National Museum in Prague. A digital caliper was used for measurements. All figures were prepared using Corel Draw 20 program and SEM pictures by means of Photoshop CS6.

Systematic palaeontology

Class Polychaeta Grube, 1850

Subclass Sedentaria Lamarck, 1818

Infraclass Canalipalpata Rouse and Fauchald, 1997

Order Sabellida Levinsen, 1883

Family Serpulidae Rafinesque, 1815

Subfamily Serpulinae Rafinesque, 1815

'Clade AII *Spirobranchus*-group' *sensu* Lehrke *et al.* (2007), Kupriyanova *et al.* (2009) and Ippolitov *et al.* (2014)

Tribe Ficopomatini Pillai, 1960

Genus *Neovermilia* Day, 1961

Type species. *Neovermilia capensis* Day, 1961 (type by original designation).

Diagnosis. "Tube white, opaque, triangular to subcircular in cross-section, medial keel may be present. Granular overlay absent, though hyaline inner (bordering lumen) and hyaline outer layers may be present" (ten Hove & Kupriyanova 2009, for recent tubes). Moreover, a free anterior tube portion may be present which may grow rather long at least in some fossil tubes and has a circular cross-section. A densely spaced delicate transverse striation and annular peristomes may occur, and in at least one fossil species peristomes may become bulbous. Chambered tubulae may or may not be developed at the tube base.

***Neovermilia gundstrupensis* sp. nov.**

Figs 3–7

Etymology. After Gundstrup gravel pit where all specimens figured here were found.

Zoobank LSID. urn:lsid:zoobank.org:act:25298BE3-5904-4402-BBCC-386738F11D21

Holotype. An almost complete tube (Fig. 3) Natural History Museum of Denmark in Copenhagen, MGUH 34202.

First paratype. An almost complete coiled tube attached to *Ventriculites*, broken into two halves (Fig. 4) MGUH 34203.

Second paratype. Two incomplete tubes attached to *Ventriculites*, one of them ending with a free(?) anterior portion (Fig. 5); the latter tube is the second paratype. It was cut and polished to observe the microstructure (Figs 6B–6B1, 7C–7C3, 7D–7D8), MGUH 34204.

Type locality. Gundstrup gravel pit, Fyn, Denmark.

Type stratum. Selandian, lower part of Kerteminde Marl Formation.

Material. The holotype with the two paratypes (the first paratype broken into two pieces) and further eight pieces of marl, each containing at least one tube, some contain several tubes (see Material and Methods).

Diagnosis. Tube very slowly increasing in diameter, reaching up to about 5 mm near the aperture. Attached posterior tube portion slightly curved or tortuous, forming loops or a rather regular coil; anterior tube portion often free, straight to moderately curved, rising for some centimetres. Usually any distinct longitudinal ornamentation is lacking. Transverse ornamentation consisting of thin, well distinguishable, usually densely spaced circular striae or wrinkles which occasionally merge into weakly but never strongly developed annular peristomes. Tube wall moderately thin to averagely thick.

Description. Tube circular in cross-section, moderately increasing in diameter up to approximately 5 mm (Fig. 3A) with a large basal lateral flange and a free, well developed, anterior portion. Only a few tubes form a spiral composed of up to 3½ turns, remarkably regular with a wide gap in the centre (Fig. 4A1). In the holotype, a loop or spiral is formed by inward coiling. More often the tube is curved, serpentine or forms loops instead of spirals. Usually any distinct longitudinal ornamentation is lacking, although nearly imperceptible densely spaced longitudinal striae or wrinkles visible only under the microscope may be present. Densely spaced weak but distinct annular striae are somewhat curved forward near the tube base (Fig. 3A1). Some of



Fig. 3. *Neovermilia gundstrupensis* sp. nov., holotype, MGUH 34202. A, coiled attached portion of the tube and distal end. A1, detail of A showing ornamentation made by thin wrinkles and a basal wide flange.



Fig. 4. *Neovermilia gundstrupensis* sp. nov., first paratype, MGUH 34203. only lower half of tube preserved. **A**, overview showing tube attached to sponge *Ventriculites*. **A1-A4**, details of tube.

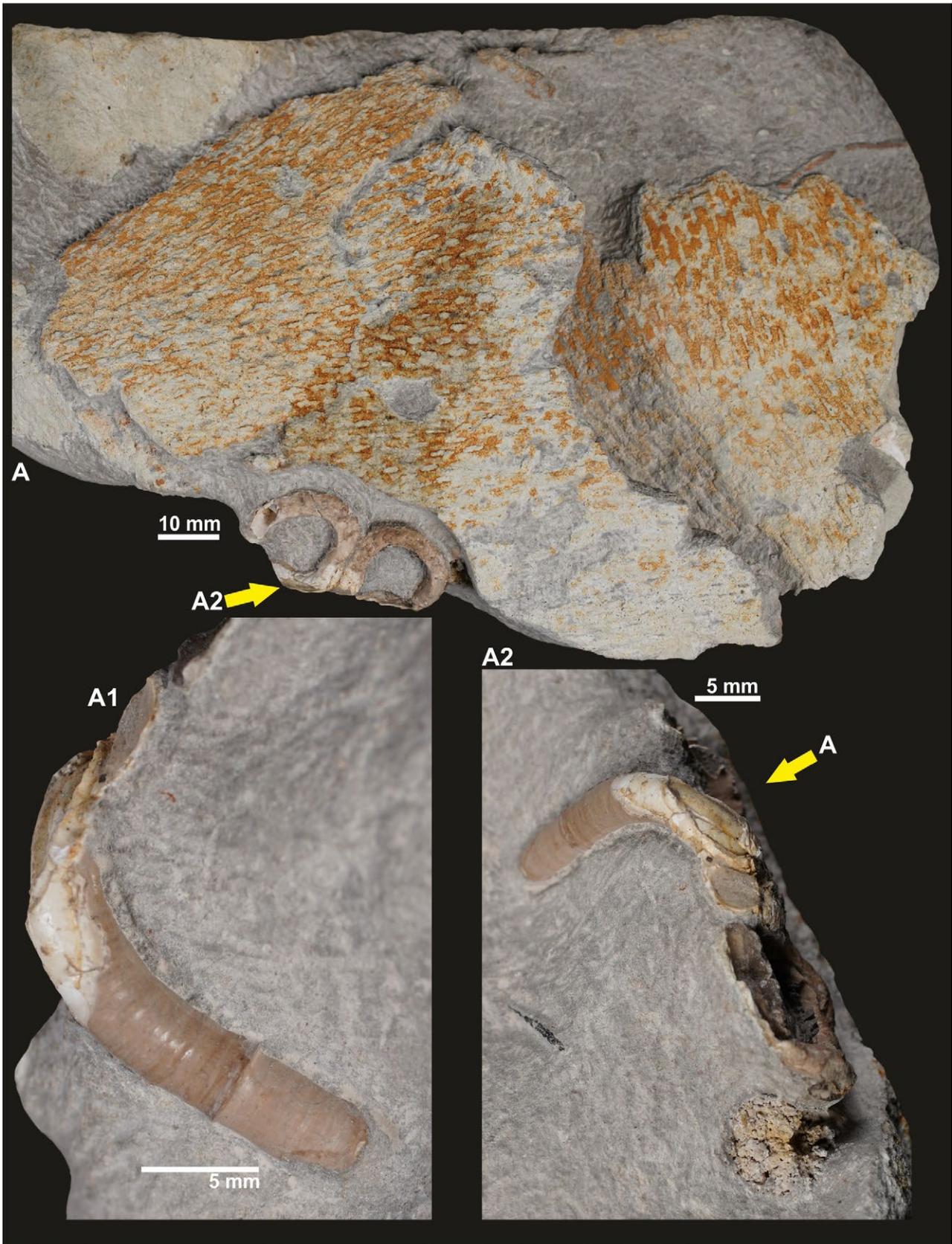


Fig. 5. *Neovermilia gundstrupensis* sp. nov., second paratype, MGUH 34204, before being cut and polished. Two coiled tubes of which one continued with an anterior free tube portion on the opposite side of the specimen. **A**, view to one side of the slab, presumably showing the undersides of the spirals. **A1**, view to the opposite side of the slab, showing the free anterior tube portion with its shiny surface preserved, also showing the delicate annular striation and very weak peristomes. **A2**, oblique lateral view, showing the connection between one of the spirals and its anterior portion.

the striae grew higher and stronger and may be considered low and short but distinct annular peristomes which may be slightly flaring but never are bulbous. They may be slightly more numerous in the posterior tube portion (Fig. 3A). wChambered tubulae are only indistinctly indicated in a few longitudinal sections; the chambers are very short in the tube's longitudinal direction but relatively wide in transverse direction, as is usual in Late Cretaceous to Danian *Neovermilia ampullacea* (J. de C. Sowerby, 1829); for well-developed tubulae of that species, see Jäger (1983, pl. 5, fig. 8). Usually, the tube wall (measured in mean 1.02 mm) consists of two layers, the outer one bright brown and slightly shiny, and the inner layer white and thinner. In tube portions where the outer layer is broken away, a densely spaced somewhat irregular annular striation becomes visible, especially at the boundary between the two layers where the tube wall, presumably due to diagenesis or weathering, is not very compact but brittle, and here and also in the inner layer the tube wall tends to flake off down to different levels.

Microstructure. The inner tube layer is composed of an irregular meshwork of needle-shaped crystals. The outer tube layer is similar, but in average the crystals are slightly longer and slightly thinner. This material of the tube wall is homogenous and corresponds to the Irregularly Oriented Prismatic structure (IOP; *sensu* Vinn *et al.* 2008, Fig. 9A; Ippolitov *et al.* 2014; Kupriyanova *et al.* 2020). However, in a single image (Fig. 7A), the crystals appear to be roughly oriented and therefore also resemble the semi-oriented irregularly oriented prismatic structure (SOIOP) (Vinn 2013b).

Discussion

Tube morphology. The present species belongs to the genus *Neovermilia* Day, 1961. Among extant serpulids, it resembles best *Neovermilia falcigera* (Roule, 1898), redescribed by Zibrowius & ten Hove (1987) from deep and cold water from Atlantic, also found as a fossil in Pliocene to Lower Pleistocene sediments in Sicily and Calabria and in various Upper Pleistocene deposits of the western and eastern Mediterranean (Zibrowius & ten Hove, 1987, Di Geronimo *et al.* 1995, 1996). The tubes of *N. gundstrupensis* and *N. falcigera* match well by size, shape of tube, spirals and loops, presence of a raising free anterior tube portion, general shape of annular peristomes, cross-section and at least occasional presence of chambered tubulae consisting of short cells, tube wall consisting of two layers. These similarities are almost the same as listed by Jäger (2005, p. 152) when comparing Turonian–Danian *N.*

ampullacea (J. de C. Sowerby, 1829) and *N. falcigera*. Additional accordances of *N. gundstrupensis* and *N. falcigera* are the usual lack of a keel, lack of a special kind of delicate transverse ornamentation composed of tiny striae and granules, and presence of weakly (*N. gundstrupensis*) or moderately (*N. falcigera*) developed annular peristomes, whereas *N. ampullacea* is more variable and may possess or lack (1) a more or less well-developed keel, at least in the posterior tube portion, (2) a transverse ornamentation characteristic for this species, and (3) annular peristomes which may range from weak via medium to considerably larger than in *N. gundstrupensis* and *N. falcigera*. In contrast, *N. falcigera* differs from *N. gundstrupensis* by possessing a thicker tube wall. Presence of a keel or comb in *N. ampullacea* is not an argument against assignment to *Neovermilia*, because extant *N. globula* (Dew, 1959) may also wear a well-developed comb.

Some tubes of the genera *Serpula* Linnaeus, 1758 *sensu stricto* and *Protula* Risso, 1826 resemble those of *Neovermilia* in outer appearance. The tubes of *N. gundstrupensis*, especially the slow to moderate increase in tube diameter, the sometimes long free anterior tube portion, the nearly total lack of distinct longitudinal ornamentation, the annular striation and the lack of strong peristomes, resemble *Protula* tubes which, however, may have a thicker tube wall and have a different microstructure and a rough, opaque surface, compared to the shiny surface of *N. gundstrupensis*. *Serpula* and especially *Protula* tubes differ from *Neovermilia* by their usually not or only slightly widened tube base, and sometimes *Protula* only adnates to its substrate without firm cementation (although rarely also *Protula* may form a wide basal seam), and *Protula* and normally also *Serpula* lack chambered tubulae, except for extant *Serpula israelitica* Amoureux, 1977 (see Sanfilippo 2009b, Fig. 5D–E).

Chambered tubulae occur not only in *Neovermilia*, but also in several species of *Pyrgopolon* (*Pyrgopolon*) de Montfort, 1808 and *Spirobranchus* Blainville, 1818, for example in *S. triqueter* (Linnaeus, 1758) which differs from *N. gundstrupensis* by its keel. The regular spiral formed by a few *N. gundstrupensis* tubes strongly resembles the spirals of the genus *Spiraserpula* Regenhardt, 1961 which, however, mostly stay smaller and, although some of their spirals may show an umbilicus, do not show such a wide gap in the centre as in *N. gundstrupensis*. More important, the peristomes of *Spiraserpula* are alae-shaped (distinctly curved forward toward the tube's median line) instead of being annular.

According to personal communication of Harry A. ten Hove and Elena Kupriyanova to T.K. (20 November 2022), the extant *Neovermilia* presumably belongs to Clade A II, although to a basal side-branch of A II,

close to the branching event between clade A I *Serpula*-group and clade A II *Spirobranchus*-group; this position in the phylogenetic tree could well explain some similarities of *Neovermilia* to *Serpula* and *Spirobranchus*. A few months later, in the more actual study by Kupriyanova *et al.* (2023), *Neovermilia* is still considered a basal side-branch of a group including *Spirobranchus*, but now this group is named tribe Ficopomatini Pillai, 1960 which, together with the tribe Serpulini Rafinesque, 1815, forms the revived Subfamily Serpulinae Rafinesque, 1815. Of course, *Serpula* and *Spiraserpula* belong to the tribe Serpulini now, and *Protula* belongs to the revived Subfamily Filograninae.

By morphological similarity of the tubes and by stratigraphic occurrence, the Selandian *N. gundstrupensis* may well be considered the descendant of Turonian – Danian *N. ampullacea* (J. de C. Sowerby, 1829), which in turn may well be considered the descendant of Cenomanian *N. trachina* (Goldfuss, 1831). From Turonian to Danian, *N. ampullacea* had been the most common and most wide-spread species of *Neovermilia*, displaying widest variability of nearly all morphological features and, in some tubes, the most distinctly expressed morphological features. Its most characteristic although often only partly realised combination of features includes: large to very large (up to 10 mm in tube diameter), spiral, loop-forming or tortuous attached tube portion, steeply rising, long, straight or curved free tube portion, a single well-developed keel in the posteriormost tube portion becoming low and less obvious anteriorly and disappearing in the raised free portion, medium-sized to large annular peristomes which are mostly relatively short but may be long and bulbous, delicate transverse ornamentation consisting of tiny lines and rows of granules, tube diameter changing from rounded triangular to circular during ontogeny, tube base widened by lateral margins, well-developed chambered tubulae at the tube base, tube wall thin and consisting of two layers: a thicker outer, often bright brown outer layer and a thin white, sometimes delicately annularly striated inner layer. *N. gundstrupensis* differs from otherwise similar *N. ampullacea* mainly by negative criteria: (1) It reaches only half of the maximum tube diameter of *N. ampullacea*. (2) A longitudinal keel in the posterior tube portion is lacking. (3) Moderately or strongly developed annular peristomes as well as any bulbous peristomes are lacking. (4) Chambered tubulae are only indistinctly indicated in a few specimens.

However, *N. gundstrupensis* is morphologically close to a variety of *N. ampullacea* (or a separate new species?) occurring in the Campanian at the same localities east of Hannover in north Germany as *N. ampullacea* *sensu stricto* and is often attached to large siliceous sponges, too. This variety grows long, but increases

only slowly in tube diameter which stays smaller than in adult typical *N. ampullacea*. The ornamentation consists of delicate transverse striation, but lacks strongly developed peristomes. The tube is very thin-walled and therefore often preserved in a compressed state, whereas other serpulid tubes including ‘normal’ *N. ampullacea* from the same localities are most often preserved uncompressed. However, in contrast to *N. gundstrupensis*, this variety does not form such regular spirals.

Both *N. faxensis* (Nielsen, 1931) from the middle Danian of Faxe and the related ‘*Serpula?*’ *insiticia* (Regenhardt, 1961) from the Danian of the region around the city of Maastricht possess a similar but smaller free anterior tube portion which, however, possesses relatively much larger and therefore much more conspicuous peristomes than *N. gundstrupensis*, if peristome diameter is compared to in-between tube diameter. The maximum figures for tube diameter of *N. faxensis* and ‘*S.?*’ *insiticia* are 2 mm respectively 1.2 mm between peristomes and 3 mm respectively 1.8 mm at peristomes. Moreover, the attached posterior tube portion of ‘*S.?*’ *insiticia* differs from *N. gundstrupensis* by its tendency to form a high trochospiral which most often is a truncated cone, less often a cylinder or an inverse cone (Jäger 1993). In some specimens of ‘*S.?*’ *insiticia* and *N. gundstrupensis* the light yellowish respectively brownish, shiny surface of the outer tube layer is preserved.

Microstructure. Our study of microstructure of the tube-wall in *Neovermilia gundstrupensis* sp. nov. shows that the needle-like prismatic crystals are irregularly oriented and that they are comparable with Irregularly Oriented Prismatic microstructure *sensu* Vinn *et al.* (2008c, Fig. 9A). This IOP microstructure is single layered and plesiomorphic.

Also, the extant *Neovermilia falcigera* (Roule, 1898) has IOP microstructure as a plesiomorphic feature. On contrary, recent *Neovermilia sphaeropomata* (Benham, 1927) possesses more advanced Lamello-Fibriallar LF structure (see Vinn 2013a, Table 1). Vinn (2013a) documented that some types of microstructure in clade A are more advanced and that in clade B plesiomorphic microstructure is present. It is very interesting that two species of the same genus *Neovermilia* present two different kinds of microstructure. *Neovermilia* is assigned to the tribe Ficopomatini, but considered a basal side-branch, situated very close to the branching of the subfamily Serpulinae into the two tribes Ficopomatini and Serpulini. Due to this location of *Neovermilia*, it is not surprising, that IOP structure can be present as plesiomorphic microstructure in both tribes.

However, IOP structure also occurs in several other

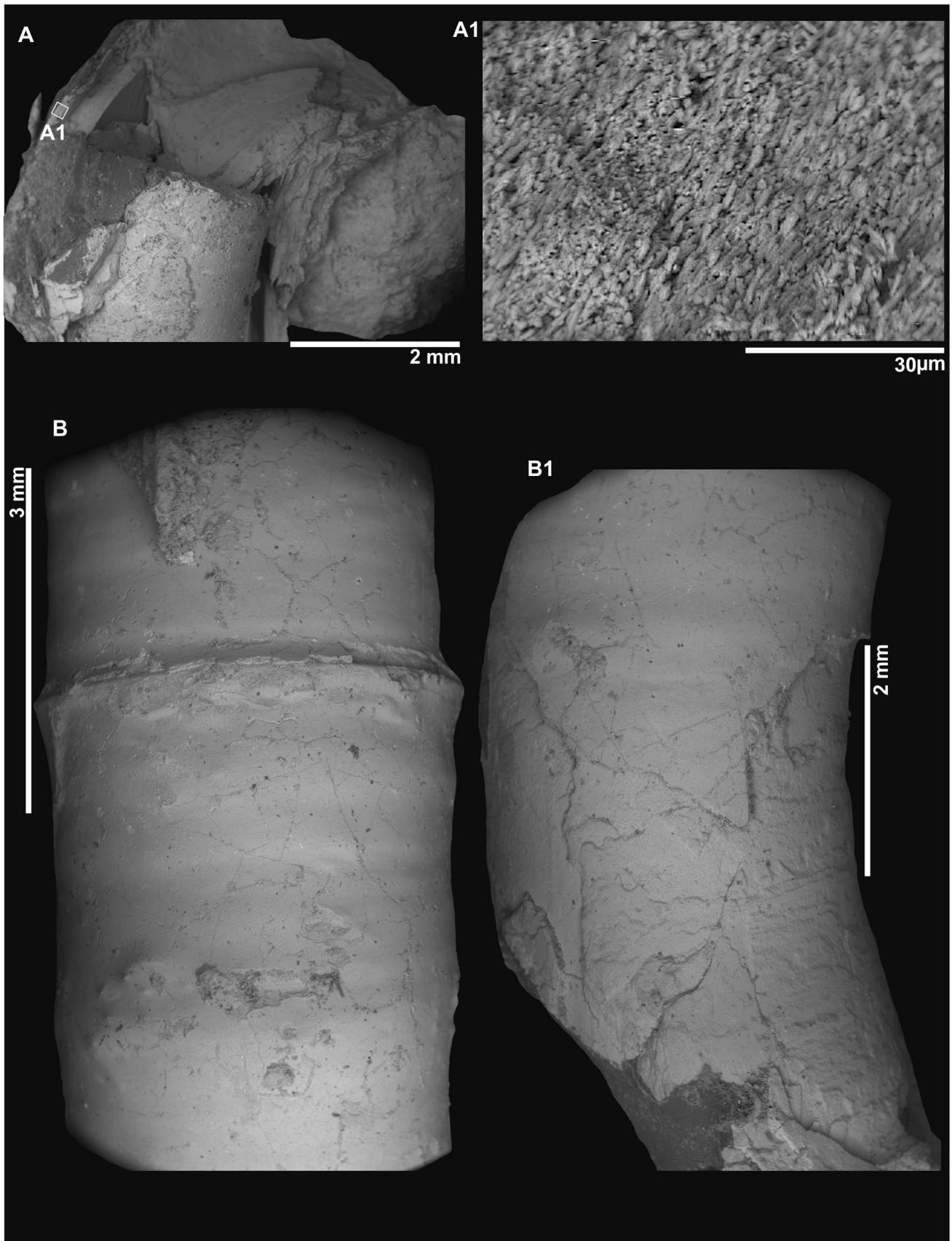


Fig. 6. *Neovermilia gundstrupensis* sp. nov. **A.** detailed view to broken tube wall. **A1.** longitudinal section through tube wall, not polished and not treated with acid. **B, B1.** same tube as Fig. 5A – 5A2, MGUH 34204. **B.** tube surface showing weak annular peristome and even weaker annular ornamentation outside peristome. **B1,** detail of white tube region in Fig. 5A1–5A2 showing tube wall flaking off down to several different levels.

not closely related serpulid genera and species of different geological age, such as *Serpula etalensis* (Piette, 1856) (tribe Serpulini?) from Upper Pliensbachian, eastern Germany (Vinn *et al.* 2008a, Fig. 1D), *Pyrgopolon mellevillei* (Nyst & le Hon, 1862) (tribe Ficopomatini) from Eocene London Clay, England (Vinn & Kupriyanova 2011, Fig. 2), *Neovermilia falcigera* (tribe Ficopomatini) from Pleistocene, Calabria, Italy (Vinn & Kupriyanova 2011, Fig. 6) and *Apomatus globifer* Théel, 1878 (see Théel 1879) (subfamily Filograninae), recent; see Vinn *et al.* (2008c, Fig. 1A, B). Therefore, it is well possible that IOP structure has developed independently several times in different phylogenetic lineages.

Only a single image (Fig. 7A) resembles the semi-oriented irregularly oriented prismatic structure (SOIOP) which is known from tubes of the genus *Protula* (Vinn 2013b). Although also the shape of *Neovermilia gundstrupensis* tubes is somewhat similar to that of *Protula*, as discussed above, in summary, the genus *Neovermilia* fits our new species best.

Palaeoecology

Remarkably, all tubes of *Neovermilia gundstrupensis* from the Selandian are attached to siliceous sponges of the genus *Ventriculites*. However, it can not be excluded that this is in part a sampling bias, because a *Ventriculites* is larger, more conspicuous in the outcrop and more attractive to the eyes of a collector than a small and abraded serpulid tube which is either solitary or attached to a small or unattractive substrate. Specimens of the typical large *Neovermilia ampullacea* as well as of its smaller thin-walled variety are common in the Campanian marly limestone east of Hannover in north Germany; also, these tubes are often found attached to *Ventriculites* as well as to other siliceous sponges (Jäger, personal observation). Therefore it is obvious that at least these fossil species of the genus *Neovermilia* show a distinct preference for

selecting large siliceous sponges as their substrates. This suggests that *Neovermilia* may have the ability to encrust some sponges whose skeleton is composed of a delicate network of thin spicules.

Once the *Neovermilia* had managed attachment to a *Ventriculites* which is a relatively large sponge, the worm enjoyed the advantage of living in a high tier of benthic habitats relatively rich in nutrient particles and relatively safe from being buried by sedimentation during lifetime. Moreover, if the sponge was still alive which however is unknown, the *Neovermilia* benefitted from nutrient-rich water currents produced by the living sponge.

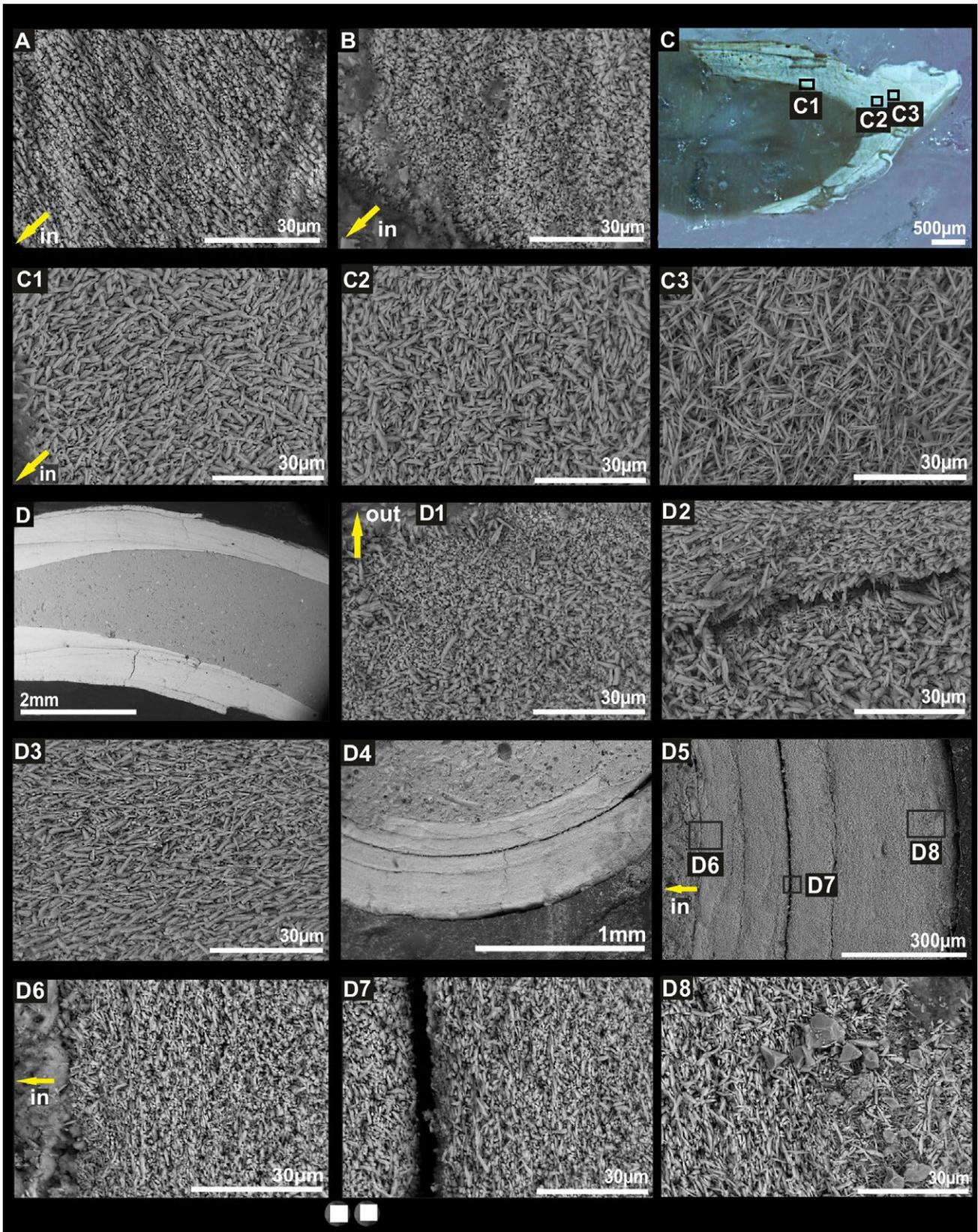
Conclusion

The new species *Neovermilia gundstrupensis* is described from the lower Selandian of Denmark. Its tube is morphologically similar to, but in some features also different from, its Turonian – Danian ancestor *N. ampullacea*. It prolongs the stratigraphically continuous lineage of Late Cretaceous to Paleocene fossil representatives of the genus *Neovermilia*. The Irregularly Oriented Prismatic (IOP) microstructure is plesiomorphic for the genus *Neovermilia*. *N. gundstrupensis* seems to preferentially encrust on the siliceous sponge *Ventriculites*, whereas *N. ampullacea* is less selective preferring sponges, but attached to various types of substrates.

Acknowledgements

We are grateful to the amateur geologists Peter Tang Mortensen, Mette Agersnap Grejsen Hofstedt and Mogens Nielsen who have spent countless hours collecting fossils in the Kerteminde Marl Formation and made them available to science. We honor all the

▼ **Fig. 7.** *Neovermilia gundstrupensis* sp. nov., microstructure of tube wall. All sections were treated with 1% acetic acid for 5 minutes. All SEM images show Irregularly Oriented Prismatic structure, IOP. Arrows point toward inner surface (in) of the tube wall or lumen, respectively toward outer surface (out) of the tube wall. **A**, polished longitudinal section showing oriented larger crystals developed in the longitudinal axis of the tube wall, and they form a substructure of IOP, similar to the semi-oriented irregularly oriented prismatic structure (SOIOP) (Vinn 2013b; 2020). **B**, polished longitudinal section showing larger non-oriented prismatic crystals and form IOP. **C,C1,C2**, same specimen which is also shown in Figs 5A–5A2 and 6B–6B1, MGUH 34204, polished longitudinal sections through inner tube layer showing sparsely packed fine crystals, IOP. **C3**, very fine needle-shaped crystals, no sharp boundary between C2 and C3. **D**, longitudinal section through the same specimen. **D1**, polished longitudinal section through outermost layer, showing sparsely packed fine crystals. **D2**, a thin gap between two layers which, however, consists of the same type of crystals. **D3**, innermost region of tube wall. **D4**, polished transverse section, turned by 180°, through inner tube layer showing sparsely packed fine crystals. **D5**, detail of D4 in higher magnification, turned by 90°. **D6,D7,D8**, details of inner, central and outer tube layers



eager amateur geologists who have collected fossils there. We greatly appreciate Sten Lennart Jakobsen for taking photographs of our Figs 3 and 4 and Elke Langstein-Jäger for her valuable help with Photoshop. We are indebted to Lenka Váchová (PD NM Prague) for her kindly taken all SEM pictures. We thank Elena Kupriyanova and Harry A. ten Hove for the results of their studies on the phylogenetic position of genus *Neovermilia*, and the reviewers Rossana Sanfilippo and Olev Vinn for considerably improving our manuscript. Additional support was obtained from Ministry of Culture of the Czech Republic (DKRVO 2019-2023/2. III.c, National Museum, 00023272).

References

- Amoureux, L. 1976. *Serpula (Paraserpula) israelitica*, nouvelle espèce de Serpulidae (Annélides Polychètes) et une petite collection annélienne de la Méditerranée orientale. Bulletin du Muséum national d'Histoire naturelle, 3e série 404, Zoologie 281, 1047–1059. <https://doi.org/10.5962/p.326713>
- Benham, W.B. 1927: Polychaeta. British Antarctic 'Terra Nova' Expedition. Natural History Reports, Zoology 7 (2), 47–182. <https://doi.org/10.5962/bhl.title.121995>
- Blainville, H.M.D. de 1818: Mémoire sur la classe des Sétipodes, partie des Vers à sang rouge de M. Cuvier, et des Annélides de M. de Lamarck. Bulletin des Sciences, par la Société Philomatique de Paris 1818, 78–85. <https://doi.org/10.3406/barb.1969.62398>
- Clausen, O.R. & Huuse, M. 1999: Topography of the Top Chalk surface, on- and offshore Denmark. Marine and Petroleum Geology 16, 677–691. [https://doi.org/10.1016/s0264-8172\(99\)00003-3](https://doi.org/10.1016/s0264-8172(99)00003-3)
- Clausen, O.R. & Huuse, M. 2002: Mid-Paleocene palaeogeography of the Danish area. Bulletin of the Geological Society of Denmark 49 (2), 171–186. <https://doi.org/10.37570/bgsgd-2003-49-13>
- Clemmensen, A. & Thomsen, E. 2005: Palaeoenvironmental changes across the Danian–Selandian boundary in the North Sea Basin. Palaeogeography, Palaeoclimatology, Palaeoecology 219, 351–394. <https://doi.org/10.1016/j.palaeo.2005.01.005>
- Cohen, K.M., Finney, S.C., Gibbard, P.L. & Fan, J.-X. 2013; updated 2022: The ICS International Chronostratigraphic Chart. Episodes 36, 199–204. <https://doi.org/10.18814/epiugs/2013/v36i3/002>
- Day, J.H. 1961: The polychaete fauna of South Africa, 6. Sedentary species dredged off Cape coasts with a few new records from the shore. Zoological Journal of the Linnean Society 44 (299), 463–560. <https://doi.org/10.1111/j.1096-3642.1961.tb01623.x>
- Dew, B. 1959: Serpulidae (Polychaeta) from Australia. Records of the Australian Museum 25 (2), 19–56. <https://doi.org/10.3853/j.0067-1975.25.1959.654>
- Di Geronimo, I., Rosso, A., Sanfilippo, R. 1995: Circalittoral to infralittoral communities encrusting the Pleistocene gravels of Motta S. Giovanni (Reggio Calabria, Italy). Géobios, Mémoire spécial 18, 119–130. [https://doi.org/10.1016/s0016-6995\(95\)80160-x](https://doi.org/10.1016/s0016-6995(95)80160-x)
- Di Geronimo, I., D'Atri, A., La Perna, R., Rosso, A., Sanfilippo, R., Violanti, D. 1997: The Pleistocene bathyal section of Archi (Southern Italy). Bollettino Società Paleontologica Italiana 36, 189–212.
- Fassari, G. & Mòllica, E. 1991: Una Nuova Specie di Serpulidae (Annelida Polychaeta) di Grotta. Animalia 18, 261–267.
- Garberoglio, R.M. & Lazo, D.G. 2011: Post-mortem and symbiotic sabellid and serpulid-coral associations from the lower Cretaceous of Argentina. Revista Brasileira de Paleontologia 14 (3), 215–228. <https://doi.org/10.4072/rbp.2011.3.02>
- Goldfuss, A. 1831: Petrefacta Germaniae 1(3), 165–240, pls 51–71. Düsseldorf: Arnz.
- Grube, A.E. 1850: Die Familien der Anneliden. Archiv für Naturgeschichte 16(1), 249–364.
- Guido, A., Jimenez, C., Achilleos, K., Rosso, A., Sanfilippo, R., Hadjioannou, L., Petrou, A., Russo, F., Mastandrea, A. 2017: Cryptic serpulid-microbialite bioconstructions in the Kakoskali submarine cave (Cyprus, Eastern Mediterranean). Facies 63, 21. <https://doi.org/10.1007/s10347-017-0502-3>
- Håkansson, E. & Pedersen, S.A.S. 1992: Geologisk kort over den danske undergrund. VARV [Special publication]. København: Tidsskriftet VARV.
- Harder, P. 1922: Om Grænsen mellem Saltholmskalk og Lellinge Grønsand og nogle Bemærkninger om Inddelingen af Danmarks ældre Tertiær. Danmarks geologiske Undersøgelse, II. Række 38, 108 pp. <https://doi.org/10.34194/raekke2.v38.6824>
- Heilmann-Clausen, C. 2010: Palæogen – Frau drivhus til kølehus. Geoviden 3, 2–11.
- Hove, H.A. ten & Hurk, P. van den 1993: A review of Recent and fossil serpulid 'reefs'; actuopalaeontology and the 'Upper Malm' limestones in NW Germany. Geologie en Mijnbouw 72, 23–67.
- Hove, H.A. ten & Kupriyanova, E.K. 2009: Taxonomy of Serpulidae (Annelida, Polychaeta): the state of affairs. Zootaxa 2036(1), 1–126. <https://doi.org/10.11646/zootaxa.2036.1.1>
- Ippolitov, A.P., Vinn, O., Kupriyanova, E.K. & Jäger, M. 2014: Written in stone: history of serpulid polychaetes through time. Memoirs of Museum Victoria 71, 123–159. <https://doi.org/10.24199/j.mmv.2014.71.12>
- Jäger, M. 1983: Serpulidae (Polychaeta, Sedentaria) aus der norddeutschen höheren Oberkreide – Systematik, Stratigraphie, Ökologie. Geologisches Jahrbuch, Reihe A 68, 3–219.
- Jäger, M. 1993: Danian Serpulidae and Spirorbidae from NE Belgium and SE Netherlands: K/T boundary extinction, survival, and origination patterns. Contributions to Tertiary and Quaternary Geology 29 (3–4), 73–137.
- Jäger, M. 2005: Serpulidae und Spirorbidae (Polychaeta, Sedentaria) aus Campan und Maastricht von Norddeutschland, den Niederlanden, Belgien und angrenzenden Gebieten. Geologisches Jahrbuch, Reihe A 157, 121–249.

- Jäger, M., Kočí, T., Schnetler K.I., Andersen, S.B. & Jacobsen, S.L. 2018: Sabellidae and Serpulidae (Polychaeta, Canalipalpata) from the Danian of Denmark, with special consideration of specimens from the Faxø quarry – preliminary report. In: Pšenička, J., Frojdová, J., Svobodová, A. & Dašková, J. (eds): Abstract Book 19th Czech-Slovak-Polish Palaeontological Conference & MIKRO 2018 workshop West Bohemian Museum in Pilsen. *Folia Musei Rerum Naturalium Bohemiae Occidentalis, Geologica et Palaeobiologica, Special Volume 2018*, pp. 32–34. Plzeň. <https://doi.org/10.1515/fbgp-2017-0002>
- Jäger, M., Kočí, T., Schnetler, K.I., Andersen, S.B., Jakobsen, S.L., Milàn, J., Bashforth, A.R. in prep: Sabellidae and Serpulidae (Polychaeta, Canalipalpata) from the Danian of Denmark, with special consideration of specimens from Faxø quarry.
- King, C. 1994: Late Paleocene microfaunas of the Harre borehole (North Jylland, Denmark). In: Nielsen, O.B. (ed.): Lithostratigraphy and biostratigraphy of the Tertiary sequence from Harre Borehole, Denmark. *Aarhus Geoscience 1*, 65–72.
- Kočí, T. & Jäger, M. 2015: Sabellid and serpulid worms (Polychaeta, Canalipalpata, Sabellida, Sabellidae, Serpulidae) from the rocky coast facies (Late Cenomanian) at Předboj near Prague. *Sborník Národního Muzea v Praze, Rada B, Přírodovědy. Acta Musei Nationalis Pragae, Series B, Historia Naturalis 71*, 31–50. <https://doi.org/10.14446/amnp.2015.31>
- Kočí, T., Jäger, M. & Morel, N. 2017: Sabellid and serpulid worm tubes (Polychaeta, Canalipalpata, Sabellida) from the historical stratotype of the Cenomanian (Late Cretaceous; Le Mans region, Sarthe, France). *Annales de Paléontologie 103*, 45–80. <http://dx.doi.org/10.1016/j.annpal.2016.11.004>
- Kočová Veselská, M., Kočí, T., Jäger, M., Mikuláš, R., Heřmanová, Z., Morel, N., Šamánek, J. 2021: Sclerobionts on tubes of the serpulid *Pyrgopolon (Pyrgopolon) deforme* (Lamarck, 1818) from the upper Cenomanian of Le Mans region, France. *Cretaceous Research 125*, 104873. <https://doi.org/10.1016/j.cretres.2021.104873>
- Kupriyanova, E.K., Hove, H.A. ten, Sket, B., Trontelj, P., Zakšek, V. & Rouse, G.W. 2009: Evolution of a unique freshwater cave dwelling serpulid polychaete *Marifugia cavatica* Absolon and Hrabě, 1930. *Systematics and Biodiversity 7*, 389–401. <https://doi.org/10.1017/s1477200009990168>
- Kupriyanova, E.K., Rzhavsky, A.V. & Hove, H.A. ten. 2020: 7.4.7 Serpulidae Rafinesque, 1815. In: Purschke, G., Böggemann, M. & Westheide, W. (eds): *Pleistoannelida, Sedentaria II. Handbook of Zoology Annelida 2*, pp. 213–275. Berlin: De Gruyter. <https://doi.org/10.1515/9783110291681-006>
- Kupriyanova, E., Hove, H.A. ten & Rouse, G.W. 2023: Phylogeny of Serpulidae (Annelida, Polychaeta) inferred from morphology and DNA sequences, with a new classification. *Diversity 15*(3), 398, 24 pp. <https://doi.org/10.3390/d15030398>
- Lamarck, J.-B. de 1818: *Histoire naturelle des animaux sans vertèbres*. 5, 612 pp. Paris: Déterville & Verdrière. <https://doi.org/10.5962/bhl.title.6484>
- Lauridsen, B.W. & Surlyk, F. 2008: Benthic faunal response to late Maastrichtian chalk–marl cyclicity at Rørdal, Denmark. *Palaeogeography, Palaeoclimatology, Palaeoecology 269*, 38–53. <https://doi.org/10.1016/j.palaeo.2008.07.001>
- Lauridsen, B.W. & Bjerager, M. 2021: The fauna of a Danian fossil Conservation Lagerstätten [sic!] from the cold-water coral mound complex at Faxø, Denmark. *Palaeogeography, Palaeoclimatology, Palaeoecology 584*, 110700, 24 pp., <https://doi.org/10.1016/j.palaeo.2021.110700>
- Lauridsen, B.W., Edvardsen, T., Blinkenberg, K.H., Stemmerik, L. 2018: Palaeoecology and survival strategies of an impoverished benthic chalk community in a mid-Danian deep shelf setting. *Palaeogeography, Palaeoclimatology, Palaeoecology 514*, 474–486. <https://doi.org/10.1016/j.palaeo.2018.10.002>
- Lehrke, J., Hove, H.A. ten, Macdonald, T.A., Bartolomaeus, T. & Bleidorn, C. 2007: Phylogenetic relationships of Serpulidae (Annelida: Polychaeta) based on 18S rDNA sequence data, and implications for opercula revolution. *Organisms, Diversity and Evolution 7*, 195–206. <https://doi.org/10.1016/j.ode.2006.06.004>
- Levinsen, G.M.R. 1883: Systematisk-geografisk Oversigt over de nordiske Annulata, Gephyrea, Chaetognathi og Balanoglossi. *Videnskabelige Meddelelser fra Dansk Naturhistoriske Forening i Kjøbenhavn 1882*, 160–251. <https://doi.org/10.5962/bhl.title.16117>
- Linnaeus, C. 1758: *Systema Naturae per regnatrionaturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima, reformata* [10th revised edition], vol. 1, 824 pp. Holmiae: Laurentius Salvius. <https://doi.org/10.5962/bhl.title.542>
- Luci, L. & Cichowolski, M. 2014: Encrustation in nautilids: a case study in the Cretaceous species *Cymatoceras perstriatum*, Neuquén Basin, Argentina. *Palaios 29*, 101–120. <http://dx.doi.org/10.2110/palo.2013.062>
- Luci, L. & Lazo, D.G. 2014: Living on an island: characterization of the encrusting fauna of large pectinid bivalves from the Lower Cretaceous of the Neuquén Basin, west-central Argentina. *Lethaia 48*(2), 205–226. <https://doi.org/10.1111/let.12100>
- Lundgren, B. 1891: Studier öfver fossilförande lösa block. *Geologiska Föreningens Stockholm Förhandlingar 13*(2) (no. 135), 111–121. <https://doi.org/10.1080/11035898309445722>
- Milàn, J., Jakobsen, S.L. & Niss, C. 2022: Fossils from Faxø Limestone, 106 pp. Faxø: Geomuseum.
- Milàn, J., Jakobsen, S.L. & Niss, C. 2023: Faxø Kalkbrud. Historien om Danmarks fossile koralrev. The story of Denmark's fossil coral reef. iii + 140 pp., many figs. Faxø: Geomuseum Faxø / Østsjælland Museum.
- Montfort, D. de 1808: *Conchyliologie systématique et classification méthodique des coquilles, 1. Coquilles univalves, cloisonnées*. lxxxvii + 409 pp., 100 figs. Paris: F. Schoell. <https://doi.org/10.5962/bhl.title.10571>
- Myrvold, K.S., Milàn, J. & Rasmussen, J.A. 2018: Two new finds of turtle remains from the Danian and Selandian (Paleocene) deposits of Denmark with evidence of predation by crocodilians and sharks. *Bulletin of the Geological Society of Denmark 66*, 211–218. <https://doi.org/10.37570/bgsg-2018-66-11>

- Nielsen, K.B. 1931: Serpulidae from the Senonian and Danian deposits of Denmark. *Meddelelser fra Dansk Geologisk Forening* 8 (1), 71–113. <https://doi.org/10.37570/bgsd-1977-26-15>
- Nyst, P.-H. & Le Hon, H. 1862: Descriptions succinctes de quelques nouvelles espèces animales et végétales fossiles, des terrains Tertiaires éocènes des environs de Bruxelles, 10 pp. Bruxelles: Académie royale des Sciences, des Lettres et des Beaux-Arts de Belgique. <https://doi.org/10.5962/bhl.title.52361>
- Ødum, H. 1926: Studier over Daniet i Jylland og paa Fyn. Danmarks geologiske Undersøgelse, II. Række 45, 306 pp. <https://doi.org/10.34194/raekke2.v45.6831>
- Piette, E. 1856: Notice sur les grès d'Aiglemont et de Rimogne. *Bulletin de la Société géologique de France* 2 (13), 188–207. <https://doi.org/10.1080/00378941.1856.10826081>
- Pillai, T.G. 1960: Some marine and brackish-water serpulid polychaetes from Ceylon, including new genera and species. *Ceylon Journal of Sciences, Biological Sciences* 3, 1–40.
- Rafinesque, C.S. 1815: Analyse de la nature ou tableau de l'univers et des corps organisés. 224 pp. Palerme: l'Auteur. <https://doi.org/10.5962/bhl.title.106607>
- Ramsdale, R. 2021: A possible serpulid tube worm of the genus *Filograna* from the upper Permian Cadeby Formation of South Yorkshire, UK. *Proceedings of the Yorkshire Geological Society* 63, pygs2020-016. <https://doi.org/10.1144/pygs2020-016>
- Regenhardt, H. 1961: Serpulidae (Polychaeta sedentaria) aus der Kreide Mitteleuropas, ihre ökologische, taxionomische und stratigraphische Bewertung. *Mitteilungen aus dem Geologischen Staatsinstitut in Hamburg* 30, 5–115.
- Risso, A. 1826–1827: Histoire naturelle des principales productions de l'Europe Méridionale et particulièrement de celles des environs de Nice et des Alpes Maritimes 3 (XVI), 1–480. Paris: F.G. Levrault. <https://doi.org/10.5962/bhl.title.58984>
- Rosenkrantz, A. 1920: Craniakalken fra Kjöbenhavn's Sydhavn. *Danmarks geologiske Undersøgelse II. Række*, 36, 79 pp. <https://doi.org/10.34194/raekke2.v36.6822>
- Rosso, A. & Sanfilippo, R. 2005: Bryozoans and serpuloids in skeletobiont communities from the Pleistocene of Sicily: spatial utilisation and competitive interactions. *Annali dell'Università degli Studi di Ferrara, Sezione di Museologia Scientifica e Naturalistica*, volume speciale 2005, 109–124.
- Roule, L. 1898: Notice préliminaire sur les espèces d'Annélides recueillies dans les explorations sous-marines du Travailleur et du Talisman. *Bulletin du Muséum National d'Histoire Naturelle* 4, 190–195. <https://doi.org/10.5962/bhl.part.14410>
- Rouse, G.W. & Fauchald, K. 1997: Cladistics and polychaetes. *Zoologica Scripta* 26 (2), 139–204. <https://doi.org/10.1111/j.1463-6409.1997.tb00412.x>
- Rouse, G.W., Pleijel, F. & Tilic, E. 2022: *Annelida*, 418 pp. London, New York: Oxford University Press. <http://doi.org/10.1093/oso/9780199692309.003.0001>
- Sanfilippo, R. 2009a: New species of *Hyalopomatus* Marenzeller, 1878 (Annelida, Polychaeta, Serpulidae) from Recent Mediterranean deep water coral mounds and comments on some congeners. *Zoosystema* 31, 147–161. <https://doi.org/10.5252/z2009n1a8>
- Sanfilippo, R. 2009b: Systematics and lifehabit in *Serpula israelitica* Amoureux, 1977 (Polychaeta Serpulidae) from the Mediterranean with remarks on other soft-bottom serpulids. *Journal of Natural History*, 43 (33–34), 2009–2025. <https://doi.org/10.1080/00222930903090991>
- Sanfilippo, R. & Mollica, E. 2000: *Serpula cavernicola* Fassari & Mollica, 1991 (Annelida Polychaeta): diagnostic features of the tubes and new Mediterranean records. *Marine Life* 10, 27–32.
- Sanfilippo, R., Vertino, A., Rosso, A., Beuck, L., Freiwald, A., Taviani, M. 2013: *Serpula* aggregates and their role in deep-sea coral communities in the southern Adriatic Sea. *Facies* 59 (4), 663–677. <https://doi.org/10.1007/s10347-012-0356-7>
- Sanfilippo, R., Rosso, A., Reitano, A. & Insacco, G. 2017: First record of sabellid and serpulid polychaetes from the Permian of Sicily. *Acta Palaeontologica Polonica* 62, 25–38. <http://dx.doi.org/10.4202/app.00288.2016>
- Sanfilippo, R., Rosso, A., Reitano, A., Viola, A. & Insacco, G. 2018: New serpulid polychaetes from the Permian of western Sicily. *Acta Palaeontologica Polonica* 63, 579–584. <https://doi.org/10.4202/app.00448.2017>
- Schlögl, J., Michalík, J., Zágorský, K. & Atrops, F. 2008: Early Tithonian serpulid-dominated cavity-dwelling fauna, and the recruitment pattern of the serpulid larvae. *Journal of Paleontology* 82, 351–361. <https://doi.org/10.1666/06-127.1>
- Schmitz, B., Pujalte, V., Molina, E., Monechi, S., Orue-Etxebarria, X., Speijer, R.P., Alegat, L., Apellaniz, E., Arenillas, I., Aubry, M.-P. *et al.* 2011: The Global Stratotype Sections and Points for the bases of the Selandian (Middle Paleocene) and Thanetian (Upper Paleocene) stages at Zumaia, Spain. *Episodes* 34, 220–243. <https://doi.org/10.18814/epiiugs/2011/v34i4/002>
- Schnetler, K.I. 2001: The Selandian (Paleocene) mollusc fauna from Copenhagen, Denmark: the Poul Harder 1920 collection. *Geology of Denmark Survey Bulletin* 37, 85 pp. <https://doi.org/10.34194/dgub.v37.5021>
- Schnetler, K.I. & Nielsen, M.S. 2018: A Palaeocene (Selandian) molluscan fauna from boulders of Kerteminde Marl in the gravel-pit at Gundstrup, Fyn, Denmark. *Cainozoic Research* 18, 3–81.
- Schwarzhan, W., Milán, J. & Carnivale, G. 2021: A tale from the middle Paleocene of Denmark: A tube-dwelling predator documented by the ichnofossil *Lepidenteron mortenseni* n. isp. and its predominant prey, *Bobbitichthys* n. gen. *rosenkrantzi* (Macrouridae, Teleostei). *Bulletin of the Geological Society of Denmark* 69, 35–52. <https://doi.org/10.37570/bgsd-2021-69-02>
- Sklenář, J., Kočí, T. & Jäger, M. 2013: Late Turonian polychaete communities recorded in the hemipelagic sediments of Bohemian Cretaceous Basin (Teplice Formation, Ohře and Dresden districts). *Bulletin of Geosciences* 88, 675–695. <https://doi.org/10.3140/bull.geosci.1412>
- Sorgenfrei, Th. & Buch, A. 1964: Deep tests in Denmark 1935–1959. *Danmarks Geologiske Undersøgelser, III Række* 36, 146 pp. <https://doi.org/10.34194/raekke3.v36.6941>

- Sowerby, J. de C. 1829: The mineral conchology of Great Britain 6, 230 pp, pls 506–609. London: The author.
- Stouge, S., Hjortkjær, B.F., Rasmussen, J.A., Roncaglia, L. & Sheldon, E. 2000: Micro- and nannofossil biostratigraphy across the Danian/Selandian (Paleocene) stage boundary at Gemmas Allé, Copenhagen, Denmark. *GFF* 122, 161–162. <https://doi.org/10.1080/11035890001221161>
- Taylor, P.D. & Wilson, M.A. 2003: Palaeoecology and evolution of marine hard substrate communities. *Earth-Science Reviews* 62, 1–103. [https://doi.org/10.1016/S0012-8252\(02\)00131-9](https://doi.org/10.1016/S0012-8252(02)00131-9)
- Théel, H.J. 1879: Les Annélides Polychètes des mers de la Nouvelle-Zemble. *Kongliga Svenska Vetenskaps-Akademiens Handlingar* 16(3), 1–75.
- Thomsen, E. & Heilmann-Clausen, C. 1985: The Danian-Selandian boundary at Svejstrup with remarks on the biostratigraphy of the boundary in western Denmark. *Bulletin of the Geological Society of Denmark* 33, 341–362. <https://doi.org/10.37570/bgisd-1984-33-28>
- Vallon, L.H. & Rindsberg, A.K. 2022: Cutting through sponge and time – a new record of *Koptichmus rasmussenae* (trace fossil) from the Kerteminde Marl (middle Paleocene), Denmark. *Bulletin of the Geological Society of Denmark* 70, 131–137. <https://doi.org/10.37570/bgisd-2022-70-09>
- Vandenbergh, N., Hilgen, F.J. & Speijer, R.J. 2012: The Paleogene Period. In: Gradstein, F.M. *et al.* (eds): *The Geologic Time Scale 2012*, 855–921. Amsterdam: Elsevier. <https://doi.org/10.1016/b978-0-444-59425-9.00028-7>
- Vinn, O. 2005: The tube ultrastructure of serpulids (Annelida, Polychaeta) *Pentaditrupa subtorquata*, Cretaceous, and *Nogrobs* cf. *vertebralis*, Jurassic from Germany. *Proceedings of the Estonian Academy of Sciences, Geology* 54, 260–265. <https://doi.org/10.3176/geol.2005.4.03>
- Vinn, O. 2007: Taxonomic implications and fossilization of tube ultrastructure of some Cenozoic serpulids (Annelida, Polychaeta) from Europe. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 244 (1), 115–128. <https://doi.org/10.1127/0077-7749/2007/0244-0115>
- Vinn, O. 2008: Tube ultrastructure of the fossil genus *Rotularia* Defrance, 1827 (Polychaeta, Serpulidae). *Journal of Paleontology* 82, 206–212. <https://doi.org/10.1666/06-125.1>
- Vinn, O. 2013a: Occurrence, Formation and Function of Organic Sheets in the Mineral Tube Structures of Serpulidae (Polychaeta, Annelida). *PLoS ONE* 8(10), e75330. <https://doi.org/10.1371/journal.pone.0075330>
- Vinn, O. 2013b: SEM study of semi-oriented tube microstructures of Serpulidae (Polychaeta, Annelida): implications for the evolution of complex oriented microstructures. *Microscopy Research and Technique* 76, 453–456. <https://doi.org/10.1002/jemt.22186>
- Vinn, O. 2020: Biomineralization of polychaete annelids in the fossil record. *Minerals* 2020, 10(10), 858. <https://doi.org/10.3390/min10100858>
- Vinn, O. 2021: Biomineralization in Polychaete Annelids: A Review. *Minerals* 2021, 11(10), 1151. <https://doi.org/10.3390/min11101151>
- Vinn, O. & Furrer, H. 2008: Tube structure and ultrastructure of serpulids from the Jurassic of France and Switzerland, its evolutionary implications. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 250(2), 129–135. <https://doi.org/10.5167/uzh-9756>
- Vinn, O. & Mutvei, H. 2009: Calcareous tubeworms of the Phanerozoic. *Estonian Journal of Earth Sciences* 58, 286–296. <https://doi.org/10.3176/earth.2009.4.07>
- Vinn, O. & Wilson, M.A. 2010: Sabellid-dominated shallow water calcareous polychaete tubeworm association from the equatorial Tethys Ocean (Matmor Formation, Middle Jurassic, Israel). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 258, 31–38. <https://doi.org/10.1127/0077-7749/2010/0080>
- Vinn, O. & Kupriyanova, E.K. 2011: Evolution of a dense outer protective tube layer in serpulids (Polychaeta, Annelida). *Carnets de Géologie, Notebooks on Geology, Brest, Letter 2011/05 (CG2011_L05)*, 137–147. <https://doi.org/10.4267/2042/43896>
- Vinn, O., Jäger, M. & Kirsimäe, K. 2008a: Microscopic evidence of serpulid affinities of the problematic fossil tube *'Serpula'etalensis* from the Lower Jurassic of Germany. *Lethaia* 41(4), 417–421. <https://doi.org/10.1111/j.1502-3931.2008.00093.x>
- Vinn, O., Mutvei, H., ten Hove, H.A. & Kirsimäe, K. 2008b: Unique Mg-calcite skeletal ultrastructure in the tube of the serpulid polychaete *Ditrupea*. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 248, 79–89. <https://doi.org/10.1127/0077-7749/2008/0248-0079>
- Vinn, O., ten Hove, H.A., Mutvei, H. & Kirsimäe, K. 2008c: Ultrastructure and mineral composition of serpulid tubes (Polychaeta, Annelida). *Zoological Journal of the Linnean Society* 154, 633–650. <https://doi.org/10.1111/j.1096-3642.2008.00421.x>
- Weedon, M.J. 1994: Tube microstructure of Recent and Jurassic serpulid polychaetes and the question of the Palaeozoic spirorbids. *Acta Palaeontologica Polonica* 39, 1–15.
- Zatoń, M., Machocka, S., Wilson, M.A., Marynowski, L. & Taylor, P.D. 2011: Origin and paleoecology of Middle Jurassic hiatus concretions from Poland. *Facies* 57, 275–300. <https://doi.org/10.1007/s10347-010-0244-y>
- Zibrowius, H. & ten Hove, H.A. 1987: *Neovermilia falcigera* (Roule, 1898) a deep- and cold-water serpulid polychaete common in the Mediterranean Plio-Pleistocene. *Bulletin of Biological Society of Washington* 7, 259–271.

