Serpula? *alicecooperi* sp. nov. – a new serpulid from the Lower Jurassic (Pliensbachian) Hasle Formation of Bornholm, Denmark

TOMÁŠ KOČÍ, JESPER MILÀN, STEN LENNART JAKOBSEN & ARDEN R. BASHFORTH

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Serpulid remains are very rare in the Lower Jurassic Hasle Formation of Bornholm, Denmark. A historical specimen mentioned, but not figured by Malling & Grönwall (1909) was reexamined and attributed to *Pentaditrupa quinquesculcata* and here figured for the first time. New finds of additional well-preserved serpulid tubes are described as *Serpula*? *alicecooperi* sp. nov, which show adaptations for a lifestyle on fine-grained sediment in a nearshore environment.

Keywords: Early Jurassic, Pliensbachian, *Serpula*, *Pentaditrupa*, Bornholm, Denmark.

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 Faxe/Østsjællands Museum, Østervej 2, DK-4640 Faxe, Denmark. Sten Lennart Jakobsen [stenlennart@yahoo.dk], Geomuseum Faxe/Østsjællands Museum, Østervej 2, DK-4640 Faxe, Denmark. Arden R. Bashfort [bashforth@snm.ku.dk], Natural History Museum of Denmark, Øster Voldgade 5-7, DK-1350 København K, Denmark.

Serpulids are polychaetes forming calcareous tubes. They represent an important part of the marine benthic communities encrusting hard substrates, both in the recent seas and in the fossil record, and they are classified as sclerobionts (Taylor & Wilson 2003; Schlögl *et al.* 2008; Sanfilippo *et al.* 2013; Guido *et al.* 2017; Breton *et al.* 2020; Kočová *et al.* 2021). Calcareous tubes are developed in all known serpulid genera (Vinn *et al.* 2008b, c; Vinn 2019, 2020), in a single genus of sabellids (*Glomerula*; Vinn *et al.* 2008a; Vinn & Wilson 2010; Vinn & Hosgör 2023; Slowiński *et al.* 2023) and in some cirratulid species of the genus *Dodecaceria* (Kočí *et al.* 2021). Calcareous tubeworms first appeared in the Permian (Sanfilippo *et al.* 2017, 2018), and they greatly diversified from the Jurassic (Goldfuss 1831; Ippolitov 2007a, b, 2010; Vinn & Wilson 2010; Jäger & Lang 2017; Kočí *et al.* 2019; Ippolitov & Martill 2020; Kočí & Fözy 2022; Slovinski *et al.* 2022) and onwards to recent (ten Hove & Kupriyanova 2009; Kupriyanova *et al.* 2020, 2023a, b; Rouse *et al.* 2022 and many references herein). The research on tube-bearing polychaetes from the Jurassic of Europe is limited, if compared to the far more extensive research of Cretaceous tube-dwelling polychaetes (Jäger 1983; Sklenář *et al.* 2013; Ippolitov *et al.* 2014; Kočí *et al.* 2017; Kočová *et al.* 2021 and many references herein).

The knowledge of serpulid tubeworms from Jurassic deposits in Denmark is poor, when compared to the research and amount of material on Cretaceous and Paleocene tubeworms (Ravn 1921, 1923; Ødum 1926; Nielsen 1931; Jäger *et al.* 2018; Milán *et al.* 2021, 2022). The first record of Jurassic serpulids from Bornholm, as *Serpula quinquesulcata* Münster, was mentioned by Malling & Grönwall (1909); it was collected from the Liassic (Lower Jurassic) *Myoconcha* bed at Stampen Å. These authors cited Moberg (1888) who described and figured *S. quinquesulcata* and *S. terquemi* Moberg, 1888 from Lower Jurassic deposits in Sweden. Today the species *Serpula quinquesulcata* is considered to belong to the genus *Pentaditrupa* Regenhardt, 1961 and is named *Pentaditrupa quinquesulcata* (Münster in Goldfuss, 1831), and *Serpula terquemi* may be considered a subjective synonym of either *Pentaditrupa quinquesulcata*, as stated by Jäger (2005) or of *Mucroserpula quinquecristata* (Münster in Goldfuss, 1831), which has sharper keels and an angular pentagonal instead of rounded pentagonal cross-section. The known occurrence of *S. quinquesulcata* Münster from Bornholm, Sweden, north-western and southern Germany as well as England was compiled by Malling & Grönwall (1909, Table 1). *Pentaditrupa quinquesulcata* is widespread in the Pliensbachian of central and western Europe; for more details, see Jäger & Schubert (2008). Cretaceous (Cenomanian to Senonian) serpulids from Bornholm were mentioned by Ravn (1921, 1923).

The aim of this paper to describe the find of a second, new species of serpulid from the Early Jurassic Hasle Formation of Bornholm, and to taxonomically revise the previous report on serpulids from the Hasle Formation by Malling & Grönwall (1909).

Geological setting

The Lower Jurassic (Pliensbachian) Hasle Formation is exposed along coastal cliffs south of the town of Hasle on the Danish island of Bornholm, located in the Baltic Sea, south of Sweden (Fig. 1). The geology of Bornholm is a complex fault block system related to movements of the NW–SE-trending Sorgenfrei–Tornquist Zone, which separates the Danish Basin from the Baltic Shield (Surlyk & Noe-Nygaard 1986; Donovan & Surlyk 2003). During the Mesozoic, the movements of the Sorgenfrei–Tornquist Zone strongly affected the sedimentation and depositional environments, and the eastern border of the fault is located only a short distance inland from the west coast of Bornholm where the Hasle Formation was deposited (Gravesen *et al.* 1982; Surlyk & Noe-Nygaard 1986; Michelsen *et al*. 2003). The Hasle Formation is a reddish-brown sandstone with hummocky and swaley cross-stratified coarse-grained siltstone and very fine-grained sandstone (Fig. 1c). Single horizons show trough cross-bedding or planar lamination, and at the base of these, the individual swales are draped with a fossiliferous conglomeratic layer of clasts of basement rocks (Surlyk &

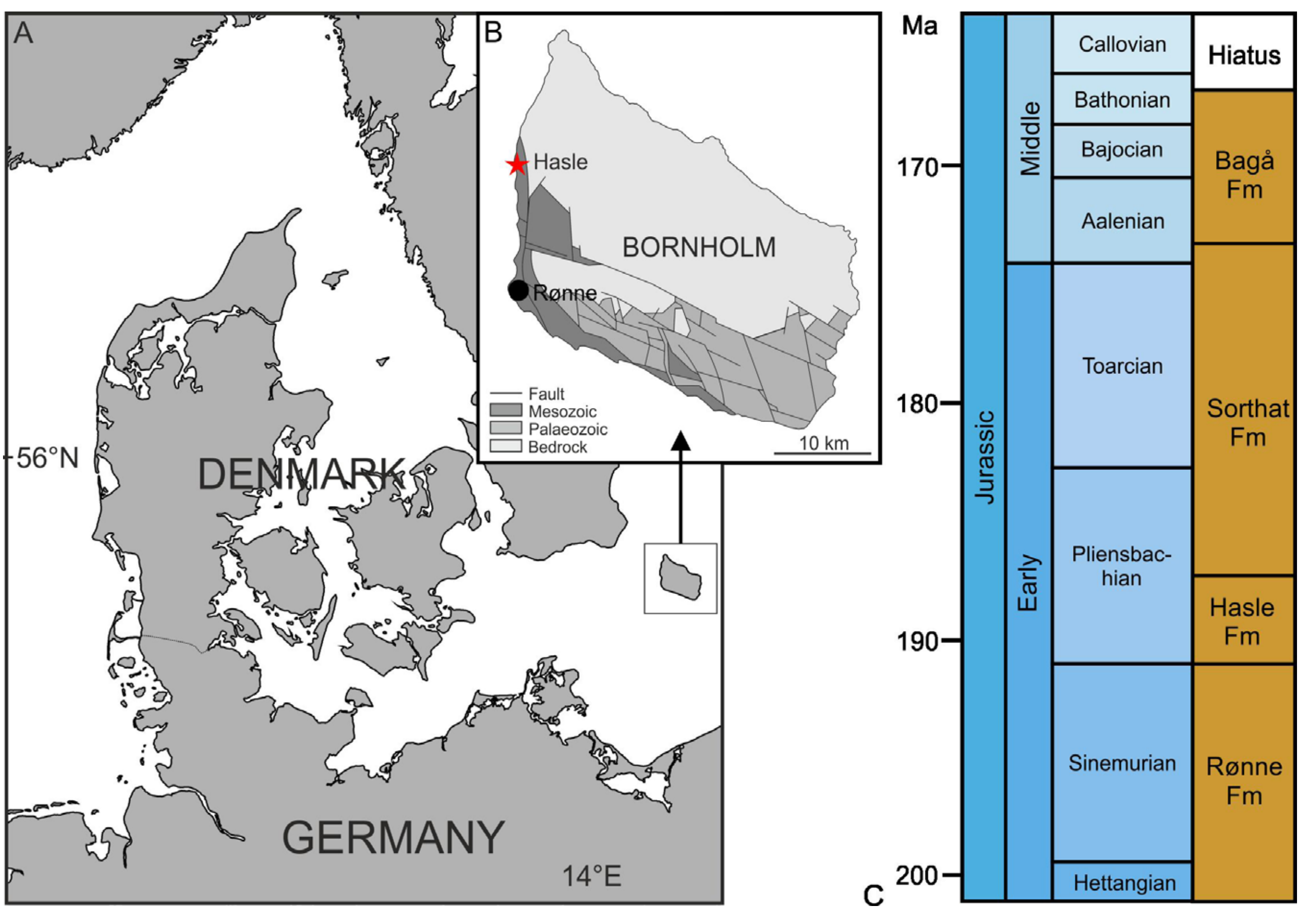

Fig. 1. Location of Bornholm and the type locality of the Hasle Formation. Further exposures of the Hasle Formation exist around Rønne, farther south at Sose Odde. **a.** Location map showing the position of Bornholm in the Baltic Sea. **b.** Outline geological map of Bornholm, showing the location of Hasle, the asterisk indicates the exposure of the Hasle Formation where the specimen was found (Duffin & Milàn 2022). **c.** Late to Middle Jurassic stratigraphy of Bornholm, modified after Sandersen *et al.* (2014).

Noe-Nygaard 1986; Larsen & Friis 1991). The Hasle Formation has been interpreted as shallow marine and has yielded a diverse marine invertebrate and vertebrate fauna. The invertebrate fauna comprises 11 species of ammonites, scaphopods, rare belemnites and several species of bivalves (Malling & Grönwall 1909; Malling 1911, 1914, 1920; Höhne 1933; Donovan & Surlyk 2003). However, due to the coarse-grained nature of the sediment at Hasle (more fine-grained at Rønne), at the type locality at Hasle, most invertebrates are poorly preserved. Condrichthyan remains are common in the form of abundant selachian teeth comprising hybodont and neoselachian species of sharks (Rees 1998), and at least two species of holocephalians (Duffin & Milàn 2017, 2022). Fish remains are abundant and represented by numerous undescribed scales. Skeletal remains and especially teeth of marine reptiles show the presence of at least three plesiosaurian taxa (Milàn & Bonde 2001; Smith 2008), in addition an osteroderm from a thallatosuchian crocodile has been found (Milàn & Mueller-Töwe 2019). Rare remains of terrestrial vertebrates are known by a theropod footprint (Milàn & Surlyk 2015), dinosaurian bone fragments and a mammaliform tooth (Molin 2021), and an isolated dinosaur tooth from? a turiasaurian sauropod (Milàn & Mateus 2024).

Material and methods

A block containing several specimens of the new serpulid species was found by amateur geologist Mette Agersnap Grejsen Hofstedt in 2023 at the type locality of the Hasle Formation, south of the Hasle harbour, Bornholm, Denmark (Fig. 1). The specimens are curated in the collections of the Natural History Museum of Denmark in Copenhagen (MGUH 34317 and MGUH 34318). The original specimen collected by Malling and mentioned by Malling & Grönwall (1909) was located in the collections of the Natural History Museum of Denmark and here taxonomically revised (MGUH 34319).

One piece of the new specimen was polished at a natural break through the tube, to show the structure of the tube wall. This section was made with an electric saw in the Palaeontological Department of the National Museum (PD NM) in Prague with the kind help of Jan Sklenář. The section was hand polished using gradually finer carborundum powder paper (200–2000 units) with water and finally Microlite powder with water. Photographs of the polished sections were made using a light microscope SZX 1200 with Canon EOS 7R camera, and SEM images were taken by using a scanning electron microscope -Hitachi S-3700 N in the Palaeontological Department of the National Museum at Prague. A digital caliper was used for measurements. All figures were prepared using the Corel Draw 20 program.

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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

'Clade AI *Serpula*-group' *sensu* Lehrke *et al*. (2007), Kupriyanova *et al*. (2008) and Ippolitov *et al*. (2014)

Tribe Serpulini Rafinesque, 1815

Genus *Serpula* Linnaeus, 1758

***Serpula*? *alicecooperi* sp. nov.**
(Figs 2, 3, 6)

Diagnosis. The tubes are straight or very slightly curved in one direction. Circular tube of moderate size, 4–5 mm in diameter. Tube-wall is two-layered, inner surface shows densely-spaced annular rings, the outer surface is unknown. There are no traces of former attachment to a substrate visible; all studied specimens seem to represent free tubes. There are no hints of longitudinal keels visible.

Derivation of name. In honor of musician Alice Cooper for his lifelong dedication to music as a performing artist.

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Type locality. Hasle sandstone, Hasle Formation, Bornholm, Denmark.

Material. One well-preserved tube and several fragmentary tubes, preserved in fine-grained sandstone block found loose on the beach below the cliff section, The tube wall is re-crystallised.

Holotype. The sample consists of two specimens preserved lying side by side in a block and its counterplate (MGUH 34317), deposited in the collections of the Natural History Museum of Denmark in Copenhagen, Fig. 2a.

Paratype. The paratype is visible in polished cross-section (MGUH 34318), Fig. 3.

Description. All studied tubes are fragments of the free anterior portion, straight or slightly curved in one direction and increase in diameter gradually. The tube is circular in cross-section, 4–5 mm in diameter, and the thickness of the tube wall is moderate. No keels are observed, but due to the firmly adhering coarse grains of the surrounding sandstone, the outer surface of the tube appears to be coarse, too, and details of the original surface ornamentation, if such had ever been present, remain unknown. The inner tube surface shows densely-spaced transverse striation, which at regular intervals form annular rings (Fig. 3).

Structure and microstructure of the tube-wall. The cross-sections show that the tube wall consists of a moderately thick dark-coloured outer layer and a very thin bright inner layer, and the longitudinal fractures show that the interior surface of the tube shows densely-spaced delicate annular striation. However, the tubes are recrystallised, and the microstructure of the tube-wall seen in Fig. 3a and 3b does not provide much information.

Remarks and relationships. Due to the relatively few characteristic morphological features of the specimens, it is difficult to state its systematic position within Serpulinae. Beside some superficial similarities to some equally poorly ornamented and hardly determinable Early Jurassic species, for example '*Serpula*' *cylindrica* Terquem & Piette, 1865 and '*Serpula*' *capitata* Phillips, 1829 (see also Tate & Blake 1876), *Serpula*? *alicecooperi* shows close similarities to the genus *Pentaditrupa* Regenhardt, 1961 as well as to '*Serpula*' *etalensis* (Piette, 1856). However, it lacks the most characteristic morphological features of both taxa.

Originally, Piette (1856) erroneously considered his '*Ancyloceras*? *etalensis*' to be a heteromorph ammonite and also compared it with scaphopods. However, according to its tube structure, '*Serpula*' *etalensis* is a true serpulid (Vinn *et al.* 2008c) and belongs to a group of Early Jurassic species representing a still unnamed genus (Jäger 1996). '*Serpula*' *etalensis* is the most typical species of this group and is characterised by many strongly developed but short annular rings on its outer tube surface which, however, are lacking in *Serpula*? *alicecooperi*; in the longitudinal fractures (Fig. 2) no such rings are visible on the outer surface of the tubes. Terquem (1855), Piette (1856) and Terquem & Piette (1865) described and figured several Early Jurassic serpulid tubes from the Lower Jurassic of France, Luxembourg and Belgium. Among these, '*Serpula*' *strangulata* Terquem (1855) is similar to '*S.*' *etalensis*; the strong rings are densely-spaced. The only difference is that the spaces between the strong rings are filled with weak rings, and it seems questionable if this small difference justifies distinguishing two species. Also '*Serpula*' *nodifera* Terquem & Piette (1865: Pl. 14, figs 9, 17, 18) belongs to the same genus as '*Serpula*' *etalensis*; it corresponds relatively well in shape and size, but the annular rings may be weaker than in '*Serpula*" *etalensis* and may be less densely and less regularly spaced (Piette (1865: Pl. 14, fig. 17). Nevertheless, even such weak and wider spaced annular rings should be visible in the longitudinal sections of the tubes of *Serpula*? *alicecooperi*, if they have such rings. On the contrary, the inner tube surface of *Serpula*? *alicecooperi* shows relatively densely-spaced delicate annular striations. '*Serpula*' *cylindracea* Terquem & Piette (1865: Pl. 14, fig. 10) corresponds rather well by its slender, only slightly curved shape, but its tube diameter is very small, only *c.* 1 mm.

Serpula? *alicecooperi* lacks the five rounded keels and pentagonal cross-section characteristic of the genus *Pentaditrupa* (although occasionally also in *Pentaditrupa* perfectly circular tubes occur; Jäger (1983)). Moreover, the tube diameter of *Serpula*? *alicecooperi* is somewhat larger and the tube wall is somewhat thinner than usual for *Pentaditrupa*. The overall structure of the tube wall of *Serpula*? *alicecooperi* seen at low magnification – thick dark outer layer, very thin bright inner layer; interior surface showing densely-spaced annular striation – is similar to that of the genus *Pentaditrupa*. Therefore, it cannot be excluded that the species *alicecooperi*, in spite of its circular cross-section, lack of keels and somewhat larger tube diameter, may belong to the genus *Pentaditrupa* instead of *Serpula*.

The species *Serpula*? *alicecooperi* was adapted to a life on a soft sandy bottom (according to Jäger & Schubert (2008); Seilacher *et al.* (2008)), because the overal outer space curvature of the tube provide stability to its freely living position or it was attached to some hard substrate by a posterior fixed part that is not preserved. Surlyk & Noe-Nygaard (1986) suggested a

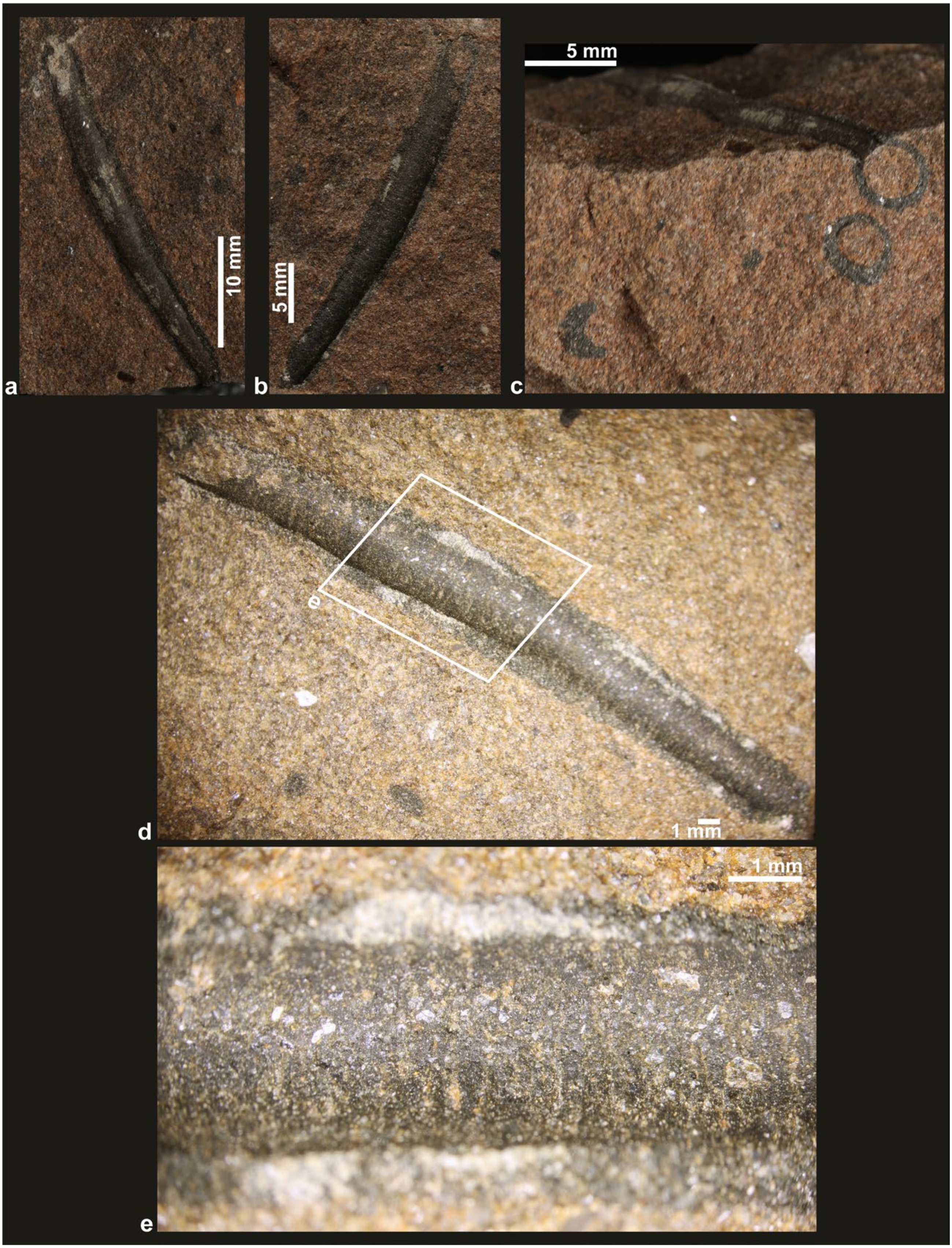

Fig. 2. a. *Serpula? alicecooperi* sp. nov., positive imprint of tube, the transverse rings are visible, Hasle sandstone, Hasle Klint, Bornholm island, Danmark. **b.** Negative imprint of tube. **c.** Circular transverse cross-section of the tube. **d.** Positive imprint showing densely spaced annular rings on the inner tube wall, the figure corresponds with fig a1. **e.** Detailed view of the densely spaced annular rings.

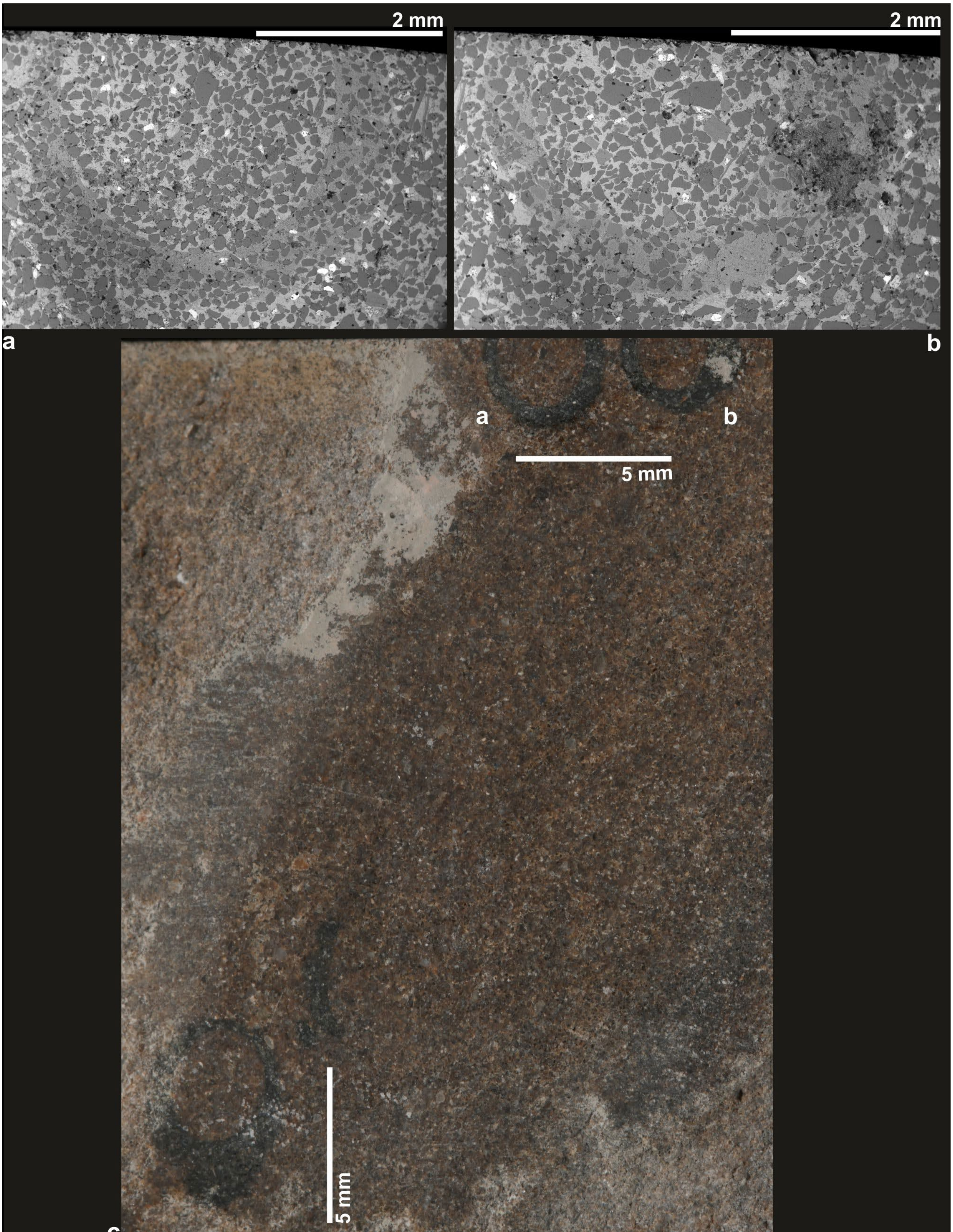

Fig. 3. *Serpula? alicecooperi* sp. nov., small piece from the large specimen. **a.** Transverse cross-section of the tube, SEM image. **b.** Transversal cross-section of the tube, SEM image. **c.** Overall view of transverse section.

palaeo-water depth of 10–40 m and an open marine shelf 1–2 km from the fault-controlled coast. These authors interpreted the Hasle sandstone as a fairly high-energy environment (sandstone and granule conglomerates, very little bioturbation).

'Clade AII *Spirobranchus*-group' *sensu* Lehrke *et al*. (2007), Kupriyanova *et al*. (2008, 2023)

Tribe Ficopomatini Pillai, 1960

Genus *Pentaditrupa*, Regenhardt, 1961

***Pentaditrupa quinquesulcata* (Münster in Goldfuss, 1831)**
(Figs 4, 5)

1831 *Serpula quinque-sulcata* Münster – Goldfuss, p. 226, pl. 67, fig. 8a–d. 1865 *Serpula pentagona*, Terq. et Piette – Terquem & Piette, p. 118, pl. 14, figs 13, 14. 1870 *Serpula subpentagona*, Tate – Tate, p. 402. (pars?) 1876 *Ditrypa quinquesulcata*, Münster – Tate & Blake, p. 438. 1888 *Serpula quinquesulcata* Münster – Moberg, p. 28, pl. 1, fig. 11. ? 1888 *Serpula Terquemi* n. sp. – Moberg, pp. 28–29, pl. 1, figs 12–13. 1909 *Serpula quinquesulcata*, Münster – Malling & Grönwall, p. 275. pars 1956 *Serpula* (*Pentaserpula*) *quinquesulcata* Münster 1831 – Parsch, pp. 228–229. 2008 *Pentaditrupa quinquesulcata* (Münster in Goldfuss, 1831) – Jäger & Schubert, pp. 57 –58, pl. 3, figs 6–13. 2010 *Pentaditrupa quinquesulcata* (Münster in Goldfuss, 1831) – Schubert, p.15, pl. 5, fig. 5.

Material. Two tubes, collected by C. Malling, MGUH 34319, from the Hasle Formation (middle part of early Pliensbachian, *Tragophylloceras ibex* zone, *Beaniceras centaurus* subzone) of Bornholm, Denmark. The tubes were described but not figured by Malling & Grönwall (1909).

Description. The tubes from Bornholm are fragments of the free anterior tube portion. The tube is rounded pentagonal in cross-section. The first tube fragment is at least 10.2 mm long but continues hidden by the adhering sediment; its diameter is 2.3 mm, a diameter of the lumen is 1.9 mm. The thickness of the tube wall may reach up to 0.8 mm. The second tube is compressed to 2 × 2.6 mm due to compaction of the sediment (Fig. 4a). The tubes bear five longitudinal keels, which are low and rounded and appear rather like rounded edges, separated by wide and shallow longitudinal depressions. Transverse ornamentation consists of delicate incremental striations, which run a bit wavy by slightly curving backward at the keels and slightly protruding between the keels, resulting in a chevron-shaped pattern (in Fig. 5 marked by arrows). The tube wall consists of two layers: The external layer is thick, and the internal layer is very thin and bright (Fig. 5a1, a2) and shows densely-spaced delicate annular striations, which are visible in the somewhat oblique cross-section through the second tube (Fig. 5a1).

Remarks and relationships. The tubes from Bornholm match those of the same species from the Pliensbachian of north and south Germany well by shape and ornamentation and by details of the tube wall. The tube diameter is comparable with measurements of tubes from Germany provided by Jäger & Schubert (2008), who stated up to 3 mm. The tube diameter, the only very slight curvature and the rounded, low keels of the tubes from Bornholm indicate that these are fragments of the anterior portions of adult specimens. The geological age (middle part of early Pliensbachian) of the Bornholm tubes matches the hitherto known age of *P. quinquesulcata*. *P. quinquesulcata* is widespread in the Pliensbachian of central and western Europe: Münster's original specimen from Theta near Bayreuth in Franconia in south Germany is from the *Gryphaea*-rich marlstone in the lower part of lower Pliensbachian. Ammon in von Gümbel (1891: 692, 697) mentioned specimens from the upper Pliensbachian and Kuhn (1947: 66, 67) from lower and upper Pliensbachian of Franconia in south Germany. The specimens studied by Jäger & Schubert (2008) are from the *valdani* subzone of lower Pliensbachian near Herford and *stokesi* subzone of upper Pliensbachian at Bielefeld-Jöllenbeck in the Herford Liassic depression, and the specimens studied by Schubert (2010) are from the lower Pliensbachium of Sommersell near Höxter; all these localities are located in Northrhine-Westphalia in northwest Germany. Jäger (unpublished) has collected tubes in lower part of lower Pliensbachian and around the boundary between the lower and upper part of upper Pliensbachian at several places in the foreland of the Swabian Alb in south Germany. Moberg (1888) described it from Kurremölla in Scania in south Sweden. Gallois (1988) mentioned it from the *Beaniceras luridum* subzone of the *ibex* zone of Soham borehole in England. In summary, there is no doubt that the two tubes from Bornholm belong to *Pentaditrupa quinquesulcata* and that this species is the characteristic representative of its genus during more or less the entire Pliensbachian.

The tubes from the Hettangian are too few in number of specimens to state anything about the geologically earliest history of the genus *Pentaditrupa*. Terquem & Piette (1865) introduced their new species '*Serpula*' *pentagona* and figured a beautiful,

Fig. 4. The specimen labelled by C. Malling, Inventory Number 1909. 36, *Centaurus* zone and described as the species *Serpula quinquesulcata* Münster in Goldfuss, 1831. The specimen is now referred to *Pentaditrupa quinquesulcata* (Münster in Goldfuss, 1831). It represents the first find of the serpulid, which was collected on Bornholm, but unfortunately not figured. **a.** Not coated with ammonium chloride. **b**. Coated with ammonium chloride.

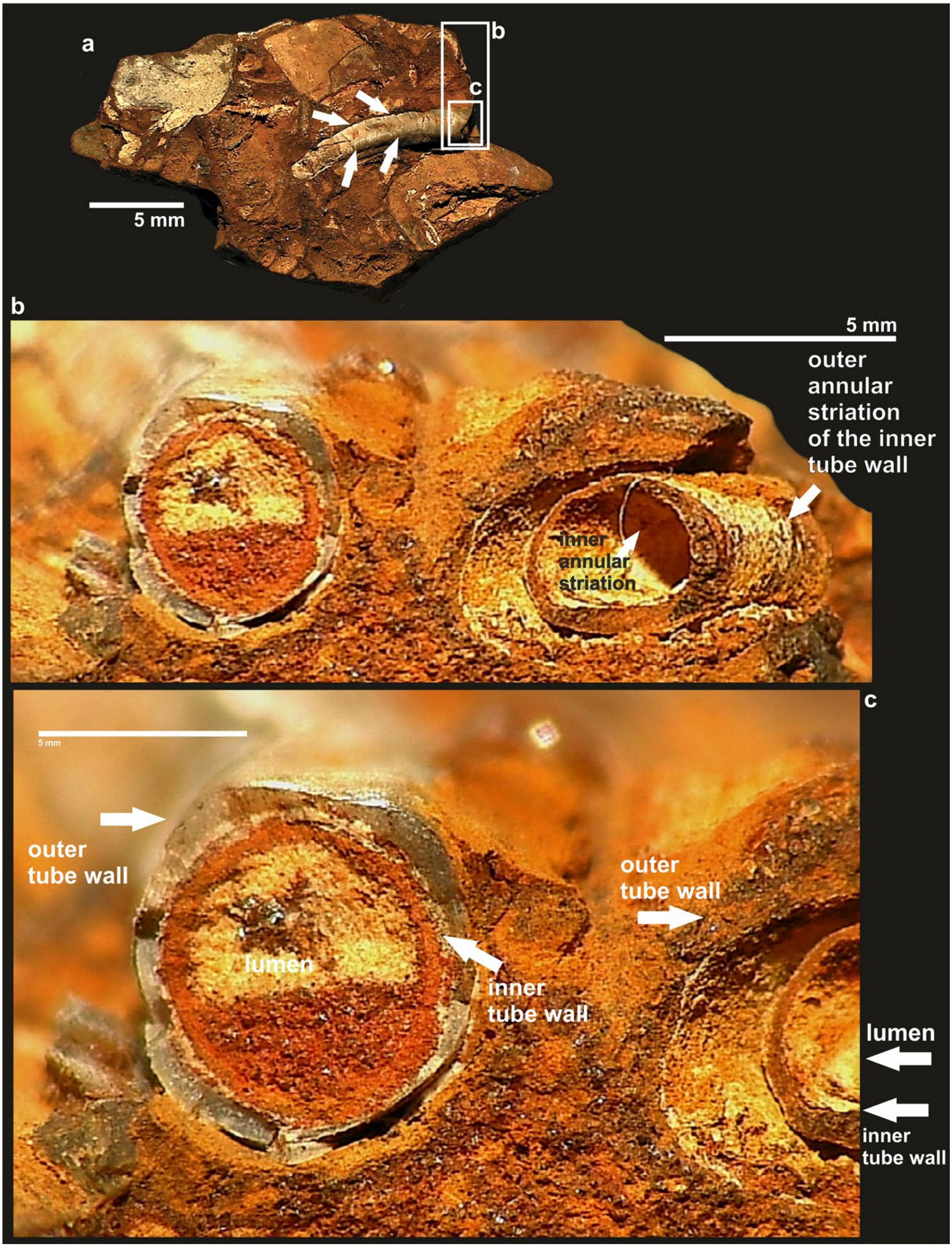

Fig. 5. a. The same specimen of *Pentaditrupa quinquesulcata* (Münster in Goldfuss, 1831). **b.** Transverse cross-section. The white arrows show external tranverse annular striation, left arrow show superficial furrows between rounded ridges. **c.** Detailed view of the pentagonal cross-section.

relatively large tube (diameter up to 4 mm) from the early Sinemurian 'Calcaire à *Ammonites bisulcatus*' of Fleigneux in Département Ardennes in northeast France. Although this is a true *Pentaditrupa* and hardly distinguishable by its morphology from a large specimen of *P. quinquesulcata*, Jäger (2005) preferred to keep it a separate species. Anyway, Terquem & Piette's species name *pentagona* is invalid, because it is a junior homonym of two older versions of the combination '*Serpula pentagona*'. The first homonymy with *Serpula pentagona* Goldfuss, 1831, a valid species name of a Late Jurassic serpulid, was already noticed by Tate (1870) who substituted Terquem & Piette's *pentagona* by uniting all *Pentaditrupa* tubes from lower Sinemurian to upper Pliensbachian under a new name '*Ditrypa*' *subpentagona* Tate, 1870. However later, in Tate & Blake (1876), Tate considered his *subpentagona* a subjective synonym of *P. quinquesulcata*, thereby he widened the stratigraphic range of *P. quinquesulcata* backwards in geological time to lower Sinemurian – upper Pliensbachian. While this is an acceptable solution, an equally acceptable alternative solution is to keep the Sinemurian and Pliensbachian tubes separate by reviving the formally valid name *subpentagona* for the former and restricting *quinquesulcata* for the latter. Anyway, this species, respectively these two species, is/are the most characteristic and most widespread Early Jurassic species of the genus *Pentaditrupa*.

Parsch (1956) stated a much longer stratigraphical range for *P. quinquesulcata* reaching from late Sinemurian ('Lias beta') to Callovian ('Dogger zeta'); very probably not only the similarities among Late Jurassic *Pentaditrupa* species had been the reason for his opinion, but also Parsch's erroneous inclusion of Middle Jurassic pentagonal tubes which, however, belong to a different genus for which later Regenhardt (1961) introduced the name *Mucroserpula.*

The second homonymy with Late Cretaceous *Serpula pentagona* Alth, 1850 was mentioned by Jäger (1983), who considered Alth's invalid species a subjective synonym of *Pentaditrupa subtorquata* (Münster in Goldfuss, 1831).

Several more Early Jurassic *Pentaditrupa* species have been named, some of which are mainly dis-

Fig. 6. Lifelike reconstruction of *Serpula? alicecooperi* sp. nov. Drawing by Lykke Bianca.

tinguished by their small or large size. In the lower Sinemurian, but in and around Rosenfeld in the foreland of the Swabian Alb in south-west Germany, Jäger (unpublished) collected many small to moderately sized pentagonal tubes whose keels vary considerably between specimens. Tubes with rounded keels may be considered small specimens of *P. subpentagona* (Tate, 1870), whereas tubes with sharp keels should rather be referred to the genus *Mucroserpula*. In these geologically relatively old samples from the early Sinemurian, distinguishing between *Pentaditrupa* and *Mucroserpula* is less obvious than in late Sinemurian, Pliensbachian and younger samples, although in the Pliensbachian of south Sweden this problem re-appears. Hence one may wonder if the sharper pentangular and slightly bilateral symmetric '*Serpula Terquemi*' Moberg, 1888 is only a variation and thus a subjective synonym of *P. quinquesulcatus* or belongs to the genus *Mucroserpula*. This question cannot be solved from Moberg's description and figures alone, but we have no fossils from the Pliensbachian of Sweden available for study. Anyway, when sorting tubes from the Pliensbachian of Germany, it is usually possible to differentiate between the rounded-keeled, usually radially symmetrical *Pentaditrupa quiquesulcata* and sharp-keeled, often slightly bilaterally symmetrical *Mucroserpula quinquecristata* (Münster in Goldfuss, 1831). It may be speculated if the similarities of Early Jurassic *Mucroserpula* with *Pentaditrupa* are due to close distance in time to a hypothetical point of phylogenetic bifurcation between the two genera. It seems obvious that fossil *Pentaditrupa* is closely related to recent *Ditrupa* and that fossil *Mucroserpula* and similar fossil *Propomatoceros* are closely related to recent *Spirobranchus* Blainville, 1818. While in the past, only few or vague details of the phylogenetic relationship between *Ditrupa* and other recent serpulid genera had been known (e.g. ten Hove & Smith 1990), the situation has improved, and in the cladograms provided by Kupriyanova *et al.* (2023) *Ditrupa* and *Spirobranchus* both are assigned to the tribe Ficopomatini, making speculation about a phylogenetic separation between *Pentaditrupa* and *Mucroserpula* somewhere around the Triassic/Jurassic boundary a bit more probable.

In the upper Sinemurian dark claystones in the northern foreland of the Swabian Alb in south-west Germany, *Pentaditrupa globiceps* (Quenstedt, 1856) is common (Jäger, unpublished). The actual position of the Quenstedt locality is uncertain. Quenstedt (1856) mentioned and stated the locality 'Breitenbach', which probably refers to a creek rather than than a village. In Quenstedt's study area several creeks with the name Breitenbach are found, one creek is located near the town Reutlingen, but we do not know if this Breitenbach creek was *sensu* Quenstedt (1856; Jäger, personal communication, 26 October 2023). Jäger collected *Pentaditrupa globiceps* (Quenstedt, 1856) in temporal outcrops near Schömberg next to the B27 road to Rottweil and between Aldingen and Trossingen in the foreland of the western part of the Swabian Alb. Tate in Tate & Blake (1876) mentioned this species also from Redcar in northeast England. *P. globiceps* is distinguishable from other Early Jurassic *Pentaditrupa* species by its small size. Also Parsch (1956) had considered this a valid species, but he was misguided by the original description of Quenstedt (1856) who erroneously stated a quadrangular cross-section similar to *Nogrobs tetragona* (J. de C. Sowerby, 1829), whereas in reality *P. globiceps* is pentagonal, and neither Parsch (1956) nor Jäger (unpublished) had ever detected a quadrangular serpulid tube of the genus *Nogrobs* de Montfort, 1808 in late Sinemurian claystones in south Germany.

In the early Pliensbachian of Yorkshire and Cleveland, the very large *Pentaditrupa gigantea* (Phillips, 1829) occurs. Originally, Phillips had described it as *Dentalium giganteum*, and for circa 170 years it has been erroneously considered a scaphopod, although its tube is calcitic and therefore well preserved at Robin Hood's Bay, where this species is common, whereas the aragonitic shells of co-occurring gastropods, scaphopods and some bivalves are dissolved and leave only imprints and steinkerns in the surrounding sediment, as usual in many Mesozoic marlstone and limestone layers. This difference in preservation between calcitic and aragonitic parts of invertebrates is well-known to geologists and experienced amateur collectors. For example, Jäger during an excursion to Robin Hood's Bay in 1992 (and presumably also other people experienced in different kinds of preservation of fossils) recognised at first sight that the supposed '*Dentalium*' *giganteum* cannot be a scaphopod, but must be a serpulid of the genus *Pentaditrupa*, due to its well-preserved tube, regularly curved shape and rounded pentagonal cross-section. Palmer (2001) was the first author who published that '*Dentalium*' *giganteum* must be a serpulid.

For decision if the spiral and strongly rounded pentagonal '*Ditrypa*' *circinata* Tate in Tate & Blake, 1876, which Tate listed from upper Sinemurian to upper Pliensbachian of Yorkshire is a valid *Pentaditrupa* species or just a subjective synonym of *P. gigantea* or *P. quinquesulcata*, a larger number of tubes from Robin Hood's Bay should be studied in more detail.

Serpula olifex (Quenstedt, 1856) occurs in the Hettangian and Sinemurium of Germany and England and is locally very common in a thin upper Sinemurian oil shale bed in the foreland of the Swabian Alb. Its tube is usually regularly curved in one direction and, if growing long enough, may form a wide open planispiral and thereby may resemble a *Pentaditrupa* tube.

However, almost all tubes of *Serpula olifex* are attached to small ammonite shells, mostly but not always to the periphery of the ammonite, where sometimes their posteriormost tube portion was overgrown by the ammonite's next whorl, proving that the serpulid encrusted a living ammonite. In the oilshale the ammonite shells are preserved totally flattened and their aragonitic shells are completely dissolved; sometimes their remains are hardly visible anymore. The also flattened but otherwise well-preserved calcitic tubes of *Serpula olifex* may erroneously be considered unattached free *Pentaditrupa* tubes. Although Seilacher *et al.* (2008) and unpublished specimens collected by Jäger show that the anteriormost tube portion of *Serpula olifex* may indeed change its direction and grow freely away from the ammonite, normally its posterior portion attached to the ammonite is longer than in *Pentaditrupa*. Moreover, three-dimensionally preserved calcified or pyritised specimens of ammonites with *Serpula olifex* encrusting the ammonite's periphery and being overgrown by the ammonites next whorl (e. g. Lange 1932; Schindewolf 1934; Merkt 1966; Müller 1966; Buys 1973; Jäger 1996; Andrew *et al.* 2011) prove that the cross-section of *Serpula olifex* is circular, not pentagonal. By its circular cross-section and by its pseudoplanktic mode of life attached to a living ammonite, *Serpula olifex* is very different from *Pentaditrupa*.

From a long geological time span ranging from the early Toarcian to the middle Albian no *Pentaditrupa* tube is known. The geological younger set of *Pentaditrupa* includes the small *P. wharfensis* (Wilckens, 1922) and *P.* cf. *wharfensis*, together ranging from upper Albian to middle Cenomanian, and the widespread and locally very common (especially in the Campanian and Maastrichtian) medium-sized *P. subtorquata* (Münster in Goldfuss, 1831), also known from upper Albian but mainly from middle Turonian to upper Danian; see Jäger (2005). *P. subtorquata*, of which many synonyms exist, is very variable in width of curvature and cross-section, which ranges from rounded pentagonal to almost perfectly circular. The 'normal' pentagonal form of *P. subtorquata* is very similar to Pliensbachian *P. quinquesulcata*, but in general, the geologically younger *Pentaditrupa* set differs from the early Jurassic *Pentaditrupa* set by never being attached to a substrate and never showing any attachment scar of a former substrate.

The pentagonal genus *Pentaditrupa* and the tusk-shaped and perfectly circular but otherwise very similar Cenozoic and recent genus *Ditrupa* Berkeley, 1835 (extant species are e. g. *Ditrupa arietina* (O. F. Müller, 1776) and *Ditrupa gracillima* Grube, 1878, which occur widespread on and partly in soft sea-bottom, are closely related. Jäger (2005) stated that the geologically youngest *Pentaditrupa* occurred in the late Danian and that phylogenetic transition from *Pentaditrupa* occurred slightly earlier in the Danian, the exact date depends on the earliest occurrence of *Ditrupa schlotheimi* Rosenkrantz, 1920 (Jäger 1993).

Discussion

The rare occurence of serpulids from the Lower Jurassic of Bornholm could be due to the nearshore, high energy environment of the Hasle Formation (Surlyk & Noe-Nygaard 1986). This environment could be poor in nutrients. The taphonomy of the tube wall in *Serpula ?alicecooperi* was caused by cementation of sandstone grains during its diagenesis and fossilisation of the original calcareous tube, however, the calcitic remains of the tube wall are observed under SEM, but we were unable to figure it, due to its poor preservation. The inner tube wall is relatively well preserved and shows annular striations and rings. The preservation of this feature enables us to distinguish between the calcareous tube of serpulids and the agglutinated tube of terebellid or pectinariid polychaetes, because the tubes of the latter genera are formed from agglutinated grains only. The question mark behind *Serpula* Linnaeus, 1758 shows that some diagnostic features are missing, e.g. the external surface of the tube wall is not preserved. The similarities with external and internal dense anullar striations and rings point to the genus *Neovermilia*. *Pentaditrupa quinquesulcata* is a typical species from the lower Jurassic of Europe, it has been reported from France, Germany, Denmark and Sweden. The two examined and redescribed specimens possess typical features of the genus *Pentaditrupa* such as pentagonal cross-section, fine transverse sculptation and two layered tube-wall.

Conclusion

Serpula quinquesulcata mentioned by Malling & Grönwall (1909) is now referred to *Pentaditrupa quinquesulcata* (Münster in Goldfuss, 1831) and is here re-examined and figured for the first time.

A new species of a serpulid worm *Serpula*? *alicecooperi* sp. nov. is described from the Lower Jurassic (Pliensbachian) Hasle Sandstone of Bornholm. SEM examination of the tube-wall of *S.*? *alicecooperi* shows the tube-wall to be recrystallised and infilled by fine-grained sandstone, however, remains of the original wall is poorly visible under SEM examination.

The morphology of the new species shows that it was adapted to free life in soft, fine-grained, bottom conditions close to the shoreface, environment with very little bioturbation, similar to the interpreted lifestyle of *Pentaditrupa quinquesulcata*.

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