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Pentaditrupa nickcavei sp. nov. and 'revived' *Pentaditrupa interjuncta* (Jessen & Ødum, 1923) (Polychaeta, Serpulidae) from the Paleocene of Denmark, with some remarks on the middle Paleocene mesofauna

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The serpulid tubeworm genus *Pentaditrupa* is characterized by its gently curved tube with pentagonal cross-section, formed by five longitudinal edges or keels. Unlike most serpulid genera and unlike Jurassic species of *Pentaditrupa*, Cretaceous and Paleocene species of *Pentaditrupa* are never found attached to solid substrates, but instead inhabited soft-bottom environments of fine-grained seafloors that later lithified into chalk, limestone, or marlstone. A new species, *Pentaditrupa nickcavei* sp. nov., is described from the lower part of the Kerteminde Marl Formation (Selandian, middle Paleocene) of the Gundstrup gravel pit, Fyn, Denmark. This species represents the first record of the genus *Pentaditrupa* from the Selandian, thus extending the stratigraphic range of this genus and its temporal overlap with its presumed descendant *Ditrupa* by several hundred thousand years. Previously, the youngest known *Pentaditrupa* tubes were dated to the late Danian (early Paleocene). Moreover, comparative studies on the microstructure of an early Danian tube from Holtug quarry, Sjælland, Denmark, resulted in "revival" of the species *Pentaditrupa interjuncta* (Jessen & Ødum, 1923), originally introduced for early Danian tubes from Voxlev, Jylland, Denmark, but since decades considered a junior synonym of Late Cretaceous *Pentaditrupa subtorquata* (Münster in Goldfuss, 1831). While in the outer aspect the tubes of Cretaceous *P. subtorquata* and Danian *P. interjuncta* are indistinguishable, there are small but distinct differences in microstructure. The early Selandian *P. nickcavei* differs from both of these geologically older species by its larger maximal tube diameter, sharper longitudinal edges or keels, and by details in microstructure.

We also document new occurrences of the serpulid *Neovermilia gundstrupensis* Kočí, Milàn & Jäger, 2023 in the Gundstrup gravel pit. *Neovermilia* and *Pentaditrupa* were characteristic faunal elements already in the Late Cretaceous and Danian limestones. Their presence in the Kerteminde Marl Formation somewhat mitigates the otherwise significant faunal turnover observed between the Danian and the Selandian. Finally, we report the first occurrence of the slit worm-snail *Tenagodus* from the Kerteminde Marl and discuss its paleoecological interactions with associated mesofauna.

Key words. Serpulids, Paleocene, Selandian, Kerteminde Marl, Gundstrup gravel pit

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The annelid family Serpulidae Rafinesque, 1815 is a highly specialised group of marine segmented worms (class Polychaeta, subclass Sedentaria; see Kupriyanova *et al.* 2023) adapted to inhabiting self-secreted calcareous tubes (hence the common name '*calcareous tubeworms*'). In most species, these tubes are attached to various hard substrates. Serpulids occur in all seas, across all depths, and within habitats of normal marine salinity. Only a few species are adapted to hypo- or hypersaline waters, and just one species is known to inhabit freshwater in karst caves. The calcareous tubes have significant fossilization potential (Jäger 1983, 2005; Sklenář *et al.* 2013; Kočí *et al.* 2017).

The oldest known fossil serpulids date back to the Permian (Sanfilippo *et al.*, 2017, 2018, Ramsdale 2021; Słowiński *et al.* 2024). Serpulids diversified extensively during the Mesozoic and Cenozoic (Ippolitov *et al.* 2014) and are currently represented by several hundred species inhabiting modern marine environments (*e.g.*, ten Hove & Kupriyanova 2009; Kupriyanova *et al.* 2020; Rouse *et al.* 2022, and references therein). Kočí *et al.* (2023) reported the first occurrence of serpulids in the Selandian Kerteminde Marl, *Neovermilia gundstrupensis* Kočí, Milàn & Jäger, 2023, as a species not reworked from the Danian sediments.

This study aims to: (1) document additional specimens of *N. gundstrupensis*, (2) describe *Pentaditrupa nickcavei* sp. nov., a second known serpulid species from the Kerteminde Marl, including a detailed analysis of its microstructure, (3) describe *P. interjuncta* from the Danian Limestone, (4) report the first occurrence of the gastropod *Tenagodus* from the Kerteminde Marl and (5) interpret the palaeoecology of the associated mesofaunal assemblage.

Geological and geographical setting

After the K–Pg boundary event, sedimentation in the Danish Basin during the early Paleocene was initially dominated by carbonates. Part of the Middle Danian Limestones are excellently exposed in the huge working quarry at Faxe, and the Early Danian Limestone in the long natural cliff of Stevns Klint, including several working and abandoned quarries in the cliff or a few kilometres further inland. In one of these abandoned quarries situated directly at the cliff east of the village of Holtug, the tube of *Pentaditrupa interjuncta* was found.

However, by the end of the Danian, carbonate sedimentation had ceased due to a major regression approximately 61.6 million years ago (Vandenberghe *et al.* 2012; Cohen *et al.* 2013, updated 2022). This regression resulted in an erosional unconformity below the overlying Selandian deposits (*e.g.*, Thomsen & Heilmann-Clausen 1985; Clemmensen & Thomsen 2005). The subsequent Selandian transgression established a new depositional regime dominated by siliciclastic sediments, including the Lellinge Greensand in eastern Denmark and its lateral equivalent, the Kerteminde Marl Formation, in deeper depositional settings towards Fyn (Clemmensen & Thomsen 2005). The Selandian Kerteminde Marl Formation is interpreted to have been deposited in an outer shelf environment within the deep neritic zone, at depths of about 100–150 m. This setting was characterized by high sedimentation rates due to significant input of reworked chalk, well-oxygenated bottom waters with low current activity, and low planktonic productivity (Clemmensen & Thomsen 2005; Heilmann-Clausen 2010). The Formation reaches a maximum thickness of up to 150 metres, thinning over the Ringkøbing–Fyn High and thickening 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 have been located in the western part of Sjælland (Clemmensen & Thomsen 2005). The Kerteminde Marl Formation is overlain by the Selandian–Thanetian Æbelø Formation, which consists predominantly of clay and represents progressively deeper depositional conditions (Clemmensen & Thomsen 2005).

In recent years, the Kerteminde Marl Formation has been recognized for its rich and diverse fauna, especially in glacially derived blocks at the Gundstrup gravel pit. Schnetler & Nielsen (2018) described a diverse mollusk fauna comprising 133 species. This mollusk assemblage was later expanded by Schnetler & Nielsen (2021), who added one more gastropod species. In the present paper, we describe the first occurrence of the gastropod *Tenagodus* Guettard, 1770, from the Kerteminde Marl. The brachiopod *Terebratulina chrysalis* (von Schlotheim, 1813) was reported by Schröder & Surlyk (2024). King (1994) documented ostracods, sponges, and echinoderm fragments from the Kerteminde Marl, all specimens are housed in the collections of the Natural History Museum of Denmark. Vertebrate remains, including abundant skeletal elements of teleost fishes (King 1994; Schwarzhans *et al.* 2021), turtles (Myrvold *et al.* 2018), and several undescribed shark teeth, are also deposited in the collection of the Natural History Museum of Denmark. Trace fossils are represented by *Lepidenteron mortenseni* (Schwarzhans *et al.*, 2021) and *Koptichnus rasmussenae* (Vallon & Rindsberg, 2022).

Material and methods

The studied material includes four rock samples containing six serpulid tubes of *Pentaditrupa nickcavei* sp. nov. from the Gundstrup gravel pit; one tube of

Pentaditrupa interjuncta (Jessen & Ødum, 1923) from the early Danian of Holtug quarry, and seven tubes of *Pentaditrupa subtorquata* (Münster in Goldfuss, 1831) from the Campanian of Misburg and Höver in northern Germany, four new specimens of the serpulid *Neovermilia gundstrupensis* Kočí, Milàn & Jäger, 2023 from the Gundstrup gravel pit, and two blocks with associated mesofauna. All figured specimens are kept in the collection of the Natural History Museum of Denamrk (MGUH & NHMD) and Østsjællands Museer (OESM).

The microstructure of the tube wall of *Pentaditrupa subtorquata* was previously studied by Vinn (2005), who analyzed the surfaces of longitudinal sections using the following procedure: „The examined tubes were ground in longitudinal direction, polished, and etched with 1% acetic acid for 1 min prior to SEM examination. Thereafter, the same tubes were re-polished and treated with a 1 : 1 mixture of 25% glutaraldehyde and 1% acetic acid, to which alcian blue was added (GA-solution), for 5–45 min before SEM study.“ Ippolitov & Rzhavsky (2008), in their paper on Recent spirorbin serpulids, noted: „The microstructure of tube wall was studied on the surfaces of longitudinal cracks without etching.“ For the present study, we applied etching to a naturally broken tube wall at the anterior part of the tube using 1% acetic acid for 3 minutes, followed by drying and examination under SEM in a low vacuum. This method has the advantage of being non-destructive

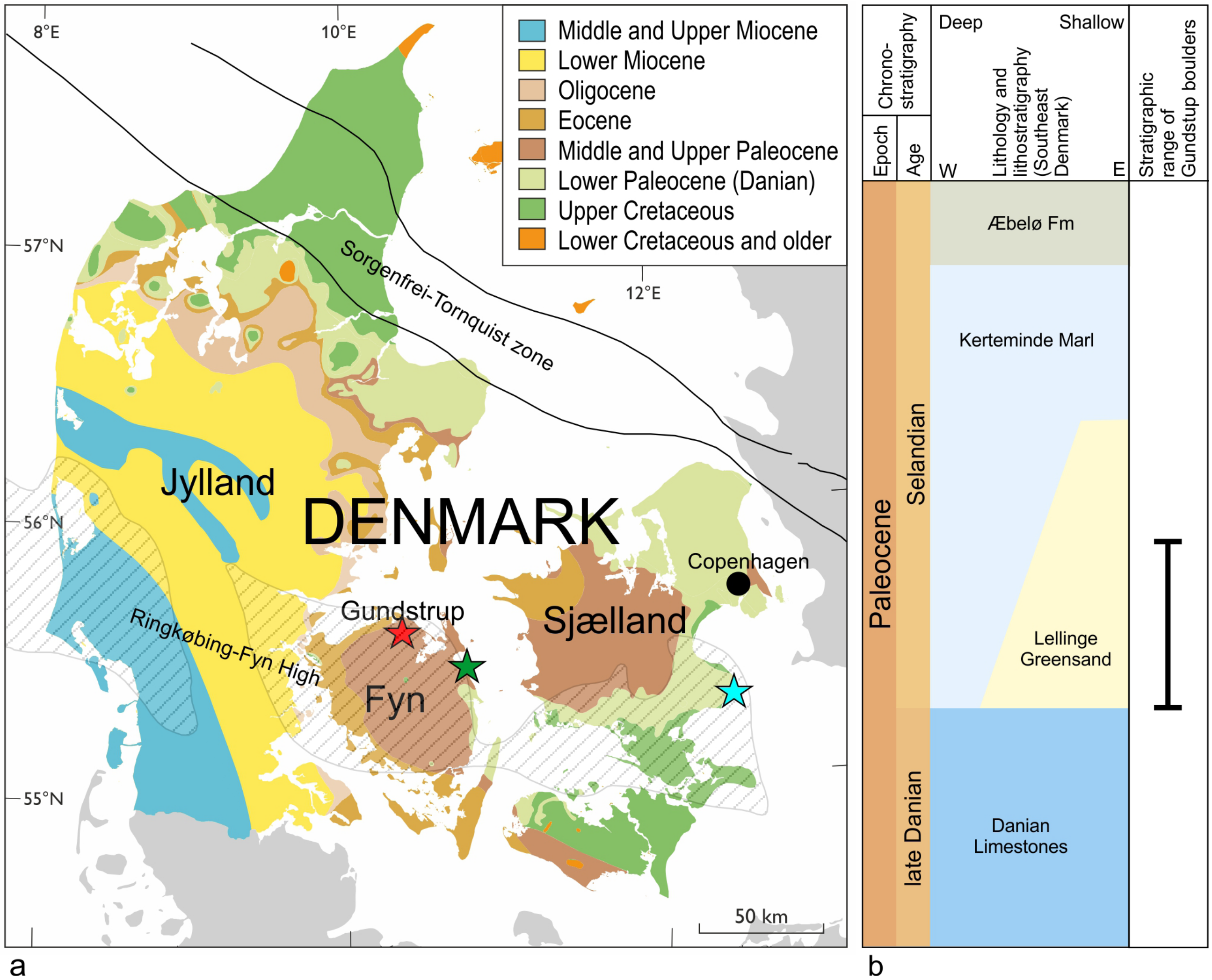

Fig. 1. a. Map of the pre-Quaternary subsurface in Denmark. The Gundstrup gravel pit is located on the isle of Fyn (55.56° N; 10.35° E), indicated by a red asterisk. Even though the boulders of Kerteminde Marl found here had been transported by Pleistocene glaciers, they have been found within the subsurface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

to the studied specimens. SEM imaging was performed using a Hitachi S-3700 N at the Palaeontological Department of the National Museum in Prague.

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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

Tribe Ficopomatini Pillai, 1960

Genus *Pentaditrupa* Regenhardt, 1961

Type species: *Pentaditrupa subtorquata* (Münster in Goldfuss, 1831) (type by original designation).

Description. While Early Jurassic representatives consist of a short posterior tube portion attached to a solid substrate and a long free tube portion, Late Cretaceous and Paleocene tubes are free, lacking any rest of an attached tube portion; they are adapted for lying freely on soft seafloor; for discussion of similarly shaped serpulid tubes, see Seilacher *et al.* (2008).

Tube small, medium-sized, or moderately large, slowly increasing in diameter, usually gently and regularly curved like an elephant's tusk, a horn, or a single whorl of a wide open spiral, less often straight or irregularly curved. The free tubes are characterized by five longitudinal ornaments equally spaced all around the circumference, causing the tube's pentagonal or pentalobate cross-section. Usually, these longitudinal ornaments are rounded edges or rounded low keels, but less often, mainly in small juvenile tube parts, they may be sharp keels, but never developed as high combs. In a few Late Cretaceous populations, longitudinal ornamentation is reduced, and the cross-section is almost circular. Transverse ornamentation is usually lacking, except for delicate, not elevated, chevron-shaped incremental lines, which protrude between the keels and retreat at the keels. No peristomes. The surface is smooth and usually a bit shiny; Vinn & Kupriyanova (2011) mentioned *Pentaditrupa* among the taxa possessing a dense outer protective tube layer, presumably an adaptation against drilling predation by gastropods and against dissolution in deeper water.

Microstructure. Concerning the method of tube construction, the tube wall consists of two main layers: (1) The thick, usually bright brown or bright yellow outer layer is the parable layer. It is built and prolonged at the aperture at the anterior end of the worm. In longitudinal section, it consists of parable-shaped = chevron-shaped increments, whose outer thighs form a thick sublayer causing a slightly reduced tube diameter at the aperture, whereas their inner thighs form a much thinner sublayer. (2) The thin inner layer is the cylinder layer. It is added to the interior surface of the tube and consists of very thin-walled cylinder-shaped increments that stick inside each other. Often the cylinder layer is pale white, transversely striated, leafy, and slightly scaling-off. (3) Additionally, in well-preserved tubes, a very thin innermost organic sheet may be present.

In contrast, in SEM images of longitudinal and transverse sections, at least of Late Cretaceous and Paleocene *Pentaditrupa* tubes, the visually most conspicuous boundary between outer and inner tube layer is located at a different level in a slightly more exterior position: inside the parable layer, with the conspicuous, strongly curved, chevron-shaped connection between outer and inner thighs of the increments of the parable layer belonging to the inner tube layer. In the present study, we follow this definition of layers and sublayers seen in SEM images, from exterior surface to interior consisting of (1) a rather thick outer layer, which represents the outer thighs of the chevron-shaped increments of the parable layer, and (2) a rather thin inner layer, which comprises (2a) the conspicuous, strongly curved connection between the outer and inner thighs of the parable layer, (2b) the inner thighs, (2c) the cylinder layer, and, if the tube is well preserved, (2d) a thin organic sheet.

In SEM images of longitudinal sections, sublayer (2a) is usually most conspicuous. It consists of long, needle-shaped spherulitic prismatic crystals. Generally, the crystals are oriented approximately (not exactly) perpendicular to the boundaries between the increments, and due to the strong curvature of these boundaries, the orientation of the crystals in the outer layer differs by up to *c.* 80 degrees from their orientation in the inner layer. In longitudinal sections, both elements – the curved boundaries and the needle-shaped spherulitic prismatic crystals – together form a characteristic pattern resembling water fountains. The crystals are longer and arranged more strictly parallel to each other in the inner layer than in the outer layer, where they are arranged roughly parallel but slightly irregularly.

In longitudinal sections, microstructure shows small but conspicuous differences in the water fountain pattern of sublayer (2a) between species from the Late Cretaceous, Danian, and Selandian ages. These differences concern (1) the relative visual predominance of boundaries between chevron-shaped increments versus visual predominance of the needle-shaped crystals, (2) the length of the crystals, and (3) maybe the grade of curvature – narrow or wide – of the water fountain pattern and of the boundaries between chevron-shaped increments.

All studied Late Cretaceous and Paleocene tubes of the genus *Pentaditrupa* have a spherulitic prismatic (SPHP) microstructure sensu Vinn (2005, Vinn *et al.* 2008c) in the inner layer and outer layer of the tube wall.

Stratigraphical range. *P. nickcavei* sp. nov. prolongs the geological record of the genus *Pentaditrupa* from Hettangian to Selandian. Hitherto, *Pentaditrupa* was known only to reach up to the Danian (Jäger 2005).

Discussion. Apart from its more or less rounded pentagonal cross-section, the tube of *Pentaditrupa* closely resembles the circular tube of its close relative and chronological successor, *Ditrupa* Berkeley, 1835. If neglecting several *Ditrupa*-like but possibly not closely related serpulid species from the Late Jurassic and Early Cretaceous of the Arctic realm, the earliest secured representative of the genus *Ditrupa* is *D. schlotheimi* Rosenkrantz, 1920 from the middle Danian (C) and late Danian (D). In consequence, the timespan of secured stratigraphic co-occurrence (although not at the same localities) of the genera *Pentaditrupa* and *Ditrupa*, which hitherto was believed to last only from Middle to Late Danian, is now prolonged up to the Selandian. As *D. schlotheimi* is very common in some facies in Denmark, the Netherlands, and Belgium, *Pentaditrupa* even survived the first bloom of the genus *Ditrupa*.

Nevertheless, the geological record of the genus *Pentaditrupa* still shows a surprisingly wide gap ranging from late Early Jurassic (Toarcian) to late Early Cretaceous (middle Albian) (Jäger 2005; Kočí *et al.* 2024). Apart from the fact that only the Early Jurassic tubes often possess a short attached posterior tube portion, whereas Late Cretaceous and Paleocene tubes entirely lack such an attached portion, the geologically old and young tubes are morphologically so similar to each other that it seems appropriate to unite them in the same genus. However, we cannot be sure: Homeomorphies between not closely related serpulid taxa are very common, as demonstrated in comparable cases of morphologically very similar ‘pairs’ of tubes, one pair characterized by quadrangular cross-section (fossil *Nogrobs* de Montfort, 1808 versus recent *Spirodiscus* Fauvel, 1909, for discussion see Kupriyanova and Ippolitov 2015), the other pair or trinity characterized by hexagonal cross-section (fossil *Tectorotularia* Regenhardt, 1961 versus fossil *Pyrgopolon* (*Hamulus*) Morton, 1834 (for discussion see Jäger in Rantuch *et al.* 2024) versus recent *Serpula crenata* Ehlers, 1908.

Pentaditrupa nickcavei **sp. nov.**
Figs 2–8

Etymology. In honor of the Australian musician, writer, actor, artist, and performer Nick Cave for his lifelong dedication to music, literature, and lyrics.

Holotype. The tube shown in Fig. 2a, MGUH 35025.

First paratype. The tube shown in Fig. 2b, MGUH 35026.

Second paratype. The tube shown in Fig. 3a, 3a1, 3a2, MGUH 35207.

Type locality. Gundstrup gravel pit, Fyn, Denmark.

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

Material. Four rock samples with 6 tubes altogether, including the holotype and two paratypes.

Diagnosis. An unattached, medium- to moderately large-sized, usually gently and regularly curved species of the genus *Pentaditrupa*. The five sides are slightly concave and meet each other laterally by forming five sharp longitudinal edges or low and narrow but sharp keels, which are not rounded even in the largest tube parts. In SEM images of longitudinal sections, the boundaries between the chevron-shaped increments predominate in visibility over the needle-shaped spherulitic prismatic crystals (Fig. 7a2, 7a3).

Description. Tube diameter gradually increasing up to *c.* 5.2 mm. The longest preserved tube length is 41.9 mm as shown in Fig. 5a, though the tubes were undoubtedly longer originally. Cross-section pentagonal with sharp or only very slightly rounded edges. Transverse ornamentation consists of densely spaced, chevron-shaped (V-shaped) delicate striae on a generally glossy surface. No peristomes. The tube wall is relatively thick, 0.6 mm in a paratype. Lumen circular, 1.2–1.3 mm in diameter in a paratype. In SEM images, the needle-shaped spherulitic prismatic crystals are relatively short in the inner layer.

Discussion. The tubes of *P. nickcavei* differ from those of *P. interjuncta* and *P. subtorquata* by their sharper longitudinal edges or low keels and by reaching a wider maximum tube diameter. Small differences in microstructure are discussed below in the General discussion chapter.

***Pentaditrupa interjuncta* (Jessen & Ødum, 1923)**
Figs 9–11

1923 *Ditrupa interjuncta* n. sp. – Jessen & Ødum, pp. 28–29, Text-Fig. 11, Pl. 2, Fig. 8a–d.
1926 *Ditrupa interjuncta* – Ødum, p. 167.
1931 *Ditrupula subtorquata* Münster. – Nielsen, p. 96.
1961 *Ditrupa* (*Pentaditrupa*) *interjuncta* (Ødum). – Regenhardt, p. 75.
? 1970 *Pentaditrupa* aff. *interjuncta* (Ødum) – Rosenkrantz, p. 426.
pars 1983 *Pentaditrupa subtorquata* (Münster in Goldfuss, 1831) – Jäger, p. 56, non Pl. 7, Figs 1–8.
pars 2005 *Pentaditrupa subtorquata* (Münster in Goldfuss, 1831) – Jäger, p. 167, non Pl. 8, Figs 1–2.

Holotype. The tube figured in Jessen & Ødum (1923, Pl. 2, Fig. 8a), Natural History Museum of Denmark, MGUH 34985. In this museum, also the other tubes of *Ditrupa interjuncta* figured in Jessen & Ødum are kept; their numbers are: Pl. 2, Fig. 8b: MGUH 34986; Pl. 2, Fig. 8c: MGUH 34987; Pl. 2, Fig. 8d: MGUH 34988; Text-Fig. 11: MGUH 34996.

Type locality. Voxlev quarry, Jylland, Denmark.

Type stratum. lower Danian, Bryozoan Limestone.

Material. A single damaged tube (OESM 13330).

Diagnosis. An unattached, medium-sized, usually gently and regularly curved species of the genus *Pentaditrupa*. *P. interjuncta* is characterized by its five blunt, but only slightly rounded and conspicuous longitudinal edges or low keels, with slightly concave or plane areas in between. In SEM images of longitudinal sections, the needle-shaped crystals predominate in visibility over the boundaries between the chevron-shaped increments. The crystals are relatively tall in the outer layer.

Description. Tube diameter gradually increasing up to *c.* 3 mm according to Jessen & Ødum's original description, but reaching only 2.3 mm in the tube from Holtug. Longest preserved tube length is 26 mm according to Jessen & Ødum, who already stated that originally that undoubtedly the tubes had been considerably longer, and *c.* 21 mm in the incomplete tube from Holtug (Fig. 9 shows only a part of its former length, after the tube had been cut for preparing transverse sections). Cross-section pentagonal with

Fig. 2. *Pentaditrupa nickcavei* sp. nov., early Selandian, Gundstrup gravel pit. a, Holotype, MGUH 35025, b. First Paratype. MGUH 35026.

Fig. 3. *Pentaditrupa nickcavei* sp. nov., early Selandian, Gundstrup gravel pit. a, a1, a2. Second Paratype, MGUH 35027.

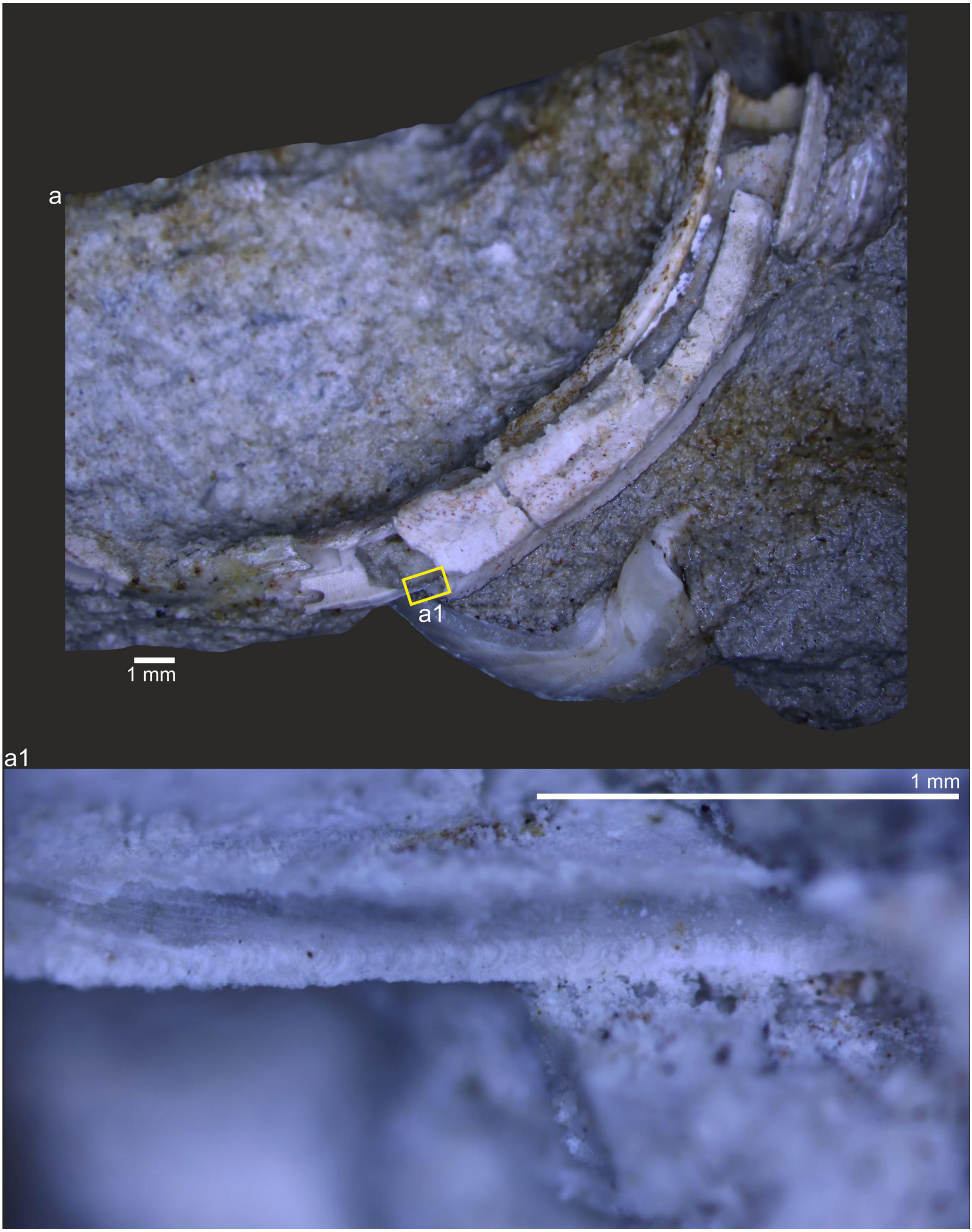

Fig. 4. *Pentaditrupa nickcavei* sp. nov., early Selandian, Gundstrup gravel pit. a. Damaged tube in sediment, which also includes a valve of the oyster *Pycnodonte* (*Phygraea*) *vesiculare* (Lamarck, 1806). The rectangle shows the region figured in a1. a1. Detail in high magnification showing chevron-shaped increments at the transition from outer to inner parable layer. (Specimen was lost during preparation).

Fig. 5. *Pentaditrupa nickcavei* sp. nov., early Selandian, Gundstrup gravel pit. a. Tube in substrate. a1. Pentagonal anterior cross-section, MGUH 35028.

rounded edges or pentalobate. On the interior surface of the tube wall, a thin organic sheet (sensu Vinn 2013a) is preserved (ios in Fig. 11b1).

Discussion. The tubes of *P. interjuncta* as well as those of *P. subtorquata* differ from the tubes of *P. nickcavei* by their more rounded longitudinal edges and by reaching only a smaller maximum tube diameter than in *P. nickcavei*. In external tube morphology and in tube diameter, *P. interjuncta* and *P. subtorquata* are usually indistinguishable. Small differences in microstructure are discussed in the General discussion chapter below.

Rosenkrantz (1970, p. 426) listed *P.* aff. *interjuncta* from the Upper Danian locality Agatdal, Greenland.

General discussion of the three studied species and their microstructure

Exterior tube morphology. The more common twisting of the longitudinal edges around the longitudinal axis in *P. interjuncta* stated by Jessen & Ødum (1923) is simply a consequence of more common twisting of

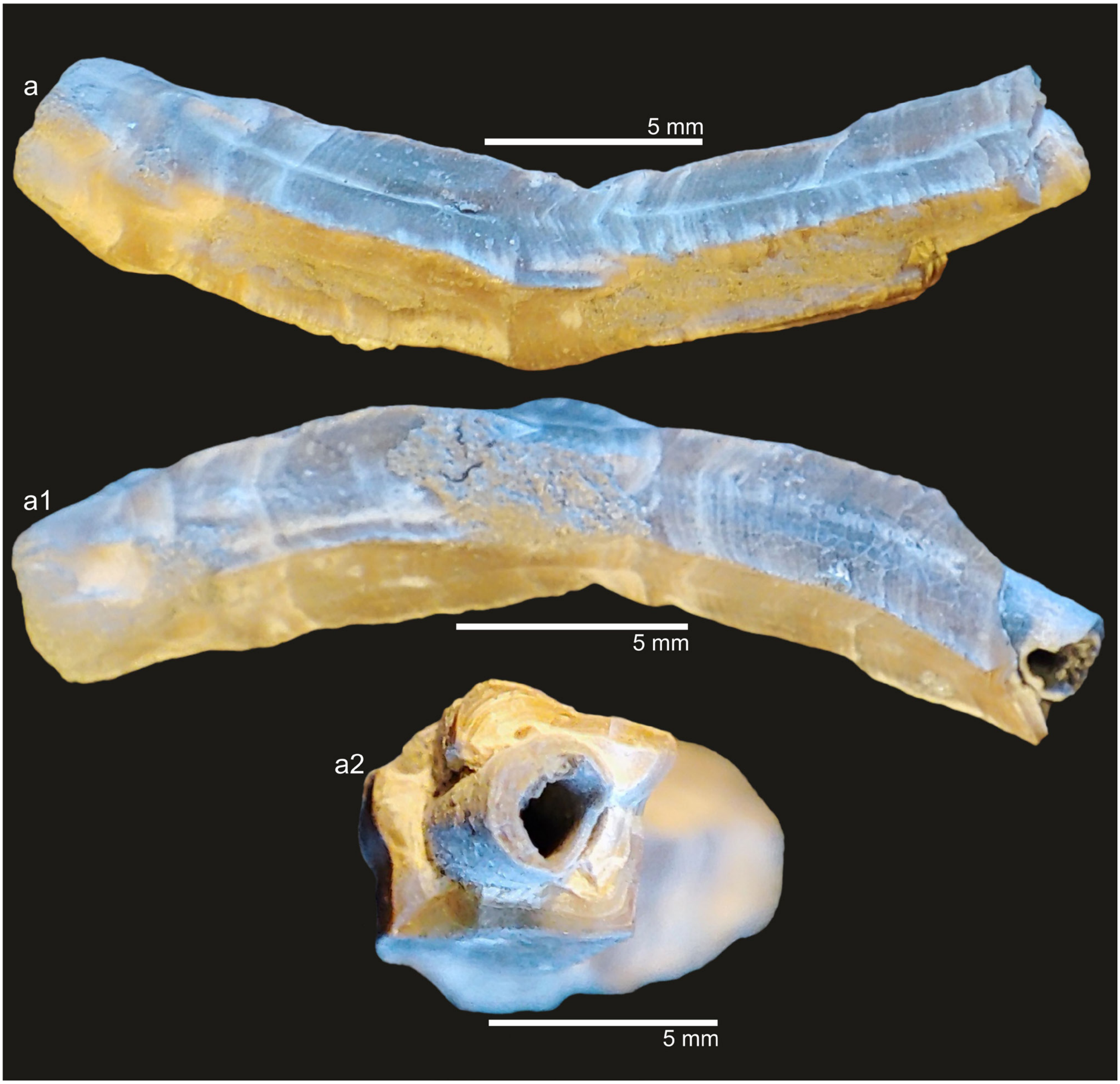

Fig. 6. *Pentaditrupa nickcavei* sp. nov., early Selandian, Gundstrup gravel pit. a, a1. Longitudinal views of the tube with longitudinal and transverse ornamentation. a2. Posterior cross-section, on the left side of the photograph, partly longitudinally broken approximately along the boundary between the outer and inner tube wall layer, MGUH 35029.

the animal around its longidinal axis during ontogeny, perhaps caused by more often changing the position and orientation of the tube including its animal by agitated water or by action of vagil marine animals. Moreover, a relatively wide morphologic variety concerning rounded longitudinal edges versus sharp keels, and convex versus plane versus concave sides between the edges respectively keels, is seen in most *Pentaditrupa* species.

Only an extremely rounded variety of Late Cretaceous *P. subtorquata* has no morphological equivalent in the two Paleocene *Pentaditrupa* species. Such a variety from the Campanian was named '*Protula pruinosa*' by Regenhardt (1961). Its longitudinal edges are inconspicuous and very much rounded, and the sides between the edges may be convex instead of concave or plain, so that the tube's cross-section becomes almost perfectly circular, resembling the genus *Ditrupa*. From around the lower/upper Campanian boundary to the upper Maastrichtian, such circular tubes co-occur with tubes of the usual *Pentaditrupa* shape in north Germany (Jäger 1983). Apart from the edges and cross-section, the circular tubes perfectly match the morphology and structure of *P. subtorquata*.

Tube microstructure. In the 21st century, SEM images showing tiny crystals and other structural details visible in high magnification in transverse, longitudinal, and surface-parallel horizontal sections became widely used and studied. Following several earlier studies (*e.g.*, Sanfilippo 1996, 1998; Sanfilippo & Mòllica 2000), researchers, predominately Olev Vinn and co-authors, studied a high number of recent and fossil serpulid species and other 'tubeworms' and classified these details (Vinn 2005, 2007, 2008, 2011, 2013a, b, 2020, 2021; Vinn & Kupriyanova 2011; Vinn & Mutvei 2009; Vinn *et al.* 2008a, b, c). They found

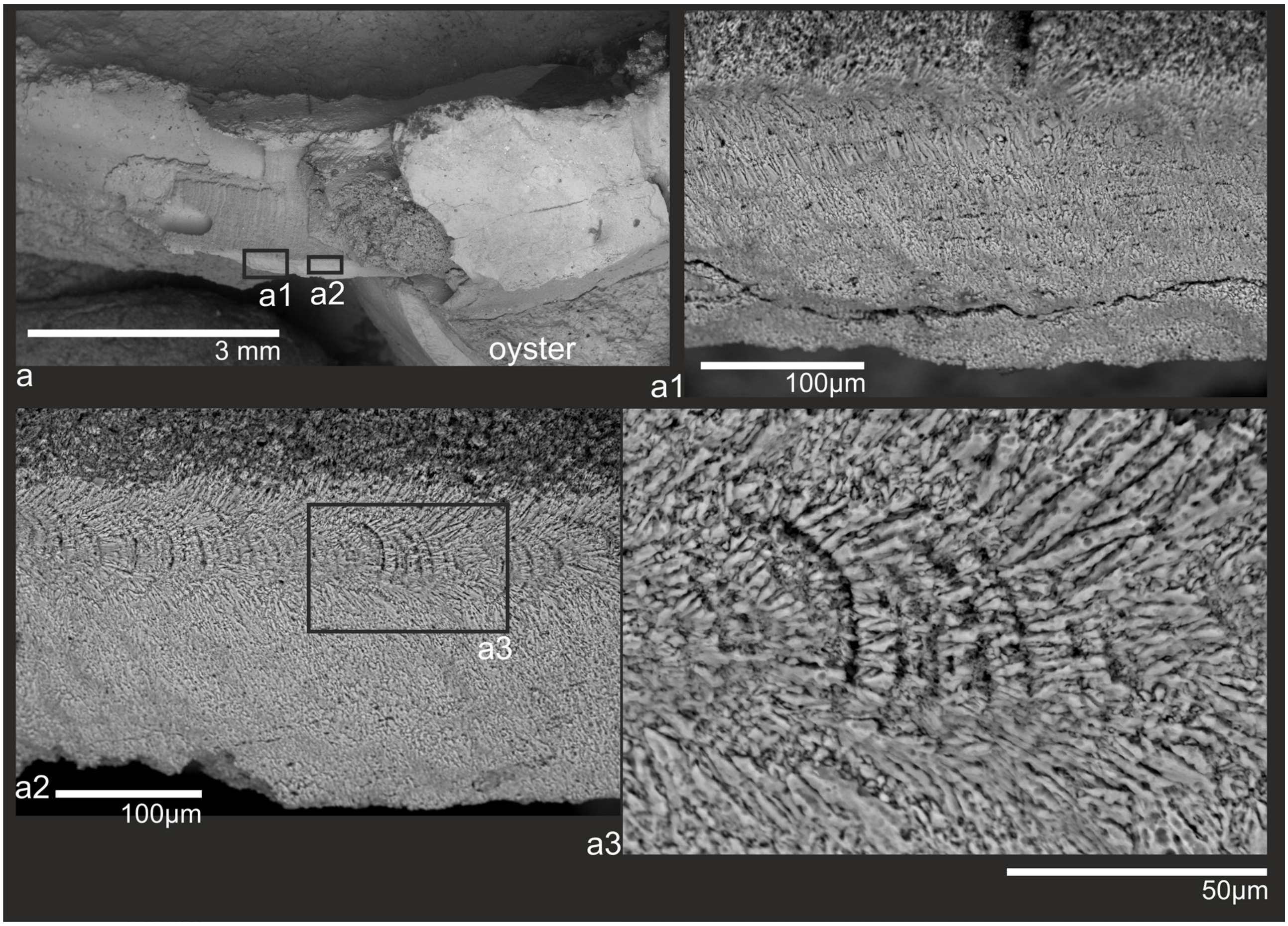

Fig. 7. Microstructure of *Pentaditrupa nickcavei* sp. nov., early Selandian, Gundstrup gravel pit, same specimen as in Fig. 4. Longitudinal section. a. Overview of broken tube wall, SEM image. a1. Outer tube layer consisting of several sublayers, which are the increments of the outer parable layer, constructed of short spherulitic prismatic crystals oriented perpendicular to the tube's longitudinal axis. a2. Inner tube layer showing growth lamellae with spherulitic prismatic crystals. a3. Detail of inner tube layer, distinctly showing the curved boundary lines between increments with short spherulitic prismatic crystals, which are arranged in a pattern resembling water fountains. The microstructure of inner and outer tube layers matches the spherulitic prismatic structure (SPHP) type sensu Vinn *et al.* (2008c).

that serpulid tubes consist of only a single layer in many species, but two, three, or even four layers in other species, and that according to the shape of the tiny crystals of which these layers consist and the orientation of these crystals as visible in transverse, longitudinal, and horizontal sections of the tube, the microstructures can be classified in at least 13 distinguishable types.

Such SEM studies constituted a conspicuous step forward in studying tube microstructure by showing hitherto unknown details. It is generally acknowledged that studies, descriptions and comparisons of microstructure are a strong and valuable tool – combined with studies on recent worm animals, their

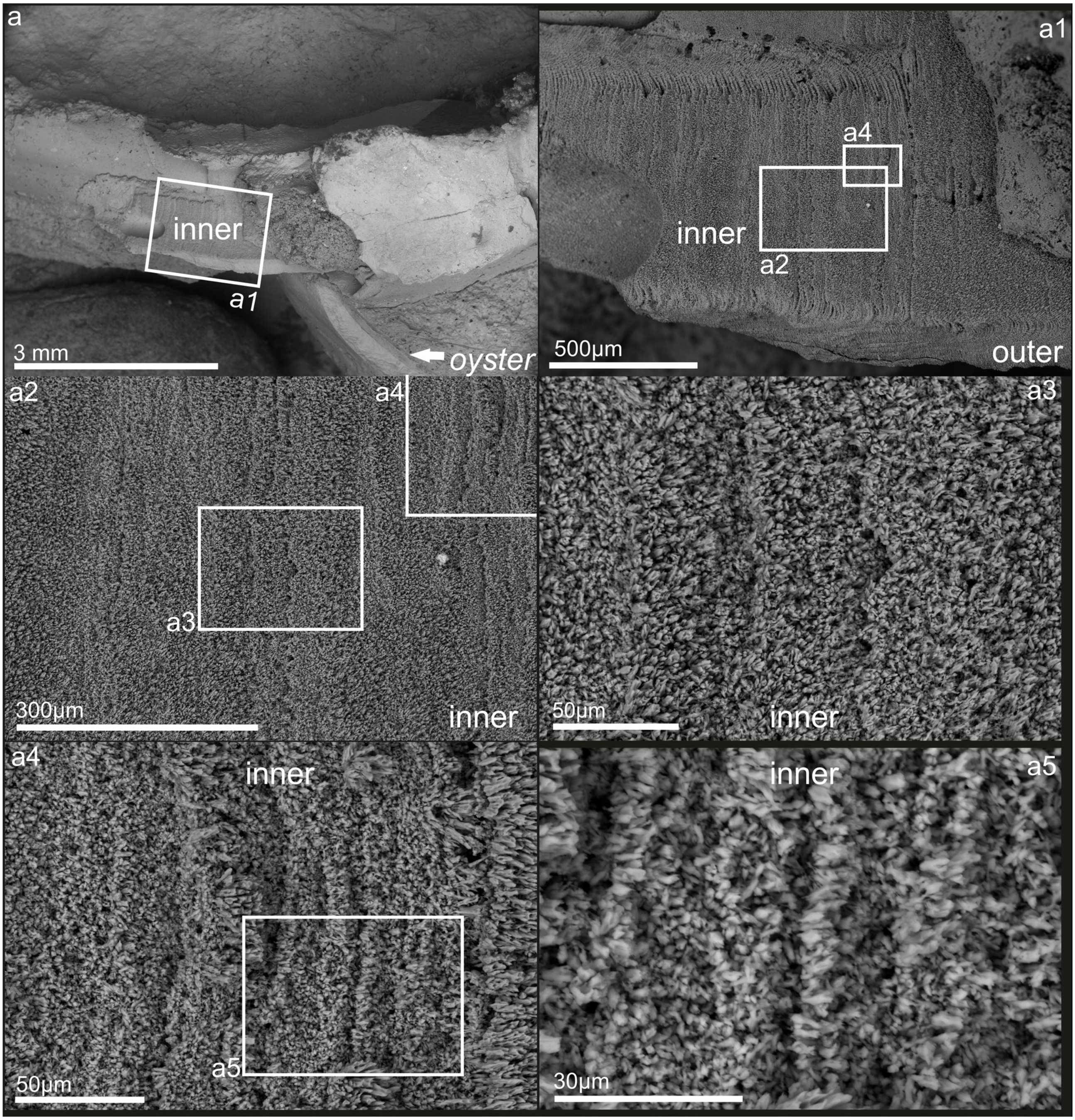

Fig. 8. Microstructure of *Pentaditrupa nickcavei* sp. nov., early Selandian, Gundstrup gravel pit, same specimen as in Fig 4. Longitudinal section. a. Overview of the interior surface of the inner tube layer. a1. Detail of a showing transverse growth lamellae consisting of short prismatic crystals. a2–a5. These growth lamellae are oriented perpendicular to the tube's longitudinal axis, whereas their short crystals are oriented parallel to the tube's longitudinal axis. The microstructure matches the spherulitic prismatic structure (SPHP) type sensu Vinn *et al*. (2008c).

opercula, exterior tube morphologies and genetics – in order to distinguish serpulid tubes from superficially similar tubes of other worm-shaped organisms, and, within family Serpulidae, to distinguish between subfamilies, tribes, genera, subgenera and, in some cases, species, and to investigate their phylogenetic relationships (*e.g.*, Kupriyanova *et al.* 2023).

While microstructure of many different species has been described, figured and discussed, not much is known yet about intraspecific or (palaeo-)geographic variability of microstructure, because usually only few SEM images of only a single tube or very few tubes of each species are provided, and, due to the usually high magnification of SEM images, they

Fig. 9. *Pentaditrupa interjuncta* (Jessen & Ødum, 1923), early Danian, Holtug quarry, OESM 13330. a. Overview. a1. Lateral view. a2. Posterior transverse section. a3. Anterior transverse section.

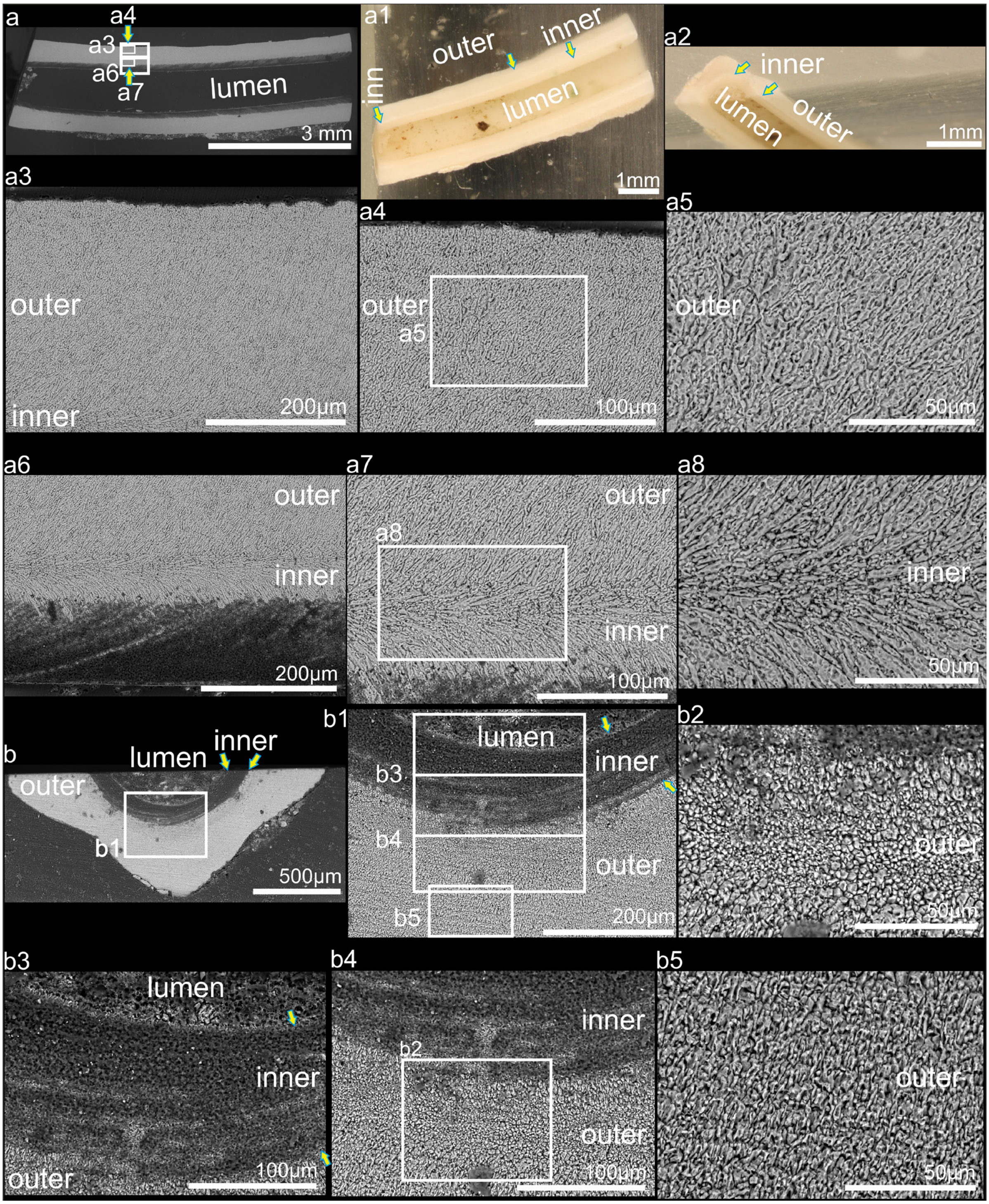

Fig. 10. Microstructure of *Pentaditrupa interjuncta* (Jessen & Ødum, 1923), early Danian, Holtug quarry. a–a8. OESM 13330. Longitudinal section. a–a2. Overviews showing the tube wall, rectangles indicate positions of detailed views in the following subfigures. a3–a7. Details of the outer tube layer in different magnifications showing approximately parallel oriented tall spherulitic prismatic crystals, which are oriented perpendicular to the inner growth lamellae. a6–a8. Details of the inner tube layer at different magnifications. a7–a8. Details of the boundary region between outer and inner tube layers, which is marked by spherulitic crystals arranged in a conspicuous pattern resembling water fountains; these crystals are oriented perpendicular to the less conspicuous chevron-shaped increments at the transition between outer and inner parable layers. b–b5. Transverse section, rectangles indicate positions of detailed views in the following subfigures. b1–b2, b4–b5. Details of the outer tube layer in different magnifications. b1, b3–b4. Details of the inner tube layer at different magnifications. – The microstructure matches the spherulitic prismatic (SPHP) type sensu Vinn *et al.* (2008c).

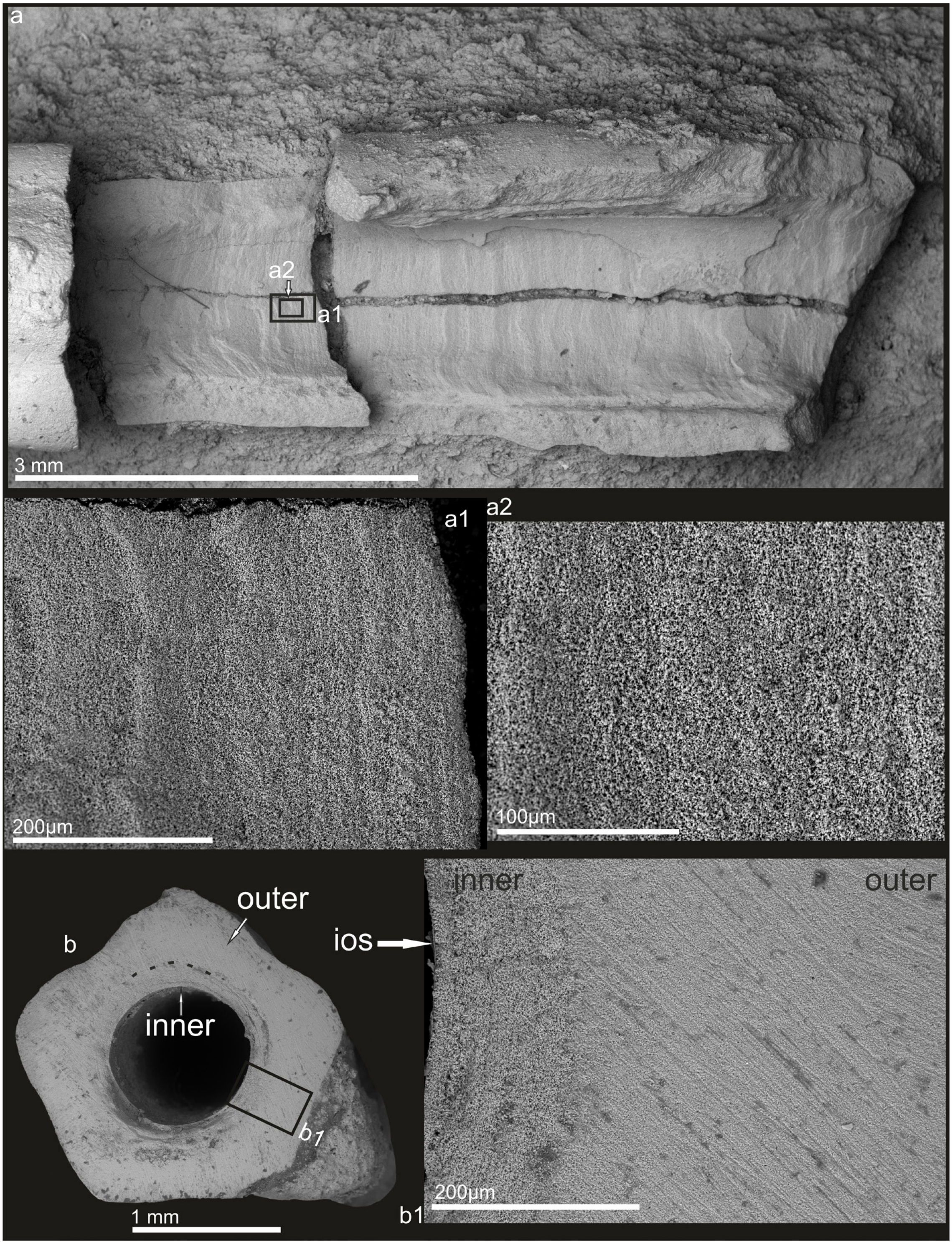

Fig. 11. Microstructure of *Pentaditrupa interjuncta* (Jessen & Ødum, 1923), early Danian, Holtug quarry, OESM 13330. a, a1, a2. Longitudinal section. a. Overview showing the tube wall of the anterior tube portion. Rectangles show positions of detailed views in the following subfigures. a1, a2. The interior surface of the tube showing the base of the inner layer, consisting of transverse incremental lamellae constructed of short prismatic crystals oriented parallel to the tube's longitudinal axis. b. Transverse section, photograph taken before treating the tube with 1% acetic acid for *c*. 3 minutes, showing the thick outer and thin inner tube wall layers; dashed line indicates boundary between them. b1. Detailed view of inner and outer layers, ios - inner organic sheet is exceptionally preserved. This organic sheet is an adaptation to strengthen the mechanical properties of the tubes in clade A (sensu Aliani et al 1995, Vinn 2011, 2013, 2021). The oblique striation in the outer layer is an artifact caused by cutting or polishing. The microstructure matches the spherulitic prismatic (SPHP) type sensu Vinn *et al.* (2008c).

Fig. 12. *Pentaditrupa subtorquata* (Münster in Goldfuss, 1831), Campanian, quarries east of Hannover. a, b, c, d. Early Campanian, Holcim quarry, Höver, OESM 13331. e, f, g. Late Campanian, Teutonia Nord quarry, Misburg, OESM 13332. a, b, c, d, e, f, g. Lateral views. a1, c1, e1. Frontal views to apertures. b1, d1, f1, g1. Transverse sections.

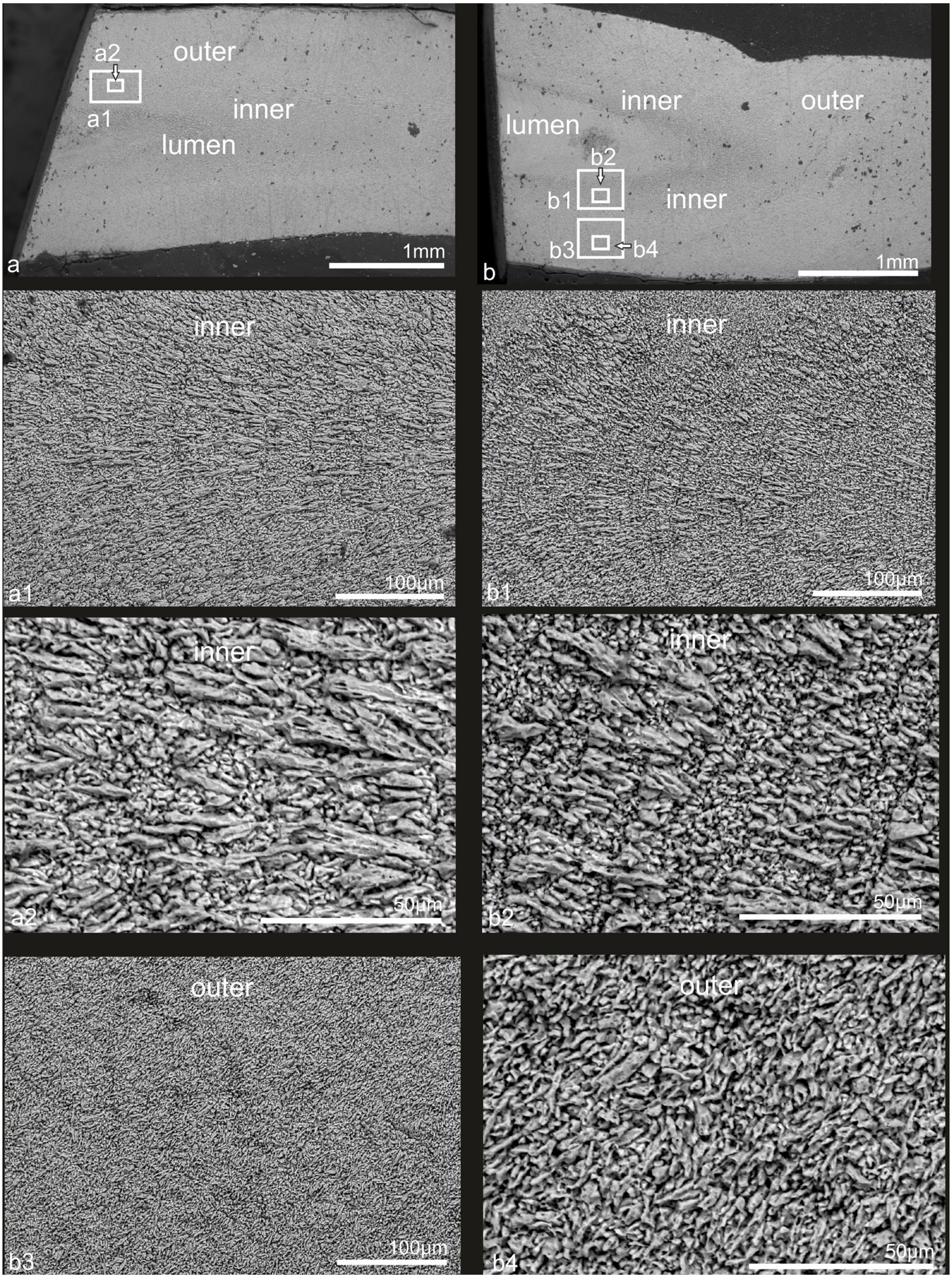

Fig. 13. Microstructure in longitudinal sections of *Pentaditrupa subtorquata*, Campanian, quarries east of Hannover, northwest Germany. a, b. Same specimen as Fig. 12b, d, early Campanian, Holcim quarry, Höver. a, b. Overviews of longitudinal sections, showing positions of details. a1, a2, b1, b2. Inner layer, consisting of regularly oriented spherulitic crystals (a2, b2) of spherulitic prismatic (SPHP) microstructure (sensu Vinn *et al*. 2008); these crystals are arranged in chevron-shaped = parable-shaped increments oriented perpendicular to the longitudinal axis of the tube. b3, b4. Outer layer with crystals of semiregular spherulitic prismatic (SPHP) microstructure.

document only a tiny portion of the entire tube. Concerning the exterior aspect of serpulid tubes, it is well-known that high morphological variability within species, together with many homeomorphisms between different taxa, impedes taxonomic-systematic research of fossil and empty recent tubes. As microstructure has a strong influence on exterior aspect, it may well be assumed that microstructure may display some intraspecific variation, too. Therefore, at least in the present state of knowledge, we should be careful not to over-estimate small differences between SEM images showing generally similar microstructure.

Moreover, tiny structures are more prone to faster crystal growth and other crystallographical and mineralogical changes by re-crystallisation than larger structures. Such changes may occur already during lifetime, or during taphocoenosis or diagenesis, or much later by subfossil or recent weathering. Hitherto, only a few studies focused on re-crystallisation in serpulid tubes in more detail; perhaps the most recent and most comprehensive study is provided by Grenier *et al.* (2024). Moreover, SEM images of perfectly plane and polished artificial sections may look different from those of rough and uneven 'planes' of natural breakage. And, of course, not perfectly longitudinal, horizontal, or transverse sections may distort the height/width ratio in the images.

Hitherto, tubes of *Pentaditrupa subtorquata* from the Campanian of Höver near Hannover, north Germany, studied by Vinn (2005: 262–263, Pl. 1, figs 3, 4, 8) seem to be the only specimens of the genus *Pentaditrupa* whose microstructure was studied and published by SEM images. In the outer tube layer, Vinn (2005: figs 3, 4) detected a semiregular spherulitic prismatic structure, abbreviated SPHP in Vinn & Kupriyanova (2011: 138–139, Tab.1), and a transverse section of the inner layer (Vinn 2005: fig. 8) shows a possibly secondary homogeneous structure composed of calcareous granules, named fine-grained homogeneous structure, abbreviated FH, in Vinn & Kupriyanova (2011: 138–139, Tab. 1).

We compared Vinn's results with SEM images of polished sections of *Pentaditrupa subtorquata* tubes with tubes of *P. nickcavei* from the early Selandian of Gundstrup gravel pit (Figs 7–8), *P. interjuncta* from the early Danian of Holtug quarry (Figs 10–11), and some more tubes of *P. subtorquata* from the same region as studied by Vinn: from the early Campanian of Höver quarry and the late Campanian of Teutonia Nord quarry at Misburg, both located east of Hannover in north Germany (Figs 13–14).

Our SEM images of the inner tube layer are quite consistent across all tubes, supporting the classification of these tubes under a single genus, *Pentaditrupa*. However, slight differences between the three species should be discussed in detail.

The outer tube layer of *Pentaditrupa nickcavei* is composed of several growth sublayers – the increments of the outer parable layer (Fig. 7a1). These increments run somewhat obliquely to the tube's longitudinal axis and consist of needle-shaped spherulitic prismatic crystals (Fig. 7a2, 7a3), which are oriented approximately, but not strictly, perpendicular to the boundaries between increments. In all three studied *Pentaditrupa* species, the crystals in the outer layer are somewhat shorter and arranged slightly less strictly parallel to each other than similar crystals in the inner layer. Our study confirms the spherulitic prismatic (SPHP) type of microstructure *sensu* Vinn *et al.* (2008c), which belongs to the oriented prismatic structures, where the long axis of the crystals has a uniform orientation and is continuous through successive growth increments (Vinn 2020). Our study shows that the outer tube layer is more or less the same in all examined tubes from the three different localities of three different geological ages.

As stated above, the transverse section in Vinn (2005, fig. 8) shows a fine-grained homogeneous structure (FH). A similar structure is also seen in *P. interjuncta* from the early Danian of Holtug quarry in the transverse section (Fig. 10b3), but in the longitudinal section of the same tube, these only seemingly fine-grained granular crystals turn out in reality to be long sphaerulitic crystals, which are arranged in the shape of beautiful „water fountains" (Fig. 10a7, 10a8). Vinn (2005) did not provide a longitudinal section of the inner tube layer of *P. subtorquata* from the Campanian. Nevertheless, other *P. subtorquata* tubes from the Campanian of the same quarry area east of Hannover show the same pattern of „water fountains" (Fig. 13a1, 13b1) as in the tubes of *P. nickcavei* and *P. interjuncta*. In the *P. interjuncta* tube from Holtug (Fig. 10a7, 10a8), the crystals are more clearly visible than the boundaries between increments; therefore, the spherulitic prismatic crystals emphasize the water fountain pattern more distinctly than in *P. nickcavei* (Fig. 7a2, 7a3) and in *P. subtorquata* (Fig. 13a1, 13b1).

We have no transverse section of the inner layer of *P. nickcavei* from the early Selandian of Gundstrup gravel pit, but in the longitudinal section (Fig. 7a2, 7a3) the beautiful 'water fountains' most conspicuously show the narrow curvature of the chevron-shaped parables (increments), whose anteriorly directed vertices (which are visible already in the lower third of the low magnification SEM image Fig. 8a1 and even in the middle of the ordinary light photograph Fig. 4a1) mark the transition between the thick outer and the thin inner parable layer. Moreover, they show that the long crystals are oriented more or less (not exactly) perpendicular to the boundary lines between the parables.

The growth increments with spherulitic prisma-

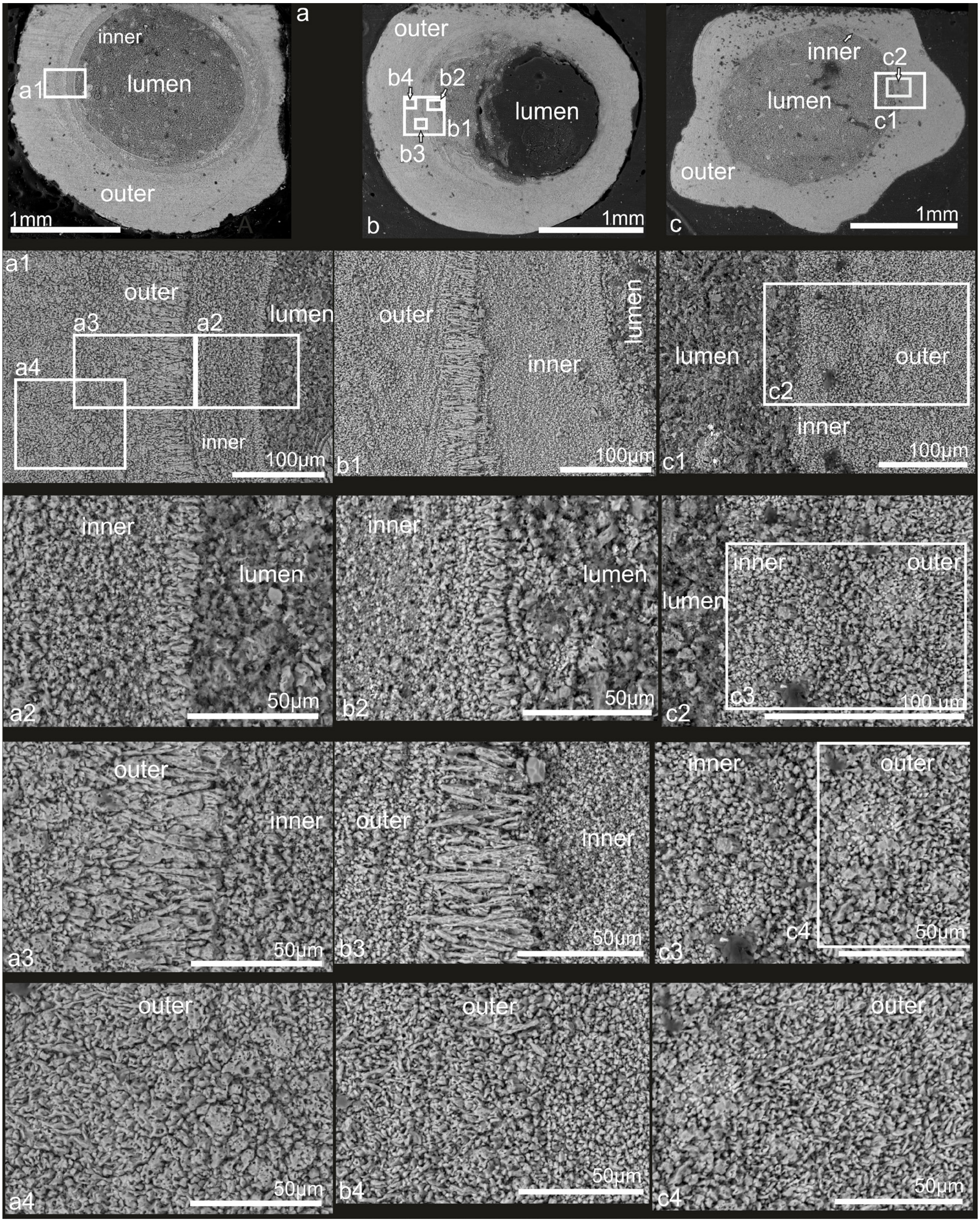

Fig. 14. Microstructure in transverse sections of *Pentaditrupa subtorquata*, Campanian, quarries east of Hannover, northwest Germany. a. Same specimen as Fig. 12b, early Campanian, Holcim quarry, Höver. b, c. Same specimen as Fig. 12e, late Campanian, Teutonia Nord quarry, Misburg. a, b, c. Overviews of transverse sections, showing positions of details. There are three layers named the outer layer, the inner layer, and the very thin innermost organic layer. a1 – a3, b1 – b3, c1 – c3. Details showing boundaries between the lumen, inner and outer layers. a3, b3. Tall prismatic crystals developed between the outer and inner layer. a4, b4, c4. Outer layer with semiregular spherulitic prismatic microstructure.

tic (SPHP) microstructure continue in the inner parable layer. Other SEM images (Fig. 8a2–8a5) of the longitudinally broken *P. nickcavei* tube show a horizontal view of the undamaged or only slightly abraded innermost part of the inner tube layer in the interior surface of the tube wall. It consists of crystals, which in this horizontal view appear to be very short, and incremental lines, which are sometimes visible as transverse striae already under a binocular microscope or even to the naked eye. This thin innermost layer can be interpreted either as a cylinder layer or as an organic sheet. Additionally, the early Danian tube from Holtug features an exceptionally preserved innermost organic sheet, as described by Vinn (2013a); see the arrow labeled 'ios' in Fig. 11b1. This organic sheet is an adaptation to strengthen the mechanical properties of the tubes in clade A (sensu Aliani *et al.* 1995; Vinn 2011, 2013, 2021).

In summary, the tube wall of *Pentaditrupa nickcavei* has two layers, the inner and the outer, both are spherulitic layers, classified as SPHP microstructure. The general construction of microstructure, as described above in the chapter on genus *Pentaditrupa*, is the same in the three species of the present study, and justifies assigning these three species to a single genus. In detail, however, there are small but distinct differences in microstructure between the three species, with regard to three features, all detectable in SEM images showing longitudinal sections of the outer sublayer of the inner tube layer – the level (2a), showing the water fountain pattern, and adjacent sublayers:
(1) The boundaries between the chevron-shaped increments predominate in visibility over the needle-shaped crystals in *P. nickcavei*, whereas in *P. interjuncta* the crystals predominate, and in *P. subtorquata*, boundaries as well as crystals are moderately visible.
(2) Although in all three *Pentaditrupa* species the crystals in the outer layer are shorter than the crystals in the inner layer, there are small differences in crystal lengths between species. In the inner tube layer, the crystals are relatively short in *P. nickcavei*, but tall in *P. subtorquata*. In the outer tube layer, the crystals are tall in *P. interjuncta*.
(3) In *P. subtoquata*, the chevron-shaped boundaries between growth increments as well as the water fountain pattern appear to be wider curved than the narrower curves in *P. interjuncta* and *P. nickcavei*. However, this widening may be only an artifact due to optical stretching caused by the non-central cutting plane in *P. subtorquata*.

Genus *Neovermilia* Day, 1961

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

Neovermilia gundstrupensis Kočí, Milàn & Jäger, 2023
Figs 15, 18h

2023 *Neovermilia gundstrupensis* sp. nov. – Kočí, Milàn & Jäger, pp. 139–146, Figs 3–7.

Additional material. 4 samples, 5 tubes altogether.

Description (short version). Tube moderately large, posterior portion coiled in some tubes. The transverse ornament consists of densely spaced annular striae. Cross-section circular. For more details, see Kočí *et al.* (2023).

Discussion. These new finds are figured (Fig. 15) to demonstrate the variability of tube shape, and to underline their common occurrence in the lower Selandian at Gundstrup pit, and their non-obligate preference of attaching their tube to sponges.

Class Gastropoda Cuvier, 1795

Subclass Caenogastropa L. R. Cox, 1960

Order Caenogastropoda *incertae sedis*

Superfamily Cerithioidea J. Fleming, 1822

Family Siliquariidae Anton, 1838

Genus *Tenagodus* Guettard, 1770

Type species. *Serpula anguina* Linnaeus, 1758 (type by subsequent designation)

Tenagodus sp.
Figs 16, 17, 18c

Material. Several large slab of Kerteminde Marl containing several damaged and poorly preserved fossils. The slabs are registred for their assiciated fauna under numbers NHMD 1986505 & NHMD 1758095.

Description. Shell medium to large-sized. Protoconch is missing. The early whorls form a regular and tight characteristic spiral, whereas the curvature of the last whorl is wider, so that the anterior portion lost direct contact with the previous whorl and may grow somewhat irregular or even partly straight. Periostracum is not preserved. Surface smooth, lacking any ornamentation. The shell wall is thin.

Discussion. The genus *Tenagodus* is known from the Middle Triassic to the Recent (Wenz 1939; Davies 1971; Squires 1990). The often cited genus *Siliquaria* is a junior objective synonym of *Tenagodus* (see Bieler 1992; Bieler & Petit 2011). The specimens from Kerteminde Marl are similar to *Tenagodus terebellus*

(Lamarck, 1818), which is recorded from the Oligocene of the North Sea Basin, the Adour Basin, northern Italy, and Iran (Harzhauser 2004), but are larger than *Tenagodus* cf. *terebellus* (Lamarck, 1818) mentioned by Harzhauser (2004: 122) from the Late Rupelian to Early Chattian of Abadehin Esfahan-Sirjan Basin in Central Iran.

Palaeoecology

Serpulids

The genus *Pentaditrupa*, characterized by its pentagonal cross-section and its short (in Early Jurassic representatives) or entirely absent (in Late Albian to

Fig. 15. *Neovermilia gundstrupensis* Kočí, Milàn & Jäger, 2023, early Selandian, Gundstrup gravel pit. a, b, c. Damaged tubes show the variability of the tube's shape of this species. a, MGUH 35030. b, MGUH 35031. c, MGUH 35032.

Selandian representatives) attached posterior tube portion, belongs to a group of phylogenetically unrelated serpulid taxa adapted to life on soft seafloor, where larger solid substrates suitable for attachment are rare or absent. Other soft-bottom dwelling serpulid species include representatives of the following genera and subgenera: *Ditrupa* Berkeley, 1835, *Nogrobs* de Montfort, 1808, *Pyrgopolon* (*Pyrgopolon*) de Montfort, 1808, *Pyrgopolon* (*Hamulus*) Morton, 1834, *Rotulispira* Chiplonkar and Tapaswi, 1973 (= *Praerotularia* Lommerzheim, 1979), *Tectorotularia* Regenhardt, 1961, *Austrorotularia* Macellari, 1984, *Rotularia* Defrance, 1827. Seilacher *et al.* (2008) discussed several representatives of this palaeoecological group in de-

Fig. 16. a, a1. Siliquarid gastropod *Tenagodus* sp., early Selandian, Gundstrup gravel pit, specimens appears as associated fauna on NHMD 1986505.

Fig. 17. a, a1, a2. Siliquariid gastropod *Tenagodus*, early Selandian, Gundstrup gravel pit, specimens appears as associated fauna on NHMD 1758095.

Fig. 18. The associated mesofauna and flora, early Selandian, Gundstrup gravel pit. a. *Pentaditrupa nickcavei* sp. nov., b. Brachiopod *Terebratulina chrysalis* (von Schlotheim, 1813). c. The siliquarid gastropod *Tenagodus* sp. d, d1. Gastropod *Aporrhais* sp., fragment of bird-foot-shaped aperture. e. Fragment of undetermined gastropod. f. Bivalve *Lima* sp. g. Gymnosperm cone. h. Serpulid *Neovermilia gundstrupensis* Kočí, Milàn & Jäger, 2023. Specimens appear as associated fauna on NHMD 1758095.

tail.

Unlike the soft-bottom dwellers *Pentaditrupa nickcavei* sp. nov. and *P. subtorquata*, *Neovermilia gundstrupensis* Kočí, Milàn & Jäger, 2023, typically has its coiled posterior tube portion attached to a large sponge *Ventriculites* (see Kočí *et al.* 2023, p. 141, Fig. 4A, A1, and p. 142, Fig. 5A) or, less commonly, to another hard substrate. This attachment suggests a dependence on such hard substrates, at least during the early stages of its life.

Vinn (2024) measured and discussed the distance between adjacent incremental lines in several serpulid tubes. In the inner layer of the Selandian tubes of *Pentaditrupa nickcavei* from the Kerteminde Marl, we observed up to six incremental lines per 50 µm, with larger tubes showing a tendency toward fewer incremental lines within the same distance. This suggests a greater distance between adjacent incremental lines in larger tubes. Our observations agree with those of Vinn (2024), who reported 5–20 growth lines per 50 µm in Cenozoic serpulids.

Di Geronimo *et al.* (2000) suggested that larger serpulid tube sizes are a response to a lower sea temperature. The relationship between the effect of temperature during tube growth, tube size, and the associated number of incremental lines cannot, however, be confirmed in the Danish serpulids. The tubes of *Pentaditrupa* and *Neovermilia* from the Kerteminde Marl are medium in size: The tube diameter of *Pentaditrupa nickcavei* reaches up to 5.2 mm; this is somewhat larger than in Late Cretaceous *P. subtorquata*. *Neovermilia gundstrupensis* reaches up to 5 mm; this is smaller than the maximum size of 10 mm (Jäger, 1983) of Late Cretaceous *Neovermilia ampullacea*. The Kerteminde Marl was deposited at a depth of 100–150 m (King 1994, 2015; Clemmensen & Thomsen 2005), where seafloor temperatures were relatively low despite a subtropical climate, with palaeotemperature estimates of 11.7–14.7°C (Buchardt 1977). Small- and large-sized serpulid tubes have not yet been found there. Absence of small tubes can easily be explained by sampling bias. Collectors often focus on specimens visible to the naked eye at outcrops, selecting only the best-preserved ones. The scarcity of large tubes may be explained by the scarcity of large substrates. For species whose tubes are attached to some hard substrate, *e.g.*, *Neovermilia*, the size of the substrate plays an important role. The correlation between the size of substrates and the size of epibionts has already been documented (*e.g.*, Kočová Veselská *et al.* 2021). A nice example of this phenomenon can be observed in the middle Danian bryozoan and corallian chalk of the Faxe quarry. These limestones were deposited in cold waters, but serpulids remained predominantly small in size. This size limitation is certainly not related to water temperature but rather to the small diameter of octocoral and scleractinian coral branches, along with the limited size of cryptic cavities within the dense coral thickets, to which many tubes are attached. These cavities were also already occupied by competing invertebrates, further limiting the growth of the serpulid tubes.

The size of serpulid tubes may also be influenced by nutrient richness and availability (Clemmensen & Thomsen 2005). The abundant supply of calcium carbonate from reworked chalk, indicated by the high sedimentation rate, may have contributed to the medium sizes of serpulid tubes in the Kerteminde Marl. Despite this, the bottom water was well-oxygenated, current activity was low, plankton production was minimal, and benthic food availability was reduced (Clemmensen & Thomsen 2005). Similarly, the larger sizes of serpulids observed in the Maastrichtian chalk deposits of Denmark (Kočí, Milàn, personal observations) can be linked to a greater supply of calcium carbonate. However, a thorough paleoecological comparison of serpulids from the Kerteminde Marl and the Maastrichtian chalk, as well as more accurate interpretations, will require further intensive sampling of the Kerteminde Marl. While serpulids from the Gundstrup gravel pit (Kerteminde Marl) have only recently been the focus of more intensive collection, those from Maastrichtian chalk and Danian limestones have been studied since the early 19th century (*e.g.*, von Hagenow 1840 for Maastrichtian serpulids from the Isle of Rügen, Germany). This suggests that collecting bias may once again be a contributing factor.

Mollusks and brachiopods

The oyster *Pycnodonte vesiculare* initially required a hard substrate for attachment during its early ontogeny, but soon became free-lying, stabilized by the increasing weight of its massive shell. The brachiopod *Terebratulina chrysalis* (Fig. 18b, arrow) was adapted to a soft substrate environment, similar to the Cretaceous species *Terebratulina striata* (Wahlenberg, 1821), which anchored itself to skeletal sand on the seafloor using a rootlet pedicle (*e.g.*, Schrøder *et al.* 2018: fig. 10; Schrøder & Surlyk 2024).

The gastropod *Tenagodus* exhibits a worm-like shell shape and slit band, features thought to be adaptations for living among seaweeds and sponges.

Due to palaeocurrents, mollusks are often found in small to large accumulations. Notable examples include two slabs: one containing approximately 30 specimens of *Kangilioptera gundstrupensis* Schnetler & Nielsen, 2018, and another with about 20 specimens of *Quadrinervus wienekei* Schnetler & Nielsen, 2018. Several specimens of the bivalve *Pteria thomseni* Schnetler & Nielsen, 2018 and the gastropods *Metacerithium hauniense* (Koenen, 1885) and *Cerithiopsis andreae* Schnetler & Nielsen, 2018 have also been found in slabs. Occasionally, concentrations of diverse species have been observed.

Bivalves are predominantly represented by infaunal species, including members of Nuculanidae, *Pholadomya* (*Bucardiomya*) *margaritacea* (Sowerby, 1821), and Cuspidariidae. Sessile bivalves, either byssate or cementing, are less common and include pectinids and *Limaria geinitzi* (von Hagenow, 1842). Boring bivalves are represented by Teredinidae, ?*Lithophaga* Röding, 1798, and ?*Netastoma* Carpenter, 1864. The dentalids were endobenthic.

The gastropod fauna includes only a few herbivorous species. All specimens of the gastropod *Scurria rieae* Schnetler & Nielsen, 2018 have been found in association with fossilized wood, probably sunken driftwood, indicating transport. Most gastropod species were carnivorous.

The presence of pelagic cephalopods suggests open marine conditions, with a soft seabed at an estimated depth of 100–150 metres in a nutrient-rich environment.

General palaeoecology

Clemmensen & Thomsen (2005, Fig. 11) described the palaeoenvironment in the Storebælt area as fully marine, with moderately good oceanic connections, a water depth of 100–150 m, and a very high sedimentation rate due to a significant input of reworked chalk. The bottom waters were well-ventilated, with low current activity. The planktonic production was low, resulting in a reduced benthic food supply. A rich and diverse non-mollusks fauna was also documented, including foraminifera, sponges, anthozoans, annelids (serpulids), decapod crustaceans, cirripedes (excluding barnacles), bryozoans, brachiopods, asteroids, ophiuroids, crinoids, echinids, chelonids, ganoids (skeletal parts, otoliths and scales in burrows), sharks (teeth) and birds (breastbone). This fauna supports the palaeoecological interpretation provided.

Schnetler and Nielsen (2018) confirmed that the mollusk fauna inhabited this environment at an estimated palaeodepth of 100–150 metres, and presumed a subtropical climate. The palaeoenvironment is linked to the transgression of the Selandian Sea, which included the erosion of underlying Danian sediments. Initially, a near-shore environment characterized the early Selandian, followed by a gradual increase in water depth, leading to the deposition of fine-grained Kerteminde Marl and, subsequently, the clay of the Æbelø Formation.

Conclusions

The serpulid tubeworm *Pentaditrupa nickcavei* sp. nov. from the Selandian (middle Paleocene) Kerteminde Marl at the Gundstrup gravel pit on Fyn, Denmark, represents the geologically youngest known species of the genus *Pentaditrupa* Regenhardt, 1961.

The species name *Pentaditrupa interjuncta* (Jessen & Ødum, 1923), after being considered a junior synonym of *P. subtorquata* for several decades, is 'revived' for Danian representatives of the genus *Pentaditrupa* from Denmark. In exterior view, the tubes of both species are usually indistinguishable, but there are small but distinct differences in microstructure.

Pentaditrupa nickcavei sp. nov. differs from the closely related Late Cretaceous to Danian *P. subtorquata* (Münster in Goldfuss, 1831) by reaching a larger tube diameter, possessing sharper longitudinal edges or low keels, and specific microstructural features.

The palaeoecology of the serpulids *Pentaditrupa nickcavei* sp. nov., *Neovermilia gundstrupensis* Kočí, Milàn & Jäger, 2023, and associated fauna is discussed.

Additionally, the siliquarid gastropod *Tenagodus* is reported for the first time from the Kerteminde Marl.

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References

Aliani, S., Bianchi, C. N., de Asmundis, C. & Meloni, R. 1995: Scanning electron microscope observations on the tube of the reef-forming serpulid *Ficopomatus enigmaticus* (Fauvel) (Annelida, Polychaeta). Bollettino di Zoologia 62, 363–367.

https://doi.org/10.1080/11250009509356090

Anton, H.E. 1838: Verzeichniss der Conchylien welche sich in der Sammlung von H.E. Anton befinden, xvi + 110 pp., Halle.

Berkeley, M.J. 1835: Observations upon the *Dentalium subulatum* of Deshayes. The Zoological Journal 5, 424–427, pl. 19, suppl. vol. pl. 18. http://biodiversitylibrary.org/page/13381128

Bieler, R. 1992: *Tenagodus* or *Siliquaria*? Unravelling taxonomic confusion in marine „worm-snails" (Cerithioidea: Siliquariidae). The Nautilus 106, 15–20. https://www.biodiversitylibrary.org/page/8271249

Bieler, R. & Petit, R.E. 2011: Catalogue of Recent and fossil "worm-snail" taxa of the families Vermetidae, Siliquariidae, and Turritellidae (Mollusca: Caenogastropoda). Zootaxa 2948, 103 pp.

Buchardt, B. 1977: Oxygen isotope ratios from shell material from the Danish middle Paleocene (Selandian) deposits and their interpretation as paleotemperature indicators. Palaeogeography, Palaeoclimatology, Palaeoecology 22, 209–230. https://doi.org/10.1016/0031-01

Carpenter, P.P. 1864: Supplementary report on the present state of our knowledge with regard to the Mollusca of the West Coast of North America. Reports of the British Association for the Advancement of Science 33 [1863], 517–686. https://www.biodiversitylibrary.org/page/29370651

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

Clausen, O.R. & Huuse, M. 2002: Mid-Paleocene palaeogeography of the Danish area. Bulletin of the Geological Society of Denmark 49, 171–186. https://doi.org/10.37570/bgsd-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/epiiugs/2013/v36i3/002

Cox, L.R. 1960: Thoughts on the classification of the Gastropoda. Proceedings of the Malacological Society of London 33, 239–261.

Cuvier, G. 1795: Second Mémoire sur l'organisation et les rapports des animaux à sang blanc, dans lequel on traite de la structure des Mollusques et de leur division en ordre, lu à la société d'Histoire Naturelle de Paris, le 11 prairial an troisième [30 May 1795]. Magazin Encyclopédique, ou Journal des Sciences, des Lettres et des Arts 1795 [1. année] (2), 433–449. http://www.biodiversitylibrary.org/page/6736775

Davies, A.M. 1971: Tertiary faunas – a text-book for oil field palaeontologists and students of geology. 1. The composition of Tertiary faunas. Revised and updated by F.E. Eames. London: George Allen and Unwin. 571 pp.

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

Defrance, M. 1827: Rotulaire. In: Levrault, F.G. (ed.): Dictionnaire des sciences naturelles 46, 321–322. Strasbourg: F. G. Levrault; Paris: LeNormant.

Di Geronimo, I., Di Geronimo, R., La Perna, R., Rosso, A. & Sanfilippo, R. 2000: Cooling evidence from Pleistocene shelf assemblages in SE Sicily. In: Hart, M.B. (ed.): Climates: Past and Present. Geological Society London, Special Publications 181, 113–120. London: The Geological Society. https://doi.org/10.1144/GSL.SP.2000.181.01.11

Ehlers, E. 1908: Die bodensässigen Anneliden aus den Sammlungen der deutschen Tiefsee-Expedition, 1–168. In: Chun, C. (ed.): Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer ''Valdivia'' 1898–1899 16 (1), 1–168, pls I–XXIII. http://www.biodiversitylibrary.org/item/18687

Fauvel, P. 1909: Deuxième note préliminaire sur les polychètes provenant des campagnes de l'Hirondelle et de la Princesse-Alice, ou déposées dans la Musée Océanographique de Monaco. Bulletin de l'Institute Océanographique de Monaco 142, 1–76. http://biodiversitylibrary.org/page/46491917

Fleming, J. 1822: The philosophy of zoology: or a general view of the structure, functions and classification of animals 2, 1–618. Edinburgh. https://www.biodiversitylibrary.org/page/28230157

Goldfuss, G.A. 1831: Petrefacta Germaniae 1 (3), 165–240, pls 51–71. Düsseldorf: Arnz.

Grenier, Chr., Berent, K., Rodríguez-Navarro, A., Vinn, O., Checa, A.G. 2024: Microstructures, crystallography and growth patterns of serpulid tubeworms (Class Polychaeta). Marine Biology 171(231), 23 pp. https://doi.org/10.1007/s00227-024-04552-w

Grube, A.E. 1850: Die Familien der Anneliden. Archiv für Naturgeschichte 16 (1), 249–364.

Guettard, J.E. 1770: Mémoires sur différentes parties des Sciences et Arts [qui referme] ... Deuxième Mémoire, qui renferme la concordance des auteurs qui ont parlé des tuyaux marins fossiles, auxquels on a comparé ceux qui se pêchent actuellement dans la mer. Classe des Tuyaux Marins. Troisième Mémoire. Sur les erreurs où l'on a été au sujet des tuyaux marins. 3(544), 71. Paris: Prault. http://www-gdz.sub.uni-goettingen.de/cgi-bin/digbib.cgi?PPN483932760

Hagenow, F. von 1840: Monographie der Rügen'schen Kreide-Versteinerungen, 2, Radiarien und Annulaten. Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefakten-Kunde 1840, 631–672.

Hagenow, F. von 1842: Monographie der Rügen'schen Kreideversteinerungen. III. Mollusken. Neues Jahrbuch für Mineralogie, Geologie und Paläontologie 1842, 528–575.

Håkansson, E. & Pedersen, S.A.S. 1992: Geologisk kort over den danske undergrund. VARV (map sheet). København: Tidsskriftet VARV.

Harzhauser, M. 2004: Oligocene gastropod faunas of the Eastern Mediterranean (Mesohellenic Trough/Greece and Esfahan-Sirjan /Central Iran). Courier Forschungsinstitut Senckenberg 248, 93–181.

Heilmann-Clausen, C. 2010: Palæogen – Fra drivhus til kølehus. Geoviden 3, 2–11.

Hove, H.A. ten & Kupriyanova, E.K. 2009: Taxonomy of Serpulidae (Annelida, Polychaeta): The state of affairs. Zootaxa

2036, 1–126. https://doi.org/10.11646/zootaxa.2036.1.1

Ippolitov, A.P. & Rzhavsky, A.V. 2008: On the tube microstructure of recent spirorbids (Annelida, Polychaeta). Doklady Biological Sciences 418 (1), 20–22. Springer Nature BV. https://doi.org/10.1134/S0012496608010079

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. 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.

Jessen, A. & Ødum, H. 1923: Senon og Danien ved Voxlev. Danmarks geologiske Undersøgelse, 2. Række 39, 73 pp.

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 Harra Borehole, Denmark. Aarhus Geoscience 1, 65–72.

King, C. 2015: A revised correlation of Tertiary rocks of the British Isles and adjacent areas of NW Europe. In: Gale, A.S. & Barry, T.L. (eds): Geological Society of London Special Report 27 [published 2016]: 724 pp. https://doi.org/10.1144/sr27

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

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 72, 135–151. https://doi.org/10.37570/bgsd-2023-72-05

Kočí, T., Milàn, J., Jakobsen, S.L. & Bashforth, A.R. 2024: *Serpula*? *alicecooperi* sp. nov. – a new serpulid from the Lower Jurassic (Pliensbachian) Hasle Formation of Bornholm, Denmark. Bulletin of the Geological Society of Denmark 73, 41–56. https://doi.org/10.37570/bgsd-2024-73-02

Koenen, A. von 1885: Ueber eine Paleocäne Fauna von Kopenhagen. Abhandlungen der königlichen Gesellschaft der Wissenschaften (Göttingen) 32, 1–128.

Kupriyanova, E.K. & Ippolitov, A.P. 2015: Deep-sea serpulids (Annelida: Polychaeta) in tetragonal tubes: on a tube convergence path from the Mesozoic to Recent. Zootaxa 4044, 151–200. http://dx.doi.org/10.11646/zootaxa.4044.2.1

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, 398, 24 pp. https://doi.org/10.3390/d15030398

Lamarck, J.-B. de 1806: Suite des Mémoires. Sur les fossiles des environs de Paris. Genre LXXIV. Huitre. Ostrea. Annales du Muséum d'Histore Naturelle 8, 156–166. Paris: Tourneisen.

Lamarck, J.-B. de 1818: Histoire naturelle des animaux sans vertèbres 5, 612 pp. Paris: Déterville & Verdière. https://doi.org/10.5962/bhl.title.6484

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 regna tria naturae, 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

Lommerzheim, A. 1979: Monographische Bearbeitung der Serpulidae (Polychaeta sedentaria) aus dem Cenoman (Oberkreide) am Südwestrand des Münsterländer Beckens. Decheniana 132, 110–195.

Macellari, C.E. 1984: Revision of serpulids of the genus *Rotularia* (Annelida) at Seymour Island (Antarctic peninsula) and their value in stratigraphy. Journal of Paleontology 58, 1098–1116. http://www.jstor.org/stable/1304869.

Montfort, D. de 1808: Conchyliologie systématique et classification méthodique des coquilles, 1. Coquilles univalves, cloisonées. lxxxvii + 409 pp., 100 figs. Paris: F. Schoell. https://doi.org/10.5962/bhl.title.10571

Morton, S.G. 1834: Synopsis of the organic remains of the Cretaceous group of the United States. viii + 88 pp., 19 pls. Philadelphia: Key and Biddle.

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/bgsd-2018-66-11

Ødum, H. 1926: Studier over Daniet i Jylland og paa Fyn. Danmarks geologiske Undersøgelse, II. Række 45, 306 pp.

Pillai, T.G. 1960: Some marine and brackish-water serpulid Polychaeta from Ceylon, including new genera and species. Ceylon Journal of Science (Biological Sciences) 3, 1–40.

Rafinesque, C.S. 1815: Analyse de la nature ou tableau de l'universe 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

Rantuch, J., Kočí, T., Jäger, M. & Váchová, L. 2024: *Tectorotularia hexagona* (Polychaeta, Serpulidae) co-existing with *Rhynchostreon suborbiculatum* (Bivalvia, Gryphaeidae) in a river-dominated marginal marine environment of Cenomanian–Turonian age in Slovakia: An example of Late Cretaceous amensalism or competition? Cretaceous Research 161(105913), 23 pp. https://doi.org/10.1016/j.cretres.2024.105913

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.

Röding, P.F. 1798: Museum Boltenianum sive Catalogus cimeliorum e tribus regnis naturæ quæ olim collegerat Joa. Fried Bolten, M. D. p. d. per XL. annos proto physicus Hamburgensis. Pars secunda continens Conchylia sive Testacea univalvia, bivalvia & multivalvia, viii + 199 pp. Hamburg: Trapp. https://www.biodiversitylibrary.org/page/16230659

Rosenkrantz, A. 1920: Craniakalken fra Kjöbenhavns Sydhavn. Danmarks geologiske Undersøgelse II. Række 36, 79 pp. https://doi.org/10.34194/raekke2.v36.6822

Rosenkrantz, A. 1970: Marine Upper Cretaceous and lowermost Tertiary deposits in West Greenland; investigations before and since 1938. Bulletin of the Geological Society of Denmark 19, 406-453.

Rouse, G.W. & Fauchald, K. 1997: Cladistics and polychaetes. Zoologica Scripta 26, 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. 1996: Micromorphology, microstructure and functional morphology of the *Josephella marenzelleri* (Polychaeta Serpulidae) tube. In: Cherchi A, ed. Autoecology of selected organisms: Achievements and problems. Bolletino della Società Paleontologica Italiana, Special Volume 3, 205–211.

Sanfilippo, R. 1998: Tube morphology and structure of the bathyal Mediterranean serpulid *Hyalopomatus variorugosus* Ben-Eliahu & Fiege, 1996 (Annelida, Polychaeta). Rivista Italiana di Paleontologia e Stratigrafia 104, 131–138.

Sanfilippo R. & Mòllica, E. 2000: *Serpula cavernicola* Fassari & Mòllica, 1991 (Annelida Polychaeta): diagnostic features of the tubes and new Mediterranean records. Marine Life 10, 27–32.

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

Schlotheim [erroneously spellt „Schlottheim“], E.F. von 1813: Beiträge zur Naturgeschichte der Versteinerungen in geognostischer Hinsicht. In: Leonhard, C.C. (ed.): Taschenbuch für die gesammte Mineralogie 7 (1), 3–134, 4 pls; Frankfurt am Main.

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.

Schnetler, K.I. & Nielsen, M.S. 2021: On the genus *Vanikoropsis* Meek, 1876 (Gastropoda, Caenogastropoda) in the Paleocene of Denmark and West Greenland with descriptions of three new species. Bulletin of the Geological Society of Denmark 69, 215–232. https://2dgf.dk/xpdf/bull69-215-232_rev..pdf

Schrøder, A.E. & Surlyk, F. 2024: The cancellothyridid brachiopod Terebratulina chrysalis from the Selandian Kerteminde Marl at Gundstrup, Denmark. Bulletin of the Geological Society of Denmark 73, 89–98. https://doi.org/10.37570/bgsd-2024-73-05

Schrøder, A.E., Sørensen, A.M. & Surlyk, F. 2018: Morphological adaptations of the brachiopods from a Late Cretaceous rocky shore, Ivö Klack, southern Sweden. Palaeogeography, Palaeoclimatology, Palaeoecology 514, 785–799. http://doi.org/10.1016/j.palaeo.2018.09.019

Schwarzhans, W., Milàn, 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

Seilacher, A., Olivero, E.B., Butts, S.H. & Jäger, M. 2008: Soft-bottom tube worms: from irregular to programmed shell growth. Lethaia 41, 349–365.

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

Słowiński, J., Clapham, M. & Zatoń, M. 2024: The Upper Permian tubular fossils from South China and their possible affinity to sabellid polychaetes. Historical Biology, 1–7. https://doi.org/10.1080/08912963.2024.2324448

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. 1821: The mineral conchology of Great Britain 3, 194 pp., pls 204–306. London: The Author.

Squires, R.L. 1990: New Paleogene siliquariid and vermetid gastropods from the Pacific coast of southwestern North America. The Veliger 33, 286–292.

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/bgsd-1984-33-28

Vallon, L.H. & Rindsberg, A.K. 2022: Cutting through sponge and time – a new record of *Koptichnus 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/bgsd-2022-70-09

Vandenberghe, 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, 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. 2011: The role of an internal organic tube lining in the biomineralization of serpulid tubes. Carnets de Geology / Notebooks on Geology, Brest 2011 (Letter 1), 13–16. https://doi.org/10.4267/2042/38798

Vinn, O. 2013a: Occurrence, Formation and Function of Organic Sheets in the Mineral Tube Structures of Serpulidae (Polychaeta, Annelida). PLoS ONE 8 (10), e75330, 1–5. 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 10, 858. https://doi.org/10.3390/min10100858

Vinn, O. 2021: Biomineralization in Polychaete Annelids: A review. Minerals 11, 1151, 1–15. https://doi.org/10.3390/min11101151

Vinn, O. 2024: Distribution of growth lines in the tube wall of serpulids (Polychaeta, Annelida). Journal of the Marine Biological Association of the United Kingdom 104, e24, 1–5. https://doi.org/10.1017/S0025315424000146

Vinn, O. & Kupriyanova, E.K. 2011: Evolution of a dense outer protective tube layer in serpulids (Polychaeta, Annelida). Carnets de Géologie 2011/05 (CG2011_L05), 137–147. https://doi.org/10.4267/2042/43896

Vinn, O. & Mutvei, H. 2009: Calcareous tubeworms of the Phanerozoic. Estonian Journal of Earth Sciences 58, 286–296. http://doi.org/10.3176/earth.2009.4.07

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, 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 Ditrupa. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 248, 79–89. http://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

Wahlenberg, G., 1821: Petrificata telluris Svecanae examinata. Nova Acta Regiae Societatis Scientiarum Upsaliensis 8, 1–116.

Wenz, W. 1938–1941: Gastropoda. Allgemeiner Teil und Prosobranchia. 1639 pp. In: Schindewolf, O.H. (ed.): Handbuch der Palaozoologie. Berlin: Gebrüder Borntraeger.