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The oldest spiral *Nogrobs* (Polychaeta, Serpulidae) from the Pliensbachian/Toarcian boundary (Oujda Mountains, eastern Morocco)

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Abstract

The rotulariid tube-dwelling polychaete *Nogrobs* (*Tetralysis*) *zekkarensis* sp. nov. (Family Serpulidae) occurs, together with a few other species of this family, in the uppermost Pliensbachian (*Pleuroceras spinatum* Zone) and lower Toarcian (*Dactylioceras tenuicostatum* Zone) section at the locality Zekkara in the Oujda Mountains (northeastern Morocco). Here, tubes of these serpulids were collected from marls and marly limestones that were deposited on a shallow siliciclastic ramp on the southwestern margin of the Tethys Ocean. The tubes

possess a distinctive spiral morphology and a two-layered microstructure. Our findings document that rotulariid serpulids originated at least during the latest Pliensbachian or earlier.

Together with morphologically similar species and comparison of their microstructures from other localities of other geological ages, these specimens triggered a revision of systematics of the subgenera of the fossil serpulid genus *Nogrobs*. The old name *Tetralysis* is revived for a subgenus of obligatorily spiral *Nogrobs* species, in which at least most individuals follow the rotulariid morphogenetic countdown program during their ontogeny, i.e., the tube is attached to a firm substrate just during an early non-spiral stage, followed by a spiral which soon breaks free and shifts to a free-lying habit adapted to soft bottoms.

Moreover, a new species name *Nogrobs (Tetraditrupa) folkestonensis* is introduced in order to replace its original name *Serpula rustica*, a junior homonym preoccupied by the same name of a different species. And the new genus name *Annuloserpula* is introduced for a group of established Early Jurassic serpulid species possessing plenty of annular peristomes.

Key words: Tubeworm, rotulariid, systematics, new genus, new species, Early Jurassic, microstructure, Eastern Morocco.

1. Introduction

Tube-dwelling polychaetes of the polychaete family Serpulidae inhabit all marine environments, ranging from nearshore, shallow-water environments down to the bathyal and hadal zones (Sanfilippo, 1998; ten Hove & Kupriyanova, 2009; Kupriyanova et al., 2011; 2014, 2020). The vast majority of serpulid species lives in waters of normal marine salinity. Only few species thrive in hyper- or hyposaline waters, and a single species lives in the freshwater of carst caves.

Their calcitic, aragonitic, or bimineralic tubes (Vinn et al., 2008a, b; Ippolitov et al., 2014; Kupriyanova et al., 2020; Vinn, 2020, 2021) are mostly attached to various types of firm substrates as sclerobionts (e.g., Sklenář et al., 2013; Vinn et al., 2023; and many other publications) or to soft substrates represented by green algae or sponges (Catra et al., 2019; Rossbach et al., 2021). In hyper- or hyposaline marine waters, or in waters of unstable salinity or temperature, serpulids can also form reefs, bioconstructions and pseudocolonies (ten Hove, 1979; Schuhmacher & Zibrowius, 1985; ten Hove & van den Hurk, 1993; Bianchi et al.,

1996; Bianchi & Morri, 1996; Antonioli et al., 2001; Guido et al., 2017; Sanfilippo et al., 2015; Rosso et al., 2015, 2020; Georgieva et al., 2019).

However, a few taxa (*Ditrupa* Berkeley, 1835; *Nogrobs* (*Tetraditrupa*) Regenhardt, 1961; *Serpula crenata* Ehlers, 1908; *Spirodiscus* Fauvel, 1909 and post-Jurassic species of *Pentaditrupa* Regenhardt, 1961) are sticking unattached in the soft, unconsolidated sediment or are free-lying at the sediment-water interface, enabling their life on soft seaground (Jäger, 2005; Cosentino & Giacobbe, 2006; Seilacher et al., 2008; Morton & Salvador, 2009; Hartley, 2014; Kupriyanova & Ippolitov, 2015; Kupriyanova & Flaxman, 2023).

Although it may be assumed that larvae of all serpulid species attach to at least a tiny substrate, for example to a few sand grains, as documented by Charles et al. (2003) for recent specimens of *Ditrupa arietina* (O.F. Müller, 1776), in practice, the term "unattached" is used for species whose very earliest attached ontogeny is normally not documented, because either tube formation has not yet started, or the earliest tube part is either not yet mineralized as in case in *Ditrupa arietina*, or is so thin and fragile that it is normally not preserved, even in recent tubes. Also in other marine invertebrates that initially attach to a firm substrate and later become recliners, such as some bivalves and brachiopods, a free-lying or reclining life habit typically refers to adult ontogenetic stages, when the size and weight of the substrate has become negligible relative to the size and weight of the individual.

Within serpulids, a part of the many exclusively fossil species of the genus *Nogrobs* de Montfort, 1808 follow the rotulariid morphogenetic countdown program (Seilacher et al. 2008) during their ontogeny, i.e., the tube is directly attached to a firm substrate only during its small initial non-spiral stage, but sometime during its spiral stage, after the physically increasingly instable connection between the anterior end of the initial tube portion and the small center of the underside of the increasingly heavier spiral had broken, it shifts to a free-lying habit adapted to soft seafloor. Finally, the entire spiral may or may not turn to a vertical orientation and continue growth by forming a straight tube portion rising vertically like a chimney. Although named after a valid and established genus of fossil serpulids, the term "rotulariid" is only meant to be only an informal morphological and palaeoecological term, not a valid name of Zoological Nomenclature.

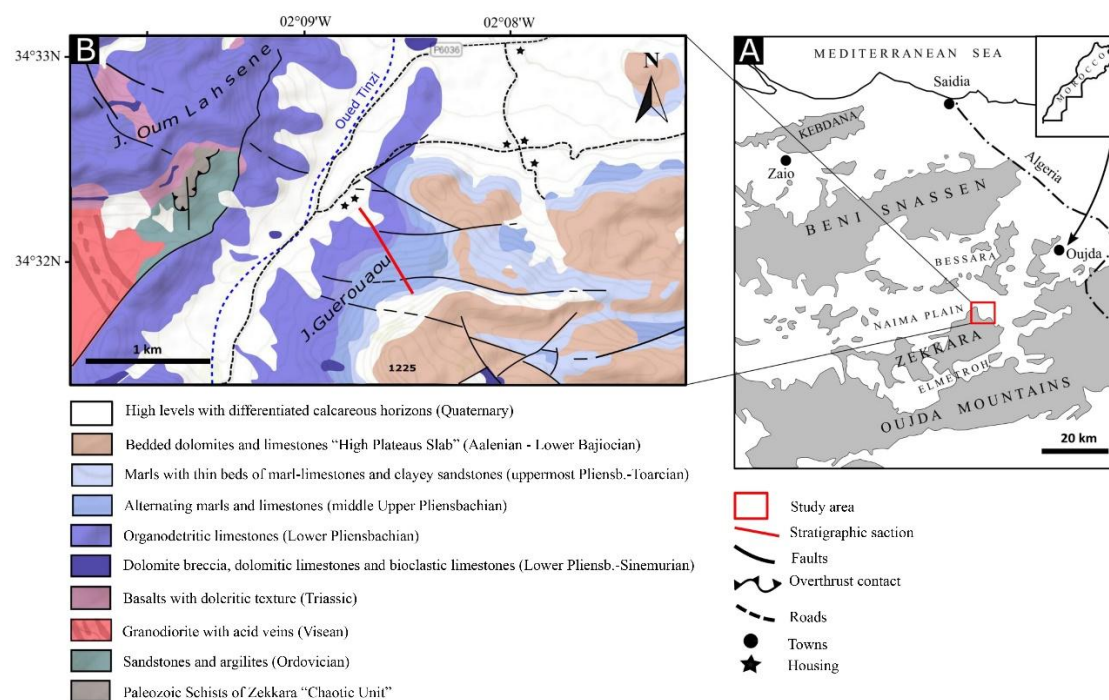
The oldest fossils of serpulids are recorded from Permian rocks (Sanfilippo et al., 2017, 2018; Ramsdale, 2021; Słowiński et al., 2024a). Serpulids gradually but dramatically diversified during the Jurassic. However, the Jurassic serpulids of the NW African Maghreb domain that

belonged to the southern Tethyan margin (Frizon de Lamotte et al., 2011) are poorly explored (Hauptmann, 1990; Ait Addi, 2015), with the exception of the Bajocian of Morocco (Schlögl et al., 2017) and the late Callovian of Israel (Wilson et al., 2008; Vinn & Wilson, 2010; Vinn et al., 2024). Schlögl et al. (2017) documented free-lying quadrangular tubes of *Nogrobs moroccensis* Jäger & Kočí, 2017 in Schlögl et al., 2017 from the Lower Bajocian (Middle Jurassic) of the Central High Atlas in Morocco; these tubes formed benthic biostromes or meadows in soft-bottom habitats. In the present article, we describe and figure a new and geologically oldest known species of the genus *Nogrobs*, which is also the oldest known rotulariid serpulid in a revised wider sense, from an Upper Pliensbachian/Lower Toarcian succession in the Oujda Mountains (NE Morocco). We describe its microstructure, compare it with Vinn et al. (2008b), and discuss its palaeocology and paleobiogeography.

2. Geographical, geological, and stratigraphic setting

Jebel Guerouaou is situated in eastern Morocco, in the western zone of the Oujda Mountains (Zekkara area), c. 10 km NE of Mestferki and 30 km SSW of the city of Oujda, between the plains named Naima and Metroh (Fig. 1). The Zekkara succession is located in a ravine on the NW slope of the Jebel Guerouaou (34°31'57''N and 2°08'08''W). It is easily accessible from Oujda by the national road N17 and local roads P6030 and P6036 leading to the village Mestferki.

Figure 1



The Jurassic succession of the Zekkara area encompasses Lower and Middle Jurassic deposits that terminate with conspicuous Aalenian–Bajocian rocky walls exceeding a height of 50 m. The upper Sinemurian succession is represented by supratidal carbonates with laminated stromatolitic facies, loferites, teepee structures, vadose pisoliths, and ooids deposited on an extremely shallow-water carbonate platform (Rakús, 1979). During the early Pliensbachian, this carbonate platform disintegrated, leading to the deposition of deep-shelf, well-bedded, cherty limestones mainly in the northern part of the Oujda Mountains. During the late Pliensbachian and early Toarcian, the platform differentiation continued with deposition of several tens of meters thick successions formed by the marl-limestone alternation, locally with bioclastic concentrations rich in bivalves (deposited below or near the storm wave base). In the southern and eastern parts, the Pliensbachian–Toarcian sediments were deposited in a shallower environment in the south and were reduced to dm- to cm-thick condensed deposits with hardgrounds in the east (Rakús, 1979). A new phase of carbonate platform deposition took place since the Aalenian and persisted to the Bajocian, and the marine deposition continued until the Kimmeridgian when the sea retracted from this region.

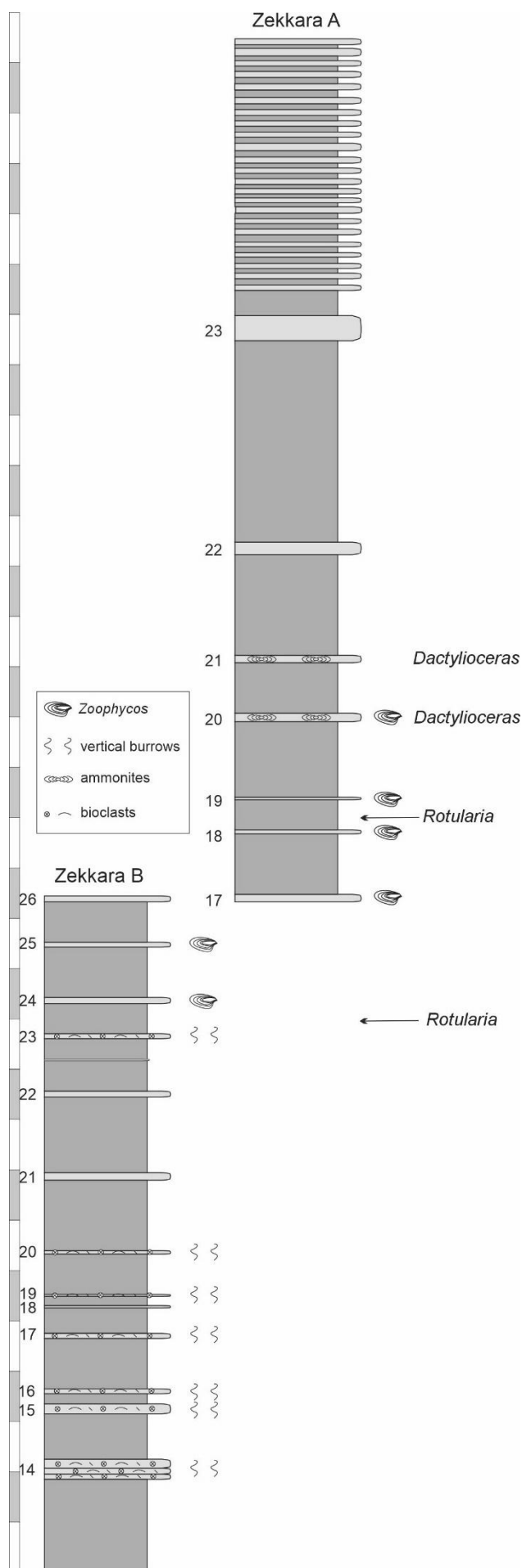
The upper Pliensbachian and Toarcian at Zekkara are locally rich in benthic macrofauna, especially ammonites, belemnites, and bivalves. Brachiopods are rare. These sediments can be subdivided into two units (Ouahhabi, 1986). The lower, 26 m-thick unit is formed by an alteration of (secondarily-dolomitized) marls and marly bioclastic limestones of the Beni Hammad Formation (marno-calcaires des Béni Hammad), locally rich in upper Pliensbachian ammonites that document the *A. margaritatus* and *P. spinatum* zones, e.g. *Amaltheus margaritatus* de Montfort, *Pleuroceras spinatum* (Bruguier), *Fuciniceras (Paltarpites) meneghinii* (Bonarelli), and *Emaciaticeras emaciatum* (Catullo) (see Ouahhabi, 1986, fig. 14). The upper unit consists of light-grey to yellowish silty marls with several thin (5–15 cm) marly limestone beds with abundant *Zoophycos*. This interval is comparable to the Béni Amyir Formation (alternances des Béni Amyir). The first stratigraphically-diagnostic ammonites occur in the bed 20 of Ouahhabi (1986, p. 30, but see also fig. 14 which does not match with the description (!)) and they belong to *Dactylioceras (Eodactylites) polymorphum* Fucini, index species of the eponymous lower Toarcian ammonite zone (i.e., equivalent of the *D. tenuicostatum* Zone).

The serpulid assemblages described here were collected in two beds – in light-gray marls in the upper part of the Beni Hammad Formation of the latest Pliensbachian (*P. spinatum* Zone) and in darker marls of the Béni Amyir Formation of the lower Toarcian (*D. tenuicostatum* Zone). First, serpulids are particularly abundant in a marly layer above the limestone bed 15

of Ouahhabi (1986, Fig. 14, this bed is marked as bed 23 at Zekkara B in Fig. 2), where they co-occur with belemnites, bivalves, echinoid spines and other echinoid fragments, crinoids and other serpulids. The stratigraphic position of this bed rich in serpulids corresponds to the uppermost part the Beni Hammad Formation, indicating that this assemblage belongs to the *P. spinatum* Zone. Second, serpulids were also found, although in lower abundance, in the marls between the limestone beds 18 and 19 (*D. tenuicostatum* Zone, Zekkara A in our Fig. 2). Although this bed did not yield any ammonites, the shift in ichnofacies towards high abundance of *Zoophycos* and the decline in abundance of larger bioclasts is typical of the lowermost Toarcian.

The biofabric of marly limestones in the *P. spinatum* Zone with occasional cm-scale bioclastic concentrations with complex internal stratification indicates that the deposition took place in the proximity of storm wave base on the middle ramp. The lowermost Toarcian marls with the *Zoophycos* ichnofacies do not show any signs of storm reworking, and were probably deposited in low-energy, outer ramp conditions below storm wave base.

Figure 2



3. Material and methods

One hundred tubes (98 specimens, because in two specimens a smaller tube is attached to a larger tube) of *Nogrobs* (*Tetralysis*) *zekkarensis* sp. nov. were studied under a binocular microscope (20 x – 40 x, Bresser), and 26 tubes (25 specimens) of them were photographed using a Sony α 7RIII. Selected specimens were studied at the Paleontological Department of the Natural History Museum in Prague with a light microscope, Olympus SZX12 by TK. Twenty best preserved specimens and specimens with epibionts were photographed with the Keyence microscope by MKV at the Geological Institute, Czech Academy of Sciences in Prague. After photography, the tubes shown in Figs 3C, 3E, 3F, 3I, 3J, 4B, 4C, 4F were embedded in plastic cast Epoxy 1200; they were polished by means of the carborundum grains paper 200, 320, 400, 600, 800, 1000, 1200, 1500, 2000 by TK. After this procedure, the specimens were dried for 48 hours. We etched all polished tubes by 1 % acetic acid for c. 3 minutes (Figs 6–9). When assessing the transverse sections of the tubes shown in Figs 10–11, we treated them for c. 10 minutes. SEM images used for microstructure tube-wall examination were taken by LV using a Hitachi S-3700 N at Palaeontological Department of National Museum in Prague.

The additional material examined for the comparison of our specimen of *Annuloserpula etalensis* (Piette, 1856) comprises 19 specimens labelled "*Ditrupa etalensis*" respectively "*Ditrupa etalense*", collected at different localities in the U.K. and stored in the collection of the British Geological Survey:

One specimen from Adderbury Oxon, UKBGS.GSM 113568.

Twelve specimens from Lightpill, Stroud, Gloucester, UKBGS.Zd 1287 (2 specimens), UKBGS.Zd 1288 (2), UKBGS.Zd 1289 (4), UKBGS.Zd 1290 (4).

One specimen from Aston Magna, Gloucestershire, UKBGS.GSM 91174.

Five specimens from Munger, Radstock, Somerset, UKBGS.GSM 91175 (1), UKBGS.GSM 91176 (1), UKBGS.GSM 91177 (1), UKBGS.GSM 91178 (1), UKBGS.GSM 91179 (1).

4. Systematic palaeontology

Phylum **Annelida** Lamarck, 1802

Class **Polychaeta** Grube, 1850

Subclass **Sedentaria** Lamarck, 1818

Infraclass **Canalipalpata** Rouse & Fauchald, 1997

Order **Sabellida** Levinsen, 1883

Family **Serpulidae** Rafinesque, 1815

Subfamily **Serpulinae** Rafinesque, 1815

Tribe **Ficopomatini** Pillai, 1960

Genus ***Nogrobs*** de Montfort, 1808

Type species. Nogrobs vermicularis de Montfort, 1808.

Diagnosis. The tube is small to medium-sized, increasing slowly to moderately in diameter. The attached tube portion may vary considerably in length between species, or, in few species, it is lacking entirely. Also the length of the free tube portion varies, but often it is long or very long. Depending on the respective subgenus, the tube may form no spiral at all, a wide open spiral, or a tightly coiled spiral in middle ontogenetic stage. The most characteristic features of the free tube portion are the four conspicuous, often wide and more or less rounded longitudinal ridges, which are equally spaced around the tube's circumference, giving the tube a characteristic rounded quadratic or, in the attached tube portion cross-section, a trapezoidal cross-section. Often the areas between the ridges are slightly concave. The attached tube portion bears two weaker longitudinal ridges at the upper/lateral edges and often an additional but weak longitudinal ridge in the middle of the upper side. Also the periphery of some of the spiral tubes may bear an additional ridge (here it is the fifth ridge), which is weakly developed in most species but prominent in few species.

Peristomes may be lacking or present. In a few species, they are very common and occur in more or less regular distances. They are oriented strictly perpendicular to the tube's longitudinal axis and often are bulbous, massive and four-part, because they are wider and higher at the longitudinal ridges than between the ridges.

Microstructure. In the present study, we mention the following seven out of the more than a dozen microstructure types and their abbreviations, as defined and detected in serpulid tubes by Olev Vinn and co-authors, e.g. Vinn et al. (2008b) and subsequent publications.

SP = Simple Prismatic

HG = Homogeneous Granular

SPHP = Heraltic Prismatic

SIOP = Spherulitic Irregularly Oriented Prismatic

IOP = Irregularly Oriented Prismatic

HAC = Homogeneous Angular Crystal

LF = Lamello-Fibrillar

Hitherto, the first five microstructure types – SP, HG, SPHP, SIOP, and IOP – are detected in the genus *Nogrobs*, the last two types are mentioned in comparison with other serpulid genera.

The vast majority of non-spiral and optionally spiral *Nogrobs* species have an unlayered SP or, if diagenetically altered, HG microstructure (Kupriyanova & Ippolitov, 2015). However, Słowiński (2024b) detected two-layered tube walls with SP and IOP microstructures. A single species which never forms a tightly coiled spiral has a two-layered tube wall with SPHP microstructure similar to SP. A single diagenetic altered HG which originally may had been an SIOP microstructure (Kupriyanova & Ippolitov, 2015).

Hitherto, microstructure is only known in two obligatorily spiral *Nogrobs* species. One of them, *Nogrobs (Tetralysis) zekkarensis* sp. nov, is introduced below; it has a two-layered tube wall with SPHP and SIOP microstructures, whereas the second species, the hitherto only known three-layered *Nogrobs*, has SP, HG and again SP microstructures.

Stratigraphic range. Late Pliensbachian to late Maastrichtian; early Paleocene (Danian)?

Discussion. The geologically long-living, species-rich and morphologically variable genus *Nogrobs* and its subgenera has a long research history. De Montfort (1808) introduced the genus *Nogrobs*, although this name was hardly remembered for almost 200 years, until Jäger (2005) revived it.

Stolizcka (1868) introduced the name *Tubulostium*, although he and many followers erroneously believed that these obligatorily spiral tubes belonged to a gastropod species.

Eudes-Deslongchamps (1878) introduced the name *Tetralysis* for, in exterior aspect, very similar spiral tubes. Because both genera differ by microstructure, we consider them different subgenera.

Nielsen (1931) introduced the name *Ditrupula*, but did not designate a type species.

Regenhardt (1961, pp. 69, 71) considered *Ditrupula* a junior subjective synonym of *Ditrupa* Berkeley, 1835. Howell (1962) tried to make the name *Ditrupula* valid by designating *Serpula*

canteriata von Hagenow, 1840 type species. However, Howell did not notice that already one year earlier, Regenhardt (1961) had chosen the same type species for his new subgenus *Tetraditrupa* of the genus *Ditrupa*. Thus Howell, when trying to make *Ditrupula* valid, he paradoxically made it invalid, because by designating the same type species, *Ditrupula* became a junior objective synonym of *Tetraditrupa*.

Although Parsch's (1956) systematic scheme of subgenera of the genus *Serpula* Linnaeus, 1758 according to the number of edges in the tube's cross-section is highly artificial, his name *Tetraserpula* is valid.

More modern research in fossil serpulids started with Regenhardt (1961), who, however, erroneously considered his *Tetraditrupa* a subgenus of genus *Ditrupa* Berkeley, 1835, and his *Glandifera* a subgenus of genus *Genicularia* Quenstedt, 1856 in Quenstedt, 1856–1858. We still consider *Tetraditrupa* and *Glandifera* valid subgenus names, but both had to change their superordinate genus to *Nogrobs*, because both possess four rounded longitudinal ridges equally spaced all around the tube, instead of five as in *Genicularia* sensu stricto or none as in *Ditrupa*. Moreover, *Glandifera* bears many typically *Nogrobs*-like bulbous four-part peristomes.

Both Lommerzheim (1979) and Jäger (1983) considered the names *Ditrupula* Nielsen, 1931, *Tetraserpula* Parsch, 1956 and *Tetraditrupa* Regenhardt, 1961 synonyms of each other, although Lommerzheim considered *Ditrupula* valid, whereas Jäger considered *Tetraserpula* valid. Jäger (2005) revived the old genus name *Nogrobs* de Montfort, 1808 and named the Jurassic species *Nogrobs* sensu stricto and the Late Cretaceous species *Nogrobs* (*Tetraditrupa*).

Moreover, Jäger (2005, p. 138) differentiated between non-spiral and spiral *Nogrobs* species, although not yet between optionally and obligatorily spiral species, and not yet by taxonomic differentiation, and stated his hypothesis that the spiral *Nogrobs* species could be occasional iterative offshoots from a continuous phylogenetic line of non-spiral *Nogrobs* species. In those days, only few obligatorily spiral *Nogrobs* species had been found respectively recognized to belong to this genus, in contrast to the already high number of non-spiral and optionally spiral species, so that the hypothesis of iterative offshoots seemed plausible. However, since then a number of additional obligatorily spiral species were found respectively recognized among already published species; see below in chapter *Nogrobs* (*Tetralysis*). Therefore, nowadays M.J. considers the obligatorily spiral species a long

continuous phylogenetic main line named *Nogrobs* (*Tetralysis*) running parallel to the non-spiral and optionally spiral line *Nogrobs* (*Nogrobs*).

However, for reasons explained in more detail below, it seems favourable to make two exceptions at the geologically oldest and geologically youngest end of the *Nogrobs* (*Tetralysis*) phylogenetic line by considering *Nogrobs* (*Tetralysis*) *zekkarensis* sp. nov. and *Nogrobs* (*Tubulostium*) *discoideum* Stoliczka, 1868 in Stoliczka, 1867–1868 two offshoots, due to different microstructure, respectively different number of tube wall layers. While consequently *Nogrobs* (*Tubulostium*) *discoideum* is nomenclatorily separated from *Nogrobs* (*Tetralysis*) at subgenus level, we still hesitate to realize a similar consequence in *N. (Tetralysis) zekkarensis*, because the microstructures of all other species of subgenus *N. (Tetralysis)*, including its type species *N. (T.) quadrangularis* (Lamarck, 1818), are still unknown. At the present incomplete state of knowledge, it cannot be excluded that this type species of *N. (Tetralysis)* may have a similar microstructure as *N. (T.) zekkarensis*, and in this case the introduction of a new subgenus name would be unnecessary.

Hitherto, no fossil *Nogrobs* tube younger than late Maastrichtian is safely known, although short and questionable mentions from the early Paleocene (Danian) of Denmark cannot be ignored. *Nogrobs*-like cross-sections through tubes from the middle Eocene (Bartonian) of Spain figured in Ferràndez-Cañadell (2018, Fig. 7a–c) may alternatively well belong to the morphologically similar free anterior tube portion of the genus *Tectorotularia* Regenhardt, 1961, which is common in the Eocene.

Erroneously, Jäger (2005) assigned the recent deep-water serpulid *Spirodiscus* Fauvel, 1909 possessing a spiral *Nogrobs*-like tube, and possibly also the recent non-spiral deep-water serpulid *Bathyditrupa* Kupriyanova, 1993 which possesses a quadratic *Nogrobs*-like cross-section, to the genus *Nogrobs*. Kupriyanova & Ippolitov (2012, 2015) argued heavily against Jäger's (2005) assignment of these recent genera to fossil *Nogrobs*; and very probably they are right. The positive result of Jäger's error is the article by Kupriyanova & Ippolitov (2015), which yields plenty of valuable details not only about the soft parts and the opercula of these recent deep-sea serpulids, but also very good images showing morphologies and microstructures of the more or less *Nogrobs*-like shaped tubes in which they live. For palaeontologists, an important result of the studies by Kupriyanova & Ippolitov (2015) is to demonstrate again that serpulids living in very similarly shaped tubes may belong to very different phylogenetic lineages.

Moreover, Kupriyanova & Ippolitov state that it seems unlikely that at least most of the fossil *Nogrobs* species have living descendants in today's rather diverse deep-water fauna, because in most cases their microstructures are rather different. Nevertheless, the bulk of Jurassic and Cretaceous *Nogrobs* tubes studied by Kupriyanova & Ippolitov, with few exceptions, show either identical or similar microstructure among each other, or, in several cases of their microstructure being diagenetically altered, also these tubes may originally have had an identical or similar microstructure.

Here we present a revised scheme of subdivision of the genus *Nogrobs* into six subgenera, by using only already established subgenus names. The six subgenera differ by the courses of their tubes, especially if forming either a small tightly coiled spiral or a wide open spiral or no spiral at all, by microstructure, and by size and frequent or occasional occurrence of peristomes.

However, in four out of the six subgenera, we do not present detailed lists of species names, because in several cases, especially among the common and geographically widespread *Nogrobs* tubes from Bathonian to Tithonian for which many species names had been introduced, details of nomenclature and synonymies are not yet revised. In several rare or/and less well known species, decision between non-spiral and optionally spiral, respectively between optionally spiral and obligatorily spiral, is still unsafe. In some other cases, it is debatable if a tightly coiled spiral species belongs to either *Nogrobs* or *Tectorotularia*. In a few Jurassic species, different opinions exist if an attached tube with an additional median ridge belongs to either *Nogrobs* or *Filogranula* Langerhans, 1884. The only subgenus which is discussed here in detail, including a species list, is *Nogrobs* (*Tetralysis*), because our new species *N. (Tetralysis) zekkarensis* is assigned to this subgenus.

Subgenus ***Nogrobs* (*Nogrobs*)** de Montfort, 1808

Type species. Nogrobs vermicularis de Montfort, 1808.

Diagnosis. The tubes are optionally spiral, because within each species, some individuals don't form a spiral, while some other individuals form a tightly coiled spiral. A low or moderate number of irregularly spaced peristomes may or may not occur.

Microstructure. Among the 13 species whose microstructures were studied by Kupriyanova & Ippolitov (2015), 11 are unilayered and show either SP microstructure or are diagenetically

altered and show HG microstructure. These 11 species, most of which are assigned to "Group 1" or "Group 2" by Kupriyanova & Ippolitov (2015), belong to either *N. (Tetraserpula)* or, at least two of them, to *Nogrobs (Nogrobs)*; these are *N. (Nogrobs) quenstedti* (Roemer, 1911) from the late Bathonian of Lechstedt, northern Germany, and a similar but smaller species from the early Callovian of Egesheim, southwestern Germany. Both are unilayered with SP microstructure. However, the species contents of "Group 1" and "Group 2" of Kupriyanova & Ippolitov (2015) does not exactly match our subgenus concepts of *N. (Nogrobs)* and *N. (Tetraserpula)*.

Stratigraphic range. Probably Bajocian, certainly Bathonian to Oxfordian, perhaps also in younger strata.

Discussion. This subgenus is similar to *N. (Tetraserpula)* Parsch, 1956, see below, but differs by being able to form a small tightly coiled spiral intercalated between the attached initial tube portion and the free tube portion. However, this spiral is not formed by all individuals of the respective species. Often the spiral is followed by a relatively long uncoiled free anteriormost tube portion. In most specimens, the spiral is only indirectly attached to the substrate in its very center via the initial tube portion, whereas the whorls of the spiral are only attached to the previous whorls. Less often, all spiral whorls are directly attached to the substrate. The type species *N. (Nogrobs) vermicularis* comes from either the Bajocian or, less probably, from the Bathonian of Muttentz near Basel in Switzerland.

Subgenus ***Nogrobs (Tetraserpula)*** Parsch, 1956

Type species. "*Serpula*" *tetragona* J. de C. Sowerby, 1829 in J. de C. Sowerby, 1826–1829. Jäger (1983) stated that this combination is an invalid junior homonym of *Serpula tetragona* Renier, 1804. However, Sowerby's combination stays valid, because according to Read & Fauchald (2026), Renier's paper is considered a rejected publication (ICZN 316).

Diagnosis. The tubes do not form any spiral. Instead, an attached tube portion is directly followed by a free tube portion. Both portions may have very variable absolute and relative lengths, and in a few species the attached portion may not be developed or not preservable. A low or moderate number of irregularly spaced peristomes may or may not occur.

Microstructure. According to Kupriyanova & Ippolitov (2015), most of the studied species which we consider to belong to *N. (Tetraserpula)* are single-layered with SP or, when

weathered, HG microstructure. In contrast, Słowiński et al. (2024b) found two layers of SP and IOP microstructure in three middle Bathonian species from Gnaszyn Dolny, Poland (Słowiński et al. 2022), of which two may alternatively be considered to belong to genus *Filogranula* Langerhans, 1884, but the third, named *Nogrobs* aff. *tetragona*, is a typical representative of the non-spiral subgenus *Nogrobs* (*Tetraserpula*).

Stratigraphic range. Late Pliensbachian to Aptian.

Discussion. This subgenus is the most characteristic, most common, and most geographically widespread. Its geologically oldest known representative is "*Serpula*" *varicosa* Behrendsen, 1891 from the late Pliensbachian of Argentina.

The subgenus *N. (Tetraserpula)* shares relatively close similarities to *N. (Nogrobs)* in tube morphology, except for absence of spiral tubes in *N. (Tetraserpula)*, and in predominately unilayered tube wall with SP microstructure (Kupriyanova & Ippolitov, 2015). Therefore, it cannot be excluded that in future these two subgenera will be reunited under the older name *N. (Nogrobs)*.

Subgenus ***Nogrobs (Tetralysis)*** Eudes-Deslongchamps, 1878

Type species. "*Serpula*" *quadrangularis* Lamarck, 1818; syn. *Tetralysis quadrata* Eudes-Deslongchamps, 1878.

Diagnosis. The tubes are obligatorily spiral, because normally all individuals form a tightly coiled spiral. They bear four usually rounded longitudinal ridges. The two lower ridges, which in the spiral form the left and right border of the tube's base, may locally be a little bulbous. In some species, the upper side of the tube, which usually is situated at the outer periphery of the spiral, is slightly or distinctly convex or may form a fifth longitudinal ridge or is elevated to form a distinct sharp keel. The tube wall is two-layered with SPHP and SIOP microstructure, but hitherto is studied in only a few specimens of a single species.

Additional description. The spiral may be followed by a mostly only short, straight or slightly curved anteriormost tube portion. Transverse ornamentation is either lacking or inconspicuous and may consist of fine striation and/or the above-mentioned weak bulges, which may occur predominately in the lower lateral longitudinal ridges of the spiral and may be interpreted as an irregular transverse ornamentation.

Microstructure. Hitherto, the microstructure of only a single species of this subgenus, *N. (Tetralysis) zekkarensis* sp. nov., is studied. Its tube wall is two-layered with SPHP microstructure in the outer layer and SIOP microstructure in the inner layer.

Stratigraphic range. Late Pliensbachian to late Valanginian.

Discussion. While in *N. (Nogrobs)* only some of the individuals form a spiral and other individuals do not, in *N. (Tetralysis)* normally all individuals form a spiral. Most specimens of the subgenera *N. (Tetralysis)* and most of the spiral specimens within the subgenus *N. (Nogrobs)* follow the morphogenetic countdown program (Seilacher et al., 2008) of rotulariid serpulids.

N. (Tetralysis) zekkarensis shows some more features which makes its subgenus stand a little aside from the other subgenera. The main difference is the two-layered tube wall with SPHP microstructure in the outer layer and SIOP microstructure in the inner layer, a combination which hitherto is assumed to have originally existed, although now diagenetically altered to SPHP and HG microstructure, in a single other *Nogrobs* species, *N. (Tetraditrupa) rustica* (J. de C. Sowerby, 1829 in J. de C. Sowerby, 1826–1829), which is a junior homonym and thus replaced by *N. (Tetraditrupa) folkestonensis* nom. nov.; see below. However, the latter species, in stark contrast to *N. (Tetralysis) zekkarensis*, never forms a tightly coiled spiral, so that it is certainly not advisable to unite both species in the same subgenus only due to their similar microstructure.

While the SPHP microstructure is rather similar to the SP microstructure present in many fossil *Nogrobs* species, hitherto the SIOP microstructure had not been detected in any other fossil *Nogrobs* species. In future, when the microstructures of a higher number of *Nogrobs* species will be known, this difference may possibly result in separating either only *N. (Tetralysis) zekkarensis* or the entire subgenus *N. (Tetralysis)* from genus *Nogrobs* sensu stricto. Among recent serpulid tubes, a two-layered tube wall with SPHP microstructure in the outer layer and SIOP microstructure in the inner layer, was detected also in *Zibrovermilia zibrowii* Kupriyanova & Ippolitov (2015), whose tube, although *Nogrobs*-like quadrangular in cross-section, however, does not form any spiral and is separated from *N. (Tetralysis) zekkarensis* by c. 185 million years, so that a close phylogenetic relation seems less probable than an independent convergent origination of the combination SPHP/SIOP. Slightly more likely, as stated by Kupriyanova & Ippolitov (2015), the recent *Zibrovermilia zibrowii* is partly comparable with the Cenomanian species *N. (Tetraditrupa) folkestonensis* nom. nov.,

which also has a more or less straight tube with two layers with SPHP microstructure in the outer layer, although with diagenetically altered HG microstructure in the inner layer, and the difference in time is "only" c. 96 million years. However, the genus *Zibrovermilia* is assigned to the Subfamily Filograninae Rioja, 1923, whereas the genus *Nogrobs* is assigned to the Tribe Ficopomatini Pillai, 1960 of the Subfamily Serpulinae Rafinesque, 1815, making a close phylogenetic relationship between *N. (Tetraditrupa) folkestonensis* nom. nov. and *Z. zibrowii* very unlikely.

In contrast to other *Nogrobs* species, occurrences of species of subgenus *N. (Tetralysis)* are restricted in time and space. Some of them are only known from a single locality, some others from several localities within a restricted region. But at these few localities, they are often common or even mass-occurring. Obviously, the species of subgenus *N. (Tetralysis)* needed very special ecological conditions.

Provisional list of species of subgenus Nogrobs (Tetralysis).

(1) *Nogrobs (Tetralysis) zekkarensis* sp. nov. from the late Pliensbachian and early Toarcian of Zekkara of Morocco.

(2) "*Serpula*" *compressa* Young & Bird, 1828 (syn. "*Vermetus*" *concinus* J. de C. Sowerby, 1829 in J. de C. Sowerby, 1826–1829) from the late Toarcian, only known from the foreshore below the vertical high cliff of Blea Wyke at Ravenscar, Yorkshire, England, where at low tide plenty of tubes can be seen accumulated in slightly elevated pseudo-reefs on the recent seafloor. The surfaces of these pseudo-reefs are somewhat prepared out of the surrounding softer rock by means of recent abrading wave action of the North Sea. These accumulations are probably no true reefs, but rather more firmly solidified sediment areas, due to the higher carbonate content of the *Nogrobs* tubes.

(3) "*Serpula*" *quadrangularis* Lamarck, 1818 (syn. *Tetralysis quadrata* Eudes-Deslongchamps, 1878). This species is very common or mass-occurring at many inland localities in and near Normandy and Maine in northern France, and thus is mentioned in the explanations of several sheets of geological maps and a few geological field guides.

(4) "*Vermetus*" *tumidus* J. de C. Sowerby, 1829 in J. de C. Sowerby, 1826–1829 from the Oxfordian of Yorkshire, common at Scarborough and on the foreshore of the North Sea below the vertical cliffs at Filey Brigg.

(5) "*Spirorbis*" *thirriai* Etallon in Thurmann & Etallon, 1861–1864. This species occurs in the Oxfordian of the Jura Mountains on both sides of the boundary between Switzerland and France, for example at Liesberg and at Col de la Croix north of St. Ursanne, both located in Switzerland, and at Haute-Saône, Mont Terrible and, rather common, at Winkel, all three located in France.

(6) A rather large spiral of an unnamed species from the late Valanginian of Cressier (exact locality unknown) near Neuchâtel, Switzerland, was donated to M.J. by Mrs. Zbinden. Unfortunately, only this single specimen is known, and it is assigned to the obligatorily spiral subgenus *N. (Tetralysis)* instead to the optionally spiral *N. (Nogrobs)* only due to its sheer size, because very large spirals are unknown in *N. (Nogrobs)*. M.J., when looking for additional specimens at the nearby type locality of the Valanginian, did not detect any additional specimens. In the also nearby old quarry at Cressier, which however exposes early Hauterivian grey clay- and marlstones, M.J. only detected and collected plenty of spiral tubes of *Tectorotularia couloni* (Defrance, 1827a) (*Tectorotularia heliciformis* (Goldfuss, 1831 in Goldfuss, 1826–1844) is a junior subjective synonym), which, however, differ by morphology and grey colour from the dark red late Valanginian *Nogrobs (Tetralysis)* specimen.

(7?) The two tubes shown in the original drawing of "*Serpula*" *quadricarinata* Münster in Goldfuss, 1831 in Goldfuss, 1826–1844 from the green sandstone of Regensburg, Bavaria, southern Germany, look like representatives of the subgenus *Nogrobs (Tetralysis)*. Unfortunately, the original specimens shown in this drawing are lost and remain an unsolved mystery. Regenhardt (1961) synonymized them with *Tectorotularia rotula* (Goldfuss, 1831 in Goldfuss, 1826–1844) from the same sediment layers of the same locality and stated their provenance from Cenomanian greensand sediment by means of adhering sediment particles to be very probable, after a label stating middle Turonian Eisbuckelschichten, which, in contrast, are poor in glauconite, had caused confusion about provenance of these serpulid tubes. Indeed, *Tectorotularia rotula* is a regionally very common species in the Cenomanian greensand, which in former centuries had been quarried around the city of Regensburg. In the large quarry at Saal, located only 18 kilometers southwest of Regensburg, M.J. collected plenty of specimens of *Tectorotularia rotula* sensu stricto from early Cenomanian greensand, but none has a cross-section similar to the type specimen of "*Serpula*" *quadricarinata* as illustrated by Goldfuss. The question whether "*Serpula*" *quadricarinata* is either a very rare Cenomanian species of *N. (Tetralysis)*, or a rare extreme morphological variation of *Tectorotularia rotula*, or a Jurassic *Nogrobs* species from a different locality which had

erroneously been confused with specimens from the Cenomanian of Regensburg, remains unsolved.

***Nogrobs (Tetralysis) zekkarensis* sp. nov.**

Table 1, Figs 3–11

Material. Ninety-eight specimens including 100 tubes, of which 25 specimens (26 tubes) are photographed and studied in more detail, from the locality Zekkara.

Holotype. Fig. 4D–D2.

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Stratum typicum. Upper Pliensbachian or lower Toarcian.

Type locality. Zekkara at the NW slope of the Jebel Guerouaou, Oujda Mountains, eastern Morocco.

Derivatio nominis. After the type locality Zekkara.

Diagnosis. The tube is moderate in size. Following a straight or slightly curved initial portion, the tube forms a tightly coiled spiral of usually 3 to 3½, exceptionally 4 whorls. The first whorls are trochospiral or cylindrical, but later whorls are very low trochospiral or almost planispiral. Sinistrally coiled spirals are c. three times as common as dextrally coiled spirals.

The genus' characteristic four rounded longitudinal ridges are represented by two prominent wide, roughly wrinkled, rounded ridges on the spiral's upper side and two somewhat less prominent rounded ridges on the underside. The spiral's periphery is topped by a fifth rounded ridge. As the outer ridges on the spiral's upper side and underside are located close to the fifth ridge, together these three ridges usually appear as a single broad ridge topped by three small sub-ridges. However, close to the transition to the anteriormost free tube portion, often the fifth ridge is substituted by a narrow median furrow at the spiral's periphery. If this furrow is developed, the tube's cross-section is rounded trapezoidal and higher than wide. However, where the fifth ridge is present, the tube's cross-section is rounded triangular, trilobate or pentalobate.

A straight free anterior tube portion is often developed, but extremely short, usually reaching only up to 1 mm, rarely 1.5 mm in length.

Additional description (Table 1). In most spirals, the center of the spiral's underside displays one of the following three aspects of the posteriormost preserved tube portions: (1) an up to 2.5 mm long fragment of a straight or more often slightly curved non-spiral initial tube portion, which anteriorly continues by forming a considerably narrower curve which becomes the first whorl of the spiral (Figs 3A1, 3B1, 3E1, 4D1, 4E1, 4I1, 4J1, 4L1, 5C1) – just as can be observed, although less common, also in "classic" rotulariids, or (2) the straight or slightly curved non-spiral initial tube portion is either not formed or was not preserved, and the preserved tube starts with the narrow first curve of the spiral, or (3) the center of the spiral's underside is obscured by a concave calcitic shell fragment of a small bivalve, either an oyster or a pectinid, the opposite convex side of which was settled by the *Nogrobs* larva (best visible in Fig. 3D1, less well in Figs 3C1, 4C1, 4H1); this is seen in 11 *N. (T.) zekkarensis* spirals. In 3 spirals, only a concave impression is left on the spiral's underside where the presumed bivalve had been, 2 small spirals are attached to 2 large spirals, in 1 spiral the negative impression caused by an unidentified substrate is plain, and in 1 spiral the negative impression is also generally plain but uneven in detail. Altogether, in 18 out of the 100 spirals, the tube stayed firmly connected to a solid substrate of at least a few millimeters in diameter, at least as long as the increasing spiral did not yet reach the border of the substrate, or even for lifetime. As in all of these 18 specimens the bivalve fragment or the negative impression is located in the center of the spiral's underside, it is unlikely that, vice versa, the bivalve settled on the serpulid, and it can be excluded the both invertebrate fossils are closely associated only by chance.

The first whorls are narrowly coiled and low trochospiral (Figs 3H, 5A2) or, more often, form a narrow and low cylinder (Figs 3A2, 4E2), suggesting a strong tendency to grow upward, whereas the later formed whorls are very low trochospiral (Fig. 5A) or almost planispiral (Figs 3F2, 3I2, 4G2, 5C2), suggesting a strong tendency to increase in width. Often but not always, the spiral's upper side is slightly concave, and the underside is slightly convex. The coiling (Table 1) is mostly sinistral (76 tubes, e.g., Fig. 4I), less often dextral (24 tubes, e.g., Fig. 4E), according to the definition used by zoologists in recent spirorbin serpulids. In large spirals, usually 3–3½ whorls are visible; only a single spiral with very slender first whorls has 4 whorls altogether.

Usually the spiral tubes are solitary; only in each of two specimens one smaller spiral tube is attached to a larger spiral tube with opposite sense of coiling (e.g., Fig. 3G, 3G2). However, 31 of the 100 spirals are encrusted by the brown mineral (limonitic?) fillings of the lumina of

tiny to small non-spiral tubes built by different, mostly unidentified organisms (Figs 3B, 3J, 4K, 4L, 4L2, 5A, 5A1, 5A3, 5B, 5C, 5C1, 5C2), which are discussed below in a separate chapter, and a small percentage of these tiny encrusters may represent non-spiral initial tube portions of juveniles of *N. (T.) zekkarensis*.

The most complete tubes end with a very short straight free anterior tube portion, which usually is only c. 1 mm long (Figs 3E–E1, 3I–I1, 3J–J1, 4D–D1, 4F–F1, 4J–J1, 4K–K1, 5A–A1, 5C–C1) and only rarely reaches up to 1.5 mm (Fig. 3F, 3F1). At the transition from the spiral to the free tube portion, the tube turns slightly away from the spiral, thereby forming a slight concavity at the periphery, respectively a weak constriction (Fig. 4D, 4D1); only one specimen (Fig. 3E, 3E1) has a strong constriction. In the free tube portion, the tube diameter decreases quickly; this decrease is most conspicuous at the side facing to the spiral.

The median ridge and especially the two wide rounded ridges with their roughly wrinkled rounded bulges on the spiral's upper side (Figs 3J, 4A, 4E, 4F, 4J, 5C), but also the two similar but a little less conspicuous ridges on the underside (Fig. 3E1, 3J1, 4A1, 4E1, 4G1, 5C1), are usually well-developed. In some specimens, the bulges occur more or less regularly spaced, so that they may be considered a kind of transverse ornamentation. Moreover, there may be weak transverse wrinkles.

Due to the relatively high ridge at the periphery, the spirals may originally have looked lenticular in lateral aspect. However, due to diagenetic compression, today the spirals are more or less flattened, and the wide median ridge, which combines the outer ridges on the spiral's upper side and underside and the fifth ridge, appears to be even more prominent in frontal view or cross-section. Due to this combined wide median ridge, the tube's cross-section is rather rounded high-triangular (Fig. 3A2, 3B2, 3D2), high-trilobate (Fig. 4A2, 4B2, 4E2) or deformed-pentalobate (Fig. 3E2, 3H, 4J2) than rounded quadrangular. However, at or close to the transition from the spiral to the free anterior tube portion, the fifth ridge is often substituted by a narrow, shallow furrow, which divides the combined wide median ridge into two closely spaced halves, thereby turning the high-triangular or high-trilobate cross-section into a rounded high trapezoidal cross-section (Figs 3D2, 3F2, 3I2, 3J2, 4F2, 4I2, 4K2, 5C2), as is characteristic for the genus *Nogrobs*, even though in *N. (T.) zekkarensis* the rounded trapezoid is higher than wide. The lumen is circular.

Microstructure. The spiral tube consists of two layers (Figs 6–11). According to the system of microstructure types of Vinn et al. (2008b), the outer layer consists of tall spherulitic crystals

and matches the SPHP microstructure, and the inner layer matches the SIOP microstructure. However, the microstructure of *N. (T.) zekkarensis* was altered by recrystallization during diagenesis and does not allow to observe growth lamellae. In contrast, in the tubes of *Rotularia spirulaea* (Lamarck, 1818) and its subjective synonym *R. nummularia* (von Schlotheim, 1820), Vinn (2008) observed chevron-shaped growth lamellae. Although we polished and treated our transverse sections of *Nogrobs zekkarensis* three times, we did not detect any lamellae in our SEM images.

Discussion. Just like in "classic" rotulariids, the very first tube portion in ontogeny is unknown in *N. (T.) zekkarensis*. It can only be assumed that it is very small in diameter, thin-walled, short, non-spiral, and attached to a solid object. It may be speculated whether or not a few thin and short fragments of the small brown tube-fillings (see below) attached to more or less adult *Nogrobs* spirals represent remains of such very first tube portions settling on an adult tube of the same species. However, most of the small brown tube fillings are a bit too large in diameter or/and too long.

Just like the "classic" rotulariids from the Cretaceous to Eocene, also 82 per cent of the individuals of *N. (T.) zekkarensis* display the rotulariid morphogenetic countdown program: An attached, straight or only slightly curved, non-spiral initial tube portion is followed by a tightly coiled spiral, which is attached to a foreign substrate only indirectly via its non-spiral initial portion. Sooner or later the spiral breaks free and lies loosely horizontally or slightly obliquely on the sea-floor. Again sooner or later, latest when forming a non-spiral free anterior tube portion, the spiral is oriented vertically by c. 90 degrees and rises the non-spiral free anterior tube portion vertically like a chimney, although this chimney is only very short in *N. (T.) zekkarensis*.

However, while 82 per cent of *N. (T.) zekkarensis* individuals behave just like "classic" rotulariids, 18 per cent of the studied *N. (T.) zekkarensis* individuals show a small solid substrate, respectively its negative impression, in the center of the spiral's underside and thereby proof that these 18 per cent of the individuals must have stayed closely attached to the substrate, either at least as long as the diameter of the spiral reached the diameter of the negative impression of the not preserved substrate, or for lifetime in the specimens in which original fragments of the substrate are still present in situ in the center of the spiral's underside, just as is the case in non-rotulariid serpulids. In contrast, in the "classic" rotulariid species from Early Cretaceous to Eocene, only very rarely the original substrate or its negative impression is preserved still connected to the spiral. Moreover, while the

posteriormost preserved tube fragment of *N. (T.) zekkarensis* runs only slightly rising, almost horizontal, and therefore is often preserved at the underside of the spiral, in "classic" rotulariid species, the posteriormost tube fragment, if preserved at all, is rising freely and more or less steeply, thereby indicating a small vertical distance from its unknown substrate, before it starts to form the spiral,.

In summary, a minor though not negligible percentage of the individuals of *N. (T.) zekkarensis* shows a tendency to stay longer in ontogeny, closer and more firmly connected to their substrate than the majority of individuals of this species, as well as than the "classic" rotulariid genera. It may be speculated whether or not *N. (T.) zekkarensis* was able to select a shell fragment of a certain but limited size, stable enough for providing a safe juvenile stage, but light enough to be turned vertically together with the spiral when forming the short chimney. If so, the morphogenetic countdown program of *N. (T.) zekkarensis* could be interpreted as a geologically early transition stage from the usual attached lifestyle of most non-rotulariid serpulid taxa to the morphogenetic countdown program of "classic" rotulariid.

Accompanying fauna. As mentioned in the chapter Geographical, geological, and stratigraphic setting, the serpulid tubes and serpulid-like tube fillings described in the present article are accompanied by ammonites, belemnites, bivalves, rare brachiopods, crinoids, echinoid spines and other echinoid remains, *Zoophycos* and vertical burrows. Bivalves with a calcitic shell settled by *N. (T.) zekkarensis* tubes include oysters and pectinids, perhaps also limids. The serpulid samples studied in detail also contains one loose specimen each of the following small-sized invertebrates: a low and circular solitary coral, two different gastropod species (one is shown in Fig. 5E–E1), an interambulacral plate of a cidaroid echinoid (Fig. 5F), an ophiuroid ossicle, and a bryozoan attached to a bivalve fragment.

Table 1

Figures	Infor- mal no.	Spiral diameter (mm)	Tube diameter (mm)	Tube height (mm)	Direction of coiling
Fig. 3A–A2	1	5.5	1.25	2.45	dextrally
Fig. 3B–B2	9	5.4	1.2	1.35	dextrally
Figs 3C–C2, 6–7	3	7.9	2.1	2.1	sinistrally
Fig. 3D–D2	5	4.7	1.55	1.8	sinistrally
Figs 3E–E2, 10	6	6.6	1.45	1.65	dextrally

Figs 3F–F2, 9	7	6.05	0.75	1.3	sinistrally
Fig. 3G–G3	8	large tube 7.5, small tube 3.5	1.6	2.8	large tube dextrally, small tube sinistrally
Fig. 3H	4	4.3	2.2	2.1	sinistrally
Figs 3I–I2, 6–7	2	5.7	1.1	1.6	sinistrally
Figs 3J–J2, 8, 11	10	6.95	1.8	2.02	sinistrally
Fig. 4A–4A2	11	6.9	1.3	1.9	sinistrally
Figs 4B–4B2, 11	12	5.75	1.4	1.7	sinistrally
Figs 4C–4C2, 11	13	4.55	1.1	1.7	sinistrally
Fig. 4D–4D2	14	6.5	1.2	1.8	sinistrally
Fig. 4E–4E2	15	5.8	0.9	1.9	dextrally
Figs 4F–4F2, 11	16	6.25	0.75	1.5	dextrally
Fig. 4G–4G2	17	6.3	1.1	1.35	sinistrally
Fig. 4H–4H2	18	6.2	1.65	2.1	sinistrally
Fig. 4I–4I2	19	6.0	1.5	1.65	sinistrally
Fig. 4J–4J2	20	6.0	1.35	1.6	sinistrally
Fig. 4K–4K2	21	6.3	1.3	1.9	dextrally
Fig. 4L–L2	25	7.2	1.15	2.1	sinistrally
Fig. 5A–A3	22	5.4	1.15	1.75	sinistrally
Fig. 5B–B2	23	6.4	0.9	1.4	sinistrally
Fig. 5C–C2	24	7.2	1.05	1.45	sinistrally
not figured	26	7.7	1.1	2.45	sinistrally
not figured	27	6.7	1.1	1.8	sinistrally
not figured	28	8.2	1.2	1.45	sinistrally
not figured	29	7.1	1.2	1.4	sinistrally
not figured	30	6.7	1.2	2	sinistrally
not figured	31	7.6	1.3	1.8	sinistrally

not figured	32	8.1	1.7	1.9	sinistrally
not figured	33	6.3	1.1	2.1	sinistrally
not figured	34	7.4	1.1	1.5	sinistrally
not figured	35	7.7	1.3	1.8	sinistrally
not figured	36	5.9	1.2	2.65	sinistrally
not figured	37	7.1	0.85	1.3	sinistrally
not figured	38	6.8	1.1	1.7	sinistrally
not figured	39	7.0	1.8	2.1	sinistrally
not figured	40	6.6	1.15	1.8	sinistrally
not figured	41	5.8	1,15	1,6	sinistrally
not figured	42	5.5	0.9	2.2	sinistrally
not figured	43	6.6	0.75	1.4	sinistrally
not figured	44	7.0	1.35	2.1	sinistrally
not figured	45	8.0	1.2	2	sinistrally
not figured	46	5.6	1.05	1.95	sinistrally
not figured	47	7.4	1.1	2.05	sinistrally
not figured	48	Large tube 7.0, small tube 3.3	1.45	1.95	Large tube sinistrally, small tube dextrally
not figured	49	6.9	0.95	1.6	sinistrally
not figured	50	5.7	1.2	1.7	sinistrally
not figured	51	6.1	0.9	1.7	sinistrally
not figured	52	7.3	1.9	2.4	sinistrally
not figured	53	6.5	1.1	1.6	sinistrally
not figured	54	6.1	0.9	1.5	sinistrally
not figured	55	5.4	1.6	1.9	sinistrally
not figured	56	6.4	1.05	1.85	sinistrally

not figured	57	6.6	1.1	1.9	sinistrally
not figured	58	5.5	0.9	1.7	sinistrally
not figured	59	5.8	1.7	1.8	sinistrally
not figured	60	5.6	1.1	1.4	sinistrally
not figured	61	6.3	1.4	1.4	sinistrally
not figured	62	6.9	1.2	1.8	sinistrally
not figured	63	6.3	1.3	2.1	sinistrally
not figured	64	5.0	1.2	1.7	sinistrally
not figured	65	6.3	1.2	1.6	sinistrally
not figured	66	5.4	0.95	1.8	sinistrally
not figured	67	5.6	0.9	1.7	sinistrally
not figured	68	5.4	1.35	1.9	sinistrally
not figured	69	4.6	1.4	1.9	sinistrally
not figured	70	6.6	1.8	2.2	sinistrally
not figured	71	4.7	1.1	2.05	sinistrally
not figured	72	6.0	1.3	1.85	sinistrally
not figured	73	5.4	1.7	1.95	sinistrally
not figured	74	6.7	1.2	2.1	sinistrally
not figured	75	4.1	1.15	1.65	sinistrally
not figured	76	4.7	1.5	1.6	dextrally
not figured	77	3.8	0.9	1.45	sinistrally
not figured	78	7.2	1.3	1.7	sinistrally
not figured	79	6.6	1.45	2.15	dextrally
not figured	80	6.8	1.3	1.6	sinistrally
not figured	81	6.8	1.3	2.95	dextrally
not figured	82	6.6	1.4	1.8	dextrally
not figured	83	6.5	1.1	1.7	sinistrally

not figured	84	6.5	1.3	1.75	dextrally
not figured	85	7.0	1.4	2.05	dextrally
not figured	86	6.0	1.2	1.8	dextrally
not figured	87	5.9	1.45	1.7	dextrally
not figured	88	5.5	1.25	1.55	dextrally
not figured	89	6.4	1.65	1.95	dextrally
not figured	90	6.4	1.4	1.7	dextrally
not figured	91	5.3	1.2	1.6	dextrally
not figured	92	5.9	1.05	1.5	dextrally
not figured	93	6.1	1.4	1.6	dextrally
not figured	94	5.1	?	?	dextrally
not figured	95	5.4	?	?	dextrally
not figured	96	?	?	?	sinistrally
not figured	97	?	?	?	sinistrally
not figured	98	6.2	?	?	sinistrally

Figure 3



Figure 4

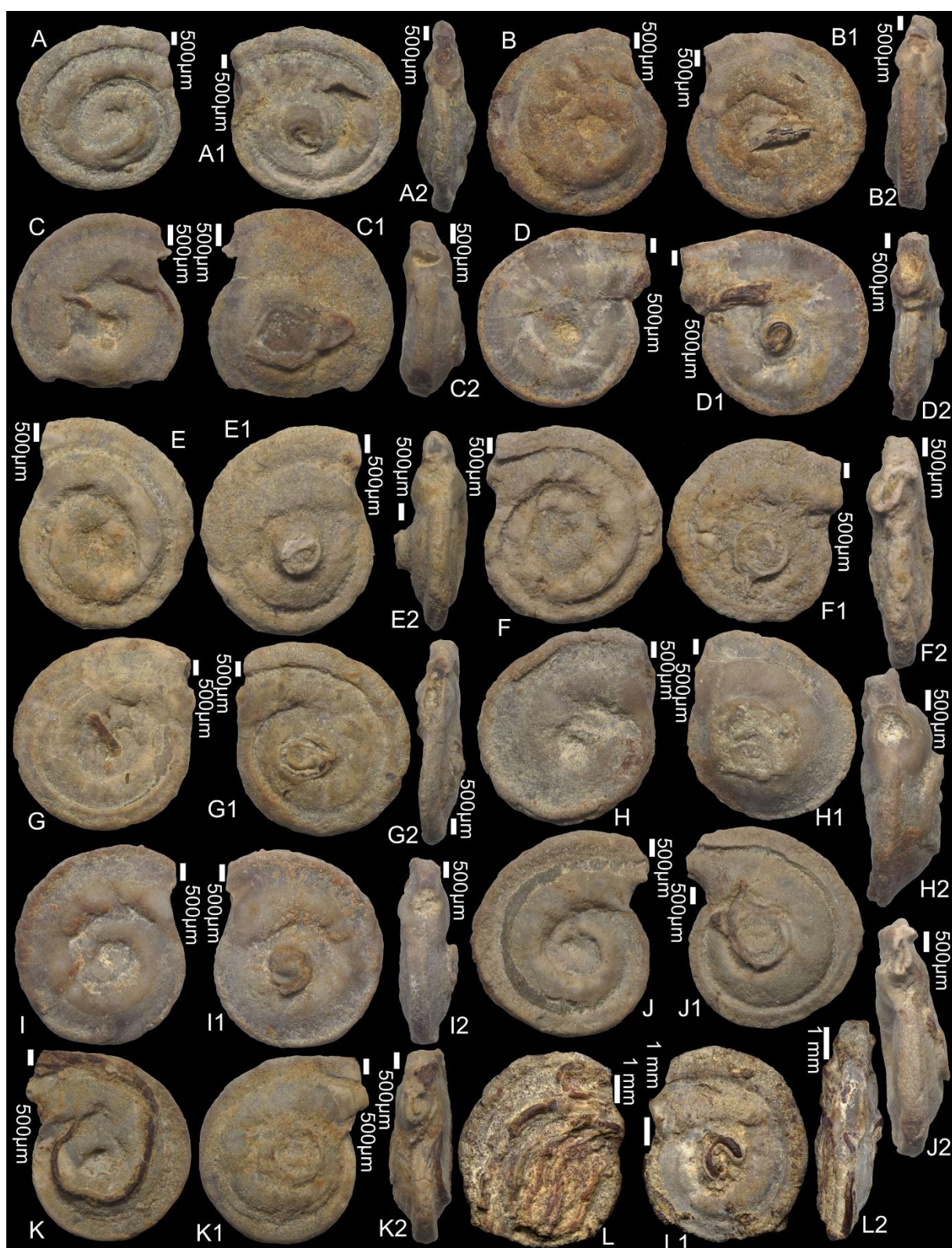


Figure 5

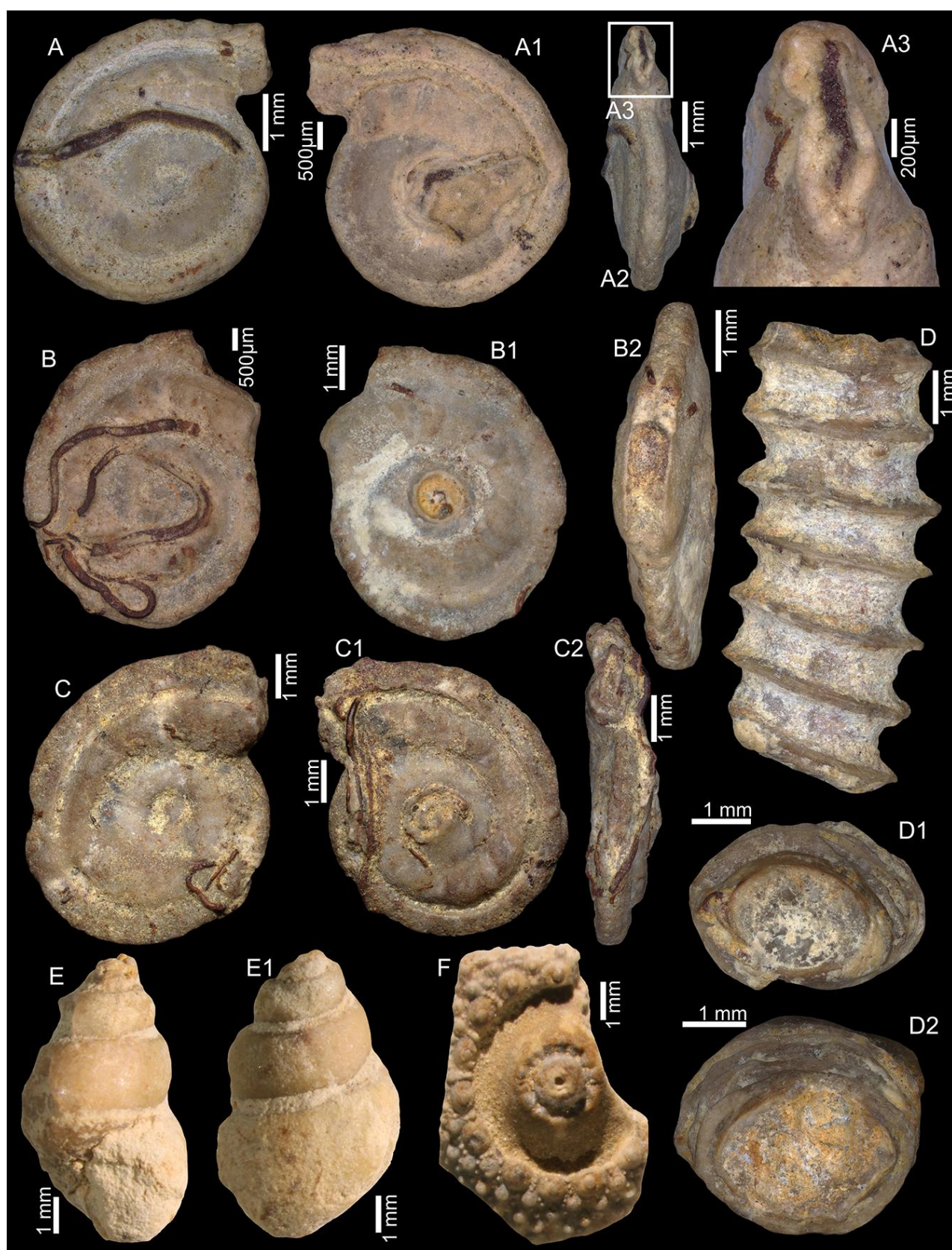


Figure 6

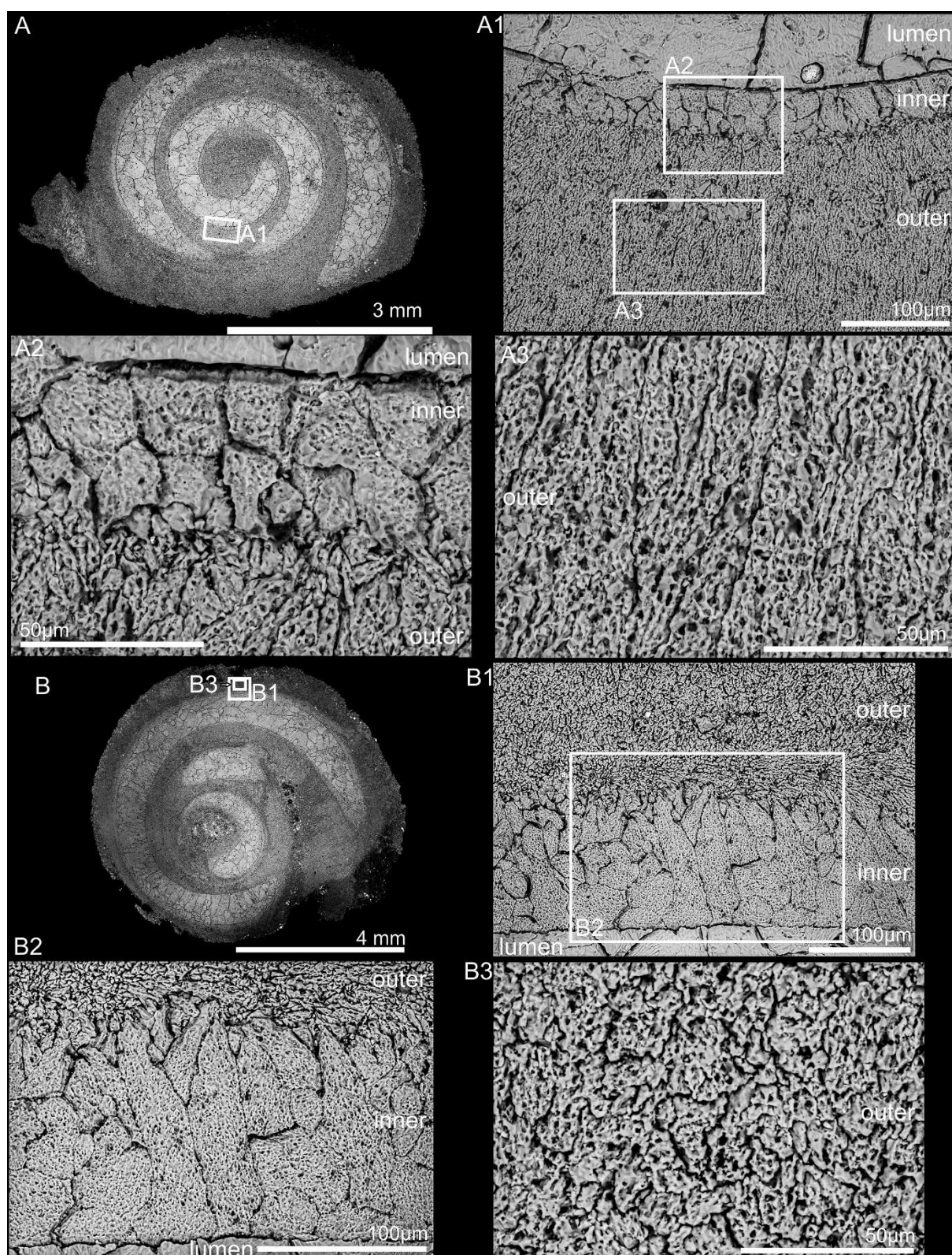


Figure 7

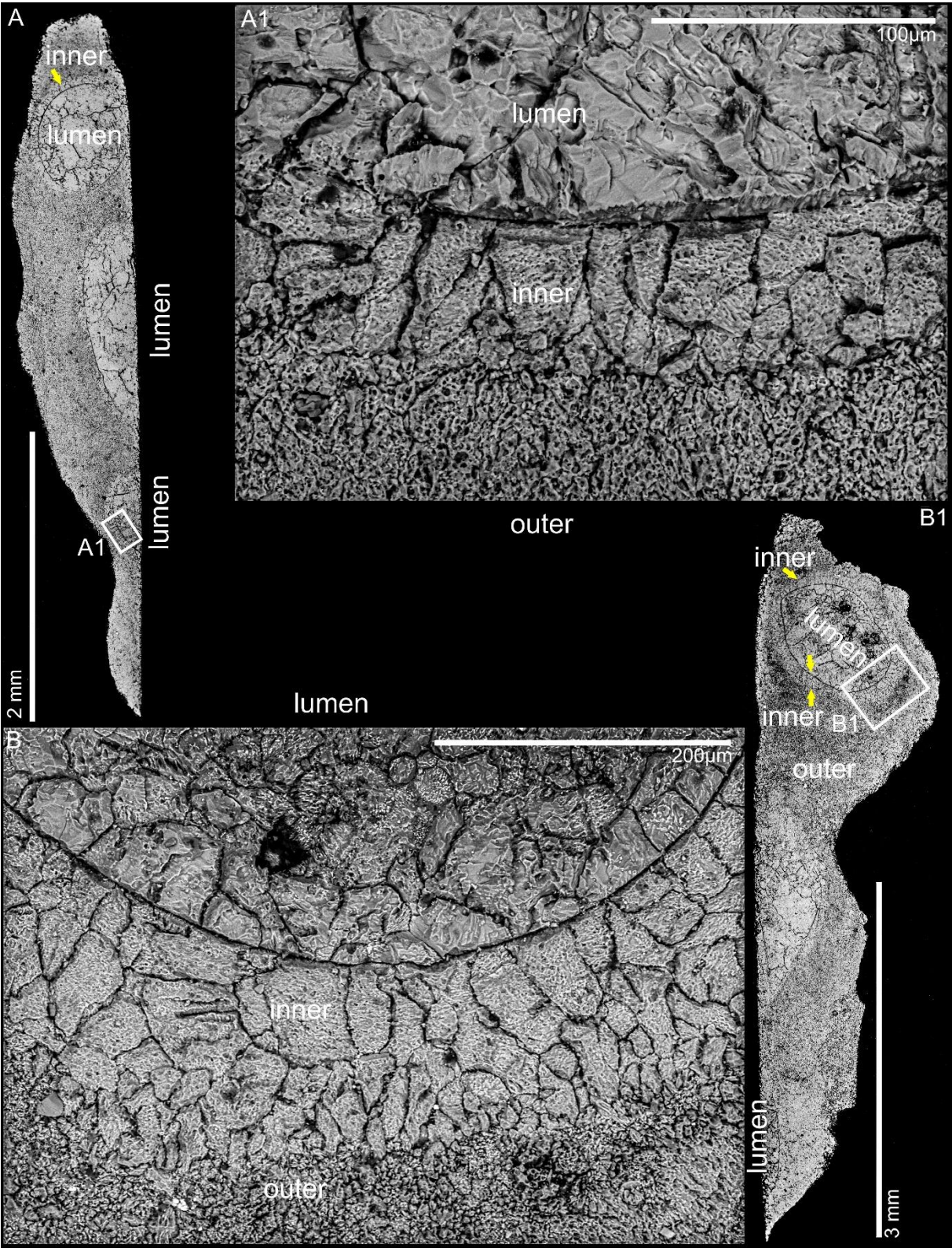


Figure 8

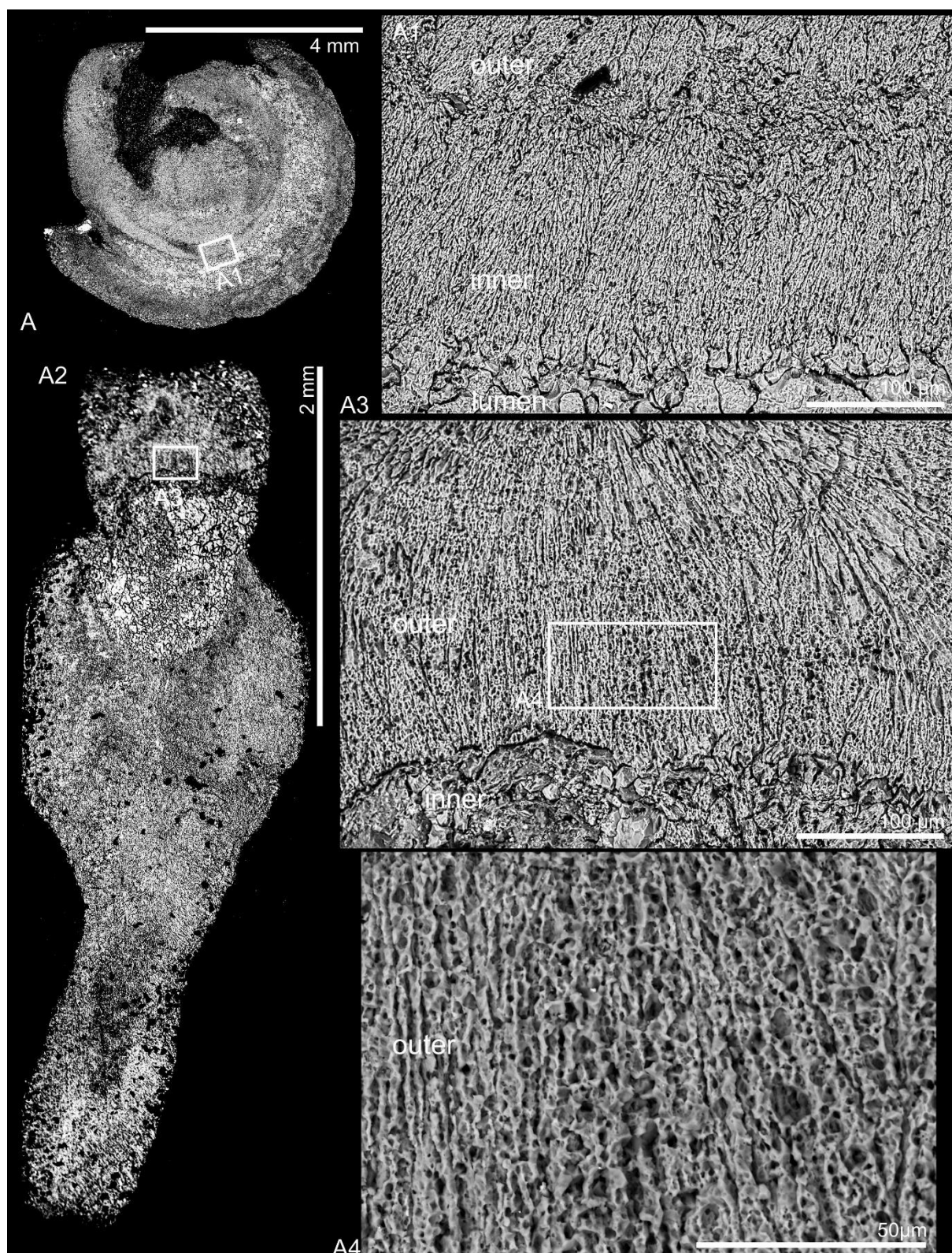


Figure 9

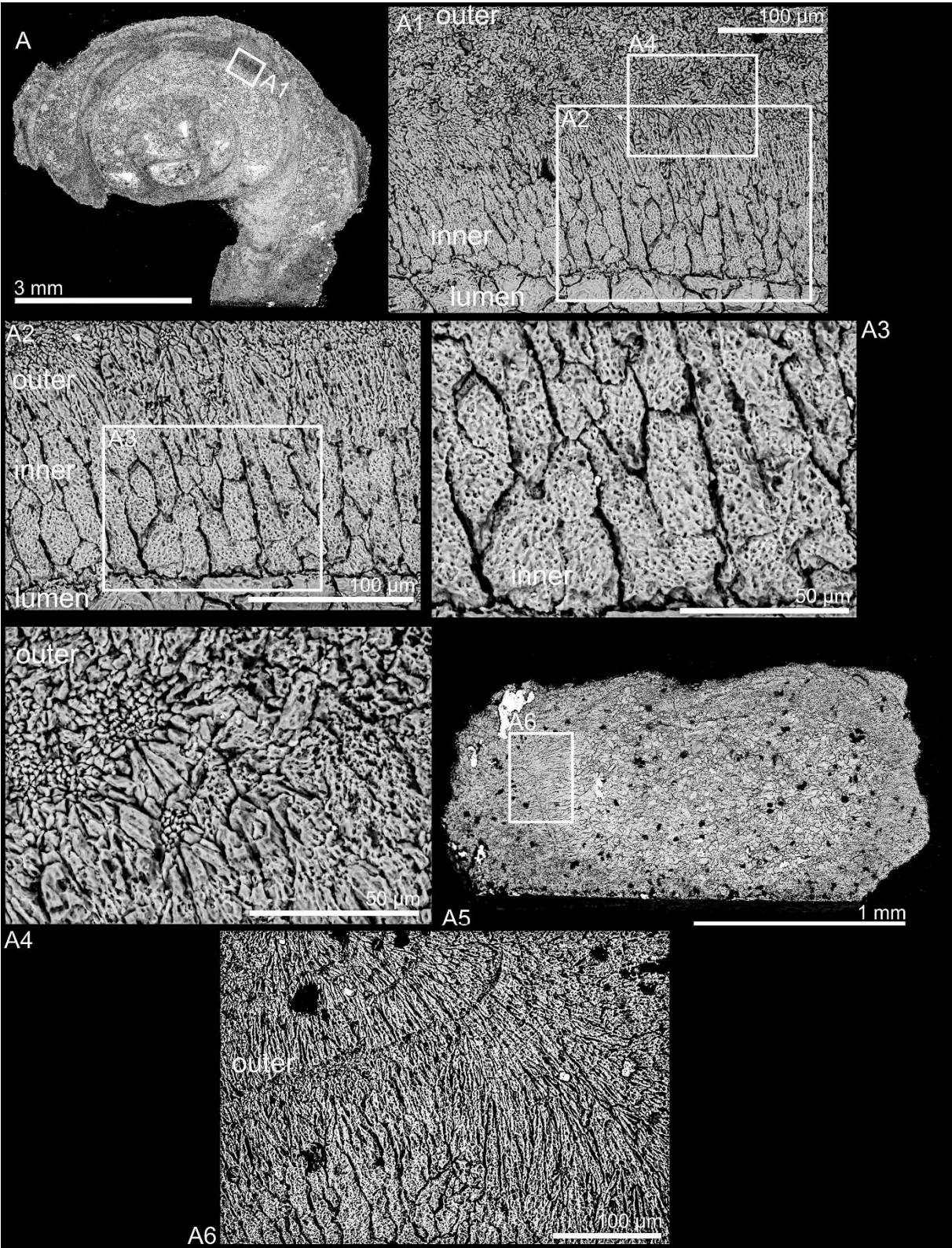


Figure 10

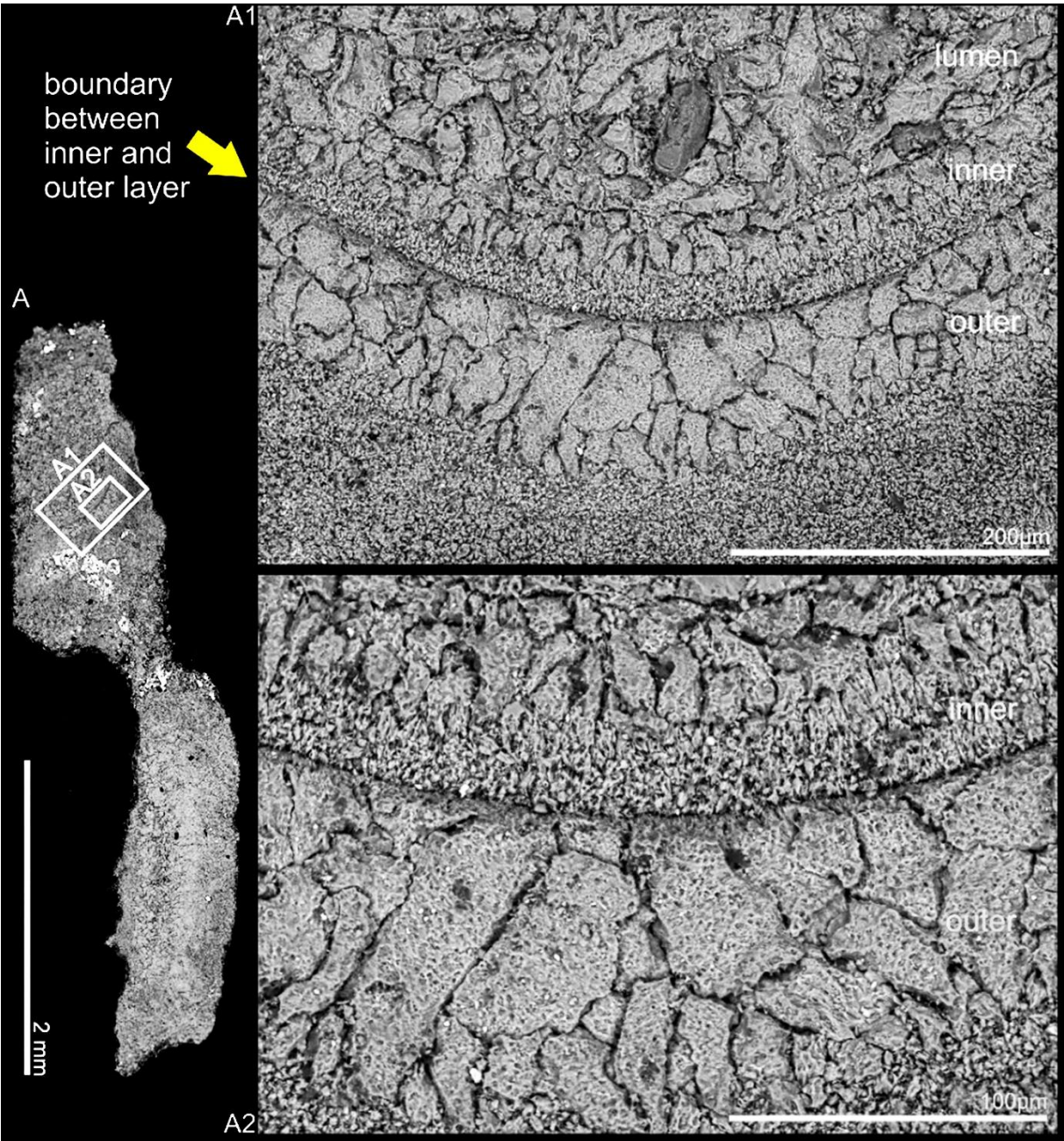
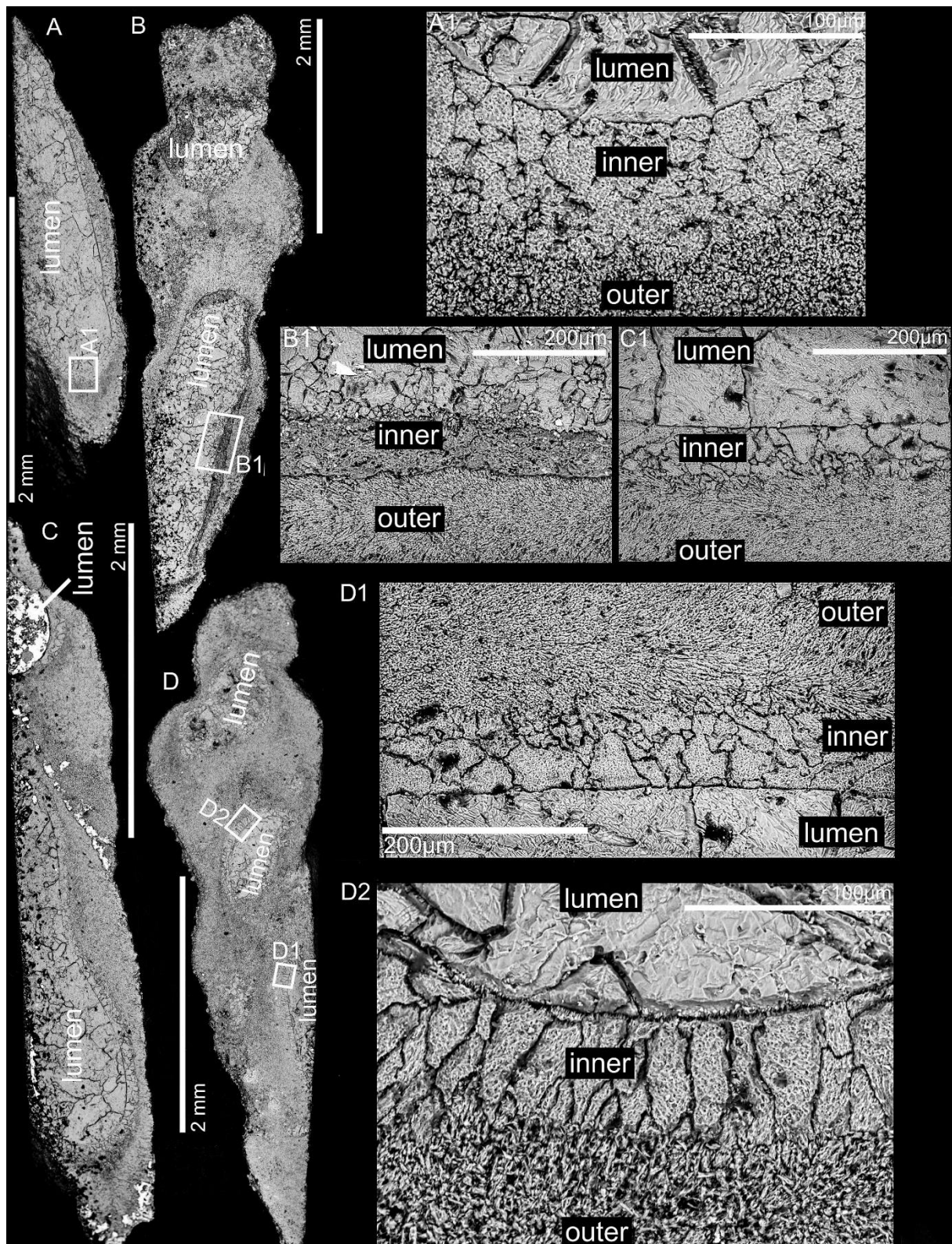


Figure 11



Subgenus *Nogrobs* (*Tubulostium*) Stoliczka, 1868 in Stoliczka, 1867–1868.

Type species. *Tubulostium discoideum* Stoliczka, 1868 in Stoliczka, 1867–1868.

Diagnosis. The tube obligatorily forms a tightly coiled spiral. It bears four usually rounded longitudinal ridges. Peristomes are lacking or inconspicuous. The tube wall is three-layered with SP, HG, and again SP microstructures.

Microstructure. Among the entire genus *Nogrobs*, *N. (Tubulostium) discoideum* is unique by its three-layered tube with SP, HG and SP microstructure (Kupriyanova & Ippolitov 2015).

Stratigraphic range. Turonian (formerly considered to be Cenomanian).

Discussion. Although the type species *N. (T.) discoideum* from the Turonian of southern India in exterior aspect matches the subgenus *Nogrobs (Tetralysis)* and although both subgenera obligatorily form a tightly coiled spiral, we keep this type species separate as a subgenus of its own, mainly due to its three-layered tube wall. Similarly, Kupriyanova & Ippolitov (2015) consider this species the only member of their "Group 3". Judging from exterior tube morphology, *N. (T.) discoideum* could well be interpreted to be geologically late, short-living offshoot from the long-living *N. (Tetralysis)* main line, although the status of the geologically youngest species of *N. (Tetralysis)*, "*Serpula*" *quadricarinata*, is uncertain (see above). However, the microstructure of *N. (Tubulostium) discoideum* is rather different from the two-layered SPHP and SIOP microstructure of *N. (Tetralysis) zekkarensis* and therefore argues against close phylogenetic relationship.

The decision to keep the species *discoideum* separate at subgenus level has also the nomenclatoric advantage to keep the other subgenus names and the other species separate from *Tubulostium* and thereby to save the other subgenus names from the danger of becoming junior synonyms of *Tubulostium*, because except for the very old name *Nogrobs*, all other subgenus names (*Tetraserpula*, *Tetralysis*, *Glandifera*, and *Tetraditrupa*) had been introduced later than the name *Tubulostium*. Moreover, there is an additional reason for keeping the species contents of *Tubulostium* small. In the 20th century, and occasionally even later, many geologists and palaeontologists followed Stoliczka's error and considered not only his type species *discoideum*, but also many other spiral serpulid tubes of the genera *Nogrobs*, *Rotularia* Defrance, 1827a, *Tectorotularia* and others to belong to gastropods named *Tubulostium*. The name *Tubulostium* had been, and occasionally still is, mentally but erroneously coupled with gastropods instead of serpulids.

Although the three-layered tube wall is unique among the genus *Nogrobs*, nevertheless its microstructure SP, HG, SP is similar to the unilayered SP microstructure or, when diagenetically altered, unilayered HG microstructure in the subgenera *N. (Nogrobs)* and *N.*

(*Tetraserpula*). *N. (T.) discoideum* may be considered an advanced unilayered SP species with an either diagenetically altered or phylogenetically intercalated additional HG layer, as suggested in Rantuch et al. (2024). However, this hypothesis does not solve the discrepancy in exterior tube morphologies, because *N. (Tubulostium) discoideum* is obligatorily spiral just like the subgenus *N. (Tetralysis)*, neither optionally spiral as *N. (Nogrobs)* nor non-spiral as *N. (Tetraserpula)*.

In summary, the problem exists that *N. (Tubulostium) discoideum* matches *N. (Tetralysis)* best by exterior tube morphology, but it matches *N. (Nogrobs)* and *N. (Tetraserpula)* only relatively best by microstructure. Unfortunately, *N. (Tetralysis) zekkarensis* is the only species of its subgenus of which the microstructure is hitherto studied. Probably the study of microstructure of the type species of *N. (Tetralysis)*, *N. (T.) quadrangularis*, would provide a solution.

Subgenus ***Nogrobs (Glandifera)*** Regenhardt, 1961

Type species. Serpula articulata J. de C. Sowerby, 1829 in J. de C. Sowerby, 1826–1829.

Diagnosis. The tubes are non-spiral and characterized by possessing numerous strongly developed, often bulbous, massive, four-piece peristomes, in some species located in more or less regular distance from each other. In some species, the attached tube portion is rather short or entirely absent.

Microstructure. Is yet unknown. Although Kupriyanova & Ippolitov (2015) listed a "*Glandifera cf. vertebralis* (J. de C. Sowerby, 1829 in J. de C. Sowerby, 1826–1829)" from the early Callovian of Egesheim in southwestern Germany with unilayered SP microstructure, the species from Egesheim is not the typical *N. (Glandifera) vertebralis* as known from the middle Callovian Lower Oxford Clay in England, but just another species of optionally spiral subgenus *N. (Nogrobs)*.

Stratigraphic range. Middle Callovian to Aptian or Albian.

Discussion. Originally, Regenhardt introduced the name *Glandifera* as a subgenus of genus *Genicularia* Quenstedt, 1856 in Quenstedt, 1856–1858, which has similar peristomes, but five longitudinal ridges and a regular pentagonal cross-section and by this may rather be related to

genus *Pentaditrupa* Regenhardt, 1961. *N. (Glandifera)* resembles *N. (Tetraserpula)* by forming no spiral at all.

Subgenus ***Nogrobs (Tetraditrupa)*** Regenhardt, 1961

Type species. *Serpula canteriata* von Hagenow, 1840. (For details, see paragraph "Discussion" in chapter "Genus *Nogrobs*".)

Diagnosis. As short fragments of the anteriormost end of the initial tube portion are only very rarely preserved, almost all specimens entirely consist of the long free tube portion. The tubes are characterized by curving gently in one direction with a gradually or quickly decreasing curvature, respectively a gradually or quickly increasing radius, of the resulting wide open, never tightly coiled spiral. In case of a gradual decrease of curvature, the spiral resembles a whorl of a relaxed watchspring; in case of a fast change from gradual to fast decrease of curvature, the tube resembles a hook with a very slightly curved or straight stalk. Moreover, the tube, especially its anterior portion, rises very gently and obliquely. In one species, each of the four rounded longitudinal edges wears a row of fine chevrons nestled inside each other. Irregular transverse swellings may occur, but no well-developed peristomes.

Microstructure. *N. (Tetraditrupa) canteriata* is single-layered and has a SP microstructure. In contrast, *N. (Tetraditrupa) folkestoneneis* nom. nov. is special by its two-layered tube wall consisting of a thin outer layer with SPHP microstructure similar to SP and a thicker inner layer with HG microstructure which is diagenetically altered and possibly originally had been an SIOP microstructure (Kupriyanova & Ippolitov, 2015).

Stratigraphic range. Late Albian to late Maastrichtian; early Paleocene (Danian) uncertain.

Discussion. Tubes of this subgenus reach a slightly larger diameter than those of the other subgenera, bear no peristomes, and are only very rarely found to have been attached; instead, they were free-lying on the soft seafloor. Often, the tube of the late Albian to middle Cenomanian *N. (Tetraditrupa) folkestonensis* is hook-shaped due to its strongly curved posterior portion and its only very gently curved or straight anterior portion. In contrast, the Maastrichtian species *N. (Tetraditrupa) canteriata* (von Hagenow, 1840) and *N. (T.) superiora* (Jäger, 1983) form a loosely coiled, wide open spiral resembling a relaxed watchspring. This small difference in morphology, together with the above mentioned

differences in microstructure and in geological age, makes *N. (Tetraditrupa) folkestonensis* different from both Maastrichtian species.

Certainly, the tube shape of subgenus *N. (Tetraditrupa)* providing a showshoe effect is an adaptation to life on the soft seafloor consisting of chalk ooze, which was widespread in Late Cretaceous time, when a very similar tube shape is also displayed by the genus *Pentaditrupa* Regenhardt, 1961 whose tubes differs from *Nogrobs* by the rounded pentagonal cross-section.

From the original description it is possible, but highly uncertain, that "*Serpula* sp. II" described but not figured by Rosenkrantz (1920) from the Danian of Copenhagen in Denmark belongs to the subgenus *N. (Tetraditrupa)*. In contrast, presumably several other mentions of the Maastrichtian species *N. (T.) canteriata* in the Danian of Denmark refer to tubes reworked from Maastrichtian chalk.

Although SP and SPHP microstructures are similar to each other, Kupriyanova & Ippolitov (2015) detected that, surprisingly, the microstructures of the two hitherto studied species of subgenus *N. (Tetraditrupa)* are rather different. While the single-layered tube wall with SP microstructure of *N. (T.) canteriata* matches the detected or, in diagenetically altered specimens, reconstructed microstructure of all species of the subgenera *N. (Nogrobs)* and *N. (Tetraserpula)* hitherto studied by Kupriyanova & Ippolitov (2015), the reconstructed original microstructure of *N. (T.) folkestonensis* nom. nov., a two-layered tube wall with SPHP and presumed SIOP microstructures, is remarkably different – not so much by the SPHP which is rather similar to the SP microstructure common in the genus *Nogrobs*, but predominantly by the combination of SPHP with the rare SIOP microstructure, a combination in genus *Nogrobs* known only in a single other species, *N. (Tetralysis) zekkarensis*, whose tube morphology differs considerably (obligatorily tightly coiled spiral versus never tightly coiled spiral in *N. (T.) folkestonensis* nom. nov.) and wide distance in geological age argue against uniting both species at subgenus level. Outside genus *Nogrobs*, this combination of SPHP and SIOP microstructures was detected by Kupriyanova & Ippolitov (2015) in their recent species *Zibrovermia zibrowii*, whose tube shape is indeed similar to *N. (T.) folkestonensis* nom. nov., but the genera *Nogrobs* and *Zibrovermia* belong to different subfamilies.

***Nogrobs (Tetraditrupa) folkestonensis* nom. nov. pro *Serpula rustica* (J. de C. Sowerby, 1829 in J. de C. Sowerby, 1826–1829).**

Remark. As stated by Jäger (2005, p. 139), the species name *Serpula rustica* J. de C. Sowerby, 1829 in J. de C. Sowerby, 1826–1829 is not valid for the late Albion to middle Cenomanian

species of *N. (Tetraditrupa)* from southern England and northern Germany, because the combination *Serpula rustica* is a junior homonym of *Serpula rustica* DeFrance, 1827b. Therefore, we introduce the new species name *folkestonensis* in order to replace the invalid species name *rustica* J. de C. Sowerby.

Derivatio nominis. After the city of Folkestone at the southern coast of England, near which the type specimen was found.

Zoobanc. urn:lsid:zoobank.org:act:08016608-6F90-46FB-844F-11C594AB7B4D

Holotype, Stratum typicum, and Type locality. The tube described and figured by J. de C. Sowerby (pl. 599, fig. 3) under the name *Serpula rustica* from the "Upper Greensand" (or rather Albian Gault Clay or Cenomanian Chalk) of East Weare Bay east of Folkestone, kept in the British Museum in London.

Occurrences. Albian: The original description states "Upper Greensand". Todd (2010) mentions that this species (as "*Tetraserpula* sp.") "Occurs uncommonly in the Gault of Folkestone (stratigraphically unlocalized)". Jäger in Krüger (2000) mentioned this species from late Albian clay in Braunschweig-Rautheim in northern Germany.

Middle Cenomanian: Gale (2002) states that this species is "apparently restricted to a single marl bed in the *C. inerme* zone; widespread in Kent, Sussex and the Isle of Wight". In northwestern Germany, this species occurs in the *Praeactinocamax primus* Event near the base of the *Acanthoceras rhotomagense* zone in the quarry near Wunstorf-Kolenfeld southwest of Hannover and at several localities in Northrhine-Westphalia.

Diagnosis. An attached tube portion was either never built or not preservable in fossils. The tube is free, long, increases slowly to gradually and reaches a medium-sized tube diameter. The tube is more or less regularly curved in one direction, but with a quickly decreasing curvature, respectively quickly increasing radius, so that the resulting tube shape rather resembles a strongly curved hook with a very slightly curved or straight stalk than a relaxed watchspring. The rounded quadrangular cross-section is even more rounded in the anterior tube portion, so that the cross-section may become almost circular near the aperture.

Discussion. The observation that an attached tube portion is always missing in this species is confirmed by similar observations by Todd (2010) and Lutz Kaecke, Hannover (personal communication). Regenhardt (1961) assigned this species to his subgenus *Genicularia* (*Glandifera*), and Gale (2002) assigned it to *Glandifera*. which he considered a genus of its

own. However, here we consider *Glandifera* another subgenus of *Nogrobs*; see above. Ziegler (2006) indicated this species from the Aptian, but presumably this is a confusion with another species or with a sediment layer of a different age.

5. Discussion

It is striking that the two geologically oldest *Nogrobs* species belonging to two different long-living subgenera are almost equally old: late Pliensbachian in *Nogrobs* (*Tetraserpula*). late Pliensbachian or early Toarcian in *Nogrobs* (*Tetralysis*). Moreover, according to Stevens (1967) also the first representatives of "*Rotularia*", although poorly preserved, appear in the Ururoan stage (Pliensbachian – Toarcian) in New Zealand. Microstructures differs between subgenera, because on the one hand the vast majority of hitherto studied tubes of *N. (Tetraserpula)* and *N. (Nogrobs)* possess an unilayered tube-wall of either SP microstructure or, if diagenetically altered, HG microstructure, whereas on the other hand the two hitherto studied tubes of *N. (Tetralysis)* have multi-layered tubes. Moreover, *N. (Tetralysis) zekkarensis* has unusual microstructure types.

The time in geological history when *N. (Tetraserpula)* and *N. (Tetralysis)* had separated from each other is unknown, but it must have happened earlier than in the latest Pliensbachian. Strangely, the oldest representatives of both subgenera, *N. (Tetraserpula) varicosa* and *N. (Tetralysis) zekkarensis*, already look rather different, and this is true also for several other *Nogrobs* species occurring in late Toarcian, Aalenian and Bajocian which either form no spiral at all as in *N. (Tetraserpula)* or always from a tightly coiled regular spiral as is *N. (Tetralysis)*. Only in the Bajocian, rare spirals of *N. (Nogrobs) vermicularis* represent the geologically oldest optional spiral species, followed by other, common and widespread species of this subgenus in the Bathonian. It seems paradox that the morphologically intermediate *N. (Nogrobs)* appeared much later in the geological record than the morphologically differentiated *N. (Tetraserpula)* (no spiral at all) and *N. (Tetralysis)* (all tubes build a spiral).

Most of the spiral Nogrobs tubes are rotulariids. Seilacher et al. (2008) reconstructed regular changes in mode of life and orientation in the course of ontogeny, termed morphogenetic countdown program. Most of the spiral tubes in the subgenera *Nogrobs* (*Nogrobs*), *N. (Tetralysis)* and *N. (Tubulostium)* follow the rotulariid morphogenetic countdown program.

The term "rotulariids", although derived from the established and valid genus name *Rotularia* Defrance, 1827a, is not a valid name according to the International Code of Zoological Nomenclature (ICZN). Instead, it is only an informal palaeoecologic term for genera, species, or individuals whose tubes follow a special morphogenetic countdown program. An overview of the research history and nomenclature of rotulariid genera (most of these had originally been introduced as subgenera of genus *Rotularia*, and all have the letter combination "...rotul..." in their names) is provided in Rantuch et al. (2024).

The rotulariid morphogenetic countdown program consists of three ontogenetic stages, of which the second stage, which is a moderately sized to large, tightly coiled, regular planispiral or trochospiral, is the most conspicuous. In the first ontogenetic stage, the rotulariid tube is very small, straight or irregularly curved, and attached to a solid substrate, just like the young tube of most other serpulids. In practice, this first stage is often not found, because mostly it is broken off from the later formed spiral, but sometimes, an anteriormost rest of the first ontogenetic stage is preserved in the center of the underside of some of the spirals. In contrast, isolated fragments of the most posterior tube portion are normally not recognized to belong to *Nogrobs*, due to its small size and lack of ornamentation characteristic of ontogenetically older *Nogrobs* tubes. The anterior end of the initial tube portion starts to rise and to grow straight and freely above the substrate, but only for a very short distance. Then suddenly the tube starts forming a very narrow, slightly rising curve, which becomes the first whorl of a tightly coiled spiral, which is the second and main ontogenetic stage.

It must be emphasized that in rotulariids the spiral had usually, with some exceptions, been attached only in the very small center of the underside, whereas the whorls of the spiral are only attached to the previous whorl of the same specimen. This is in contrast to a large number of non-rotulariid serpulid taxa, which also may form a spiral which, however, is attached to a foreign substrate by its entire underside or at least by a wide part of it. In *Tectorotularia hexagona* (Roemer, 1841 in Roemer, 1840–1841) from the Cenomanian to early Turonian of Essen, northwestern Germany, some specimens form a regular rotulariid spiral, whereas other specimens form an irregular pseudo-spiral by wrapping the tube all around a small pebble in the center, and both forms occur together in the same palaeo-population (Rantuch et al., 2024).

Gradually, the increasing spiral becomes too large and too heavy to be fixed and hold by the small and thin tube of the first stage, and suddenly the spiral breaks loose and lies freely on the seafloor.

If the rotulariid animal grows old enough, a third final stage is formed by the tube growing tangentially, straight or only slightly curved, and either horizontally or only slightly rising, away from the spiral (Wrigley, 1951; Ball, 1960; Elorza & Astibia 2017, 2018; Savazzi, 1995; 1999; Seilacher et al., 2008; Astibita et al., 2016; Hassan-Vand et al., 2018; Rantuch et al., 2024). In contrast to the classical assumed life position of rotulariids with the spiral lying horizontally on the soft seafloor, some authors observed in fossil tubes sticking in situ in the sediment (Seilacher et al., 2008) or at least assumed (McNamara, 2023), that the true life orientation of the adult rotulariid had been turned by 90 degrees from the above mentioned more or less horizontal orientation to a vertical orientation, so that the straight tube part of the third stage stands vertically like a chimney.

Hitherto, spiral species of the genus *Nogrobs* had not been included in the rotulariids, because usually their spirals stay smaller, and their tubes often have four conspicuous longitudinal rounded ridges or sharp keels causing the tubes' quadrilobate or rounded quadratic cross-section. And while the vast majority of the *Nogrobs* species forming a tightly coiled spiral lived in the Jurassic, the vast majority of the "classical" rotulariids lived in the Cretaceous, Paleocene and Eocene. However, the same rotulariid morphogenetic countdown program is followed also in *Nogrobs* (*Nogrobs*) and *N. (Tetralysis)* and a few other genera.

Nogrobs (Tetralysis), *N. (Tubulostium)*, *Tectorotularia* and *Rotularia* are similar in tube morphology, but differ in microstructure. In the "Discussion" subchapter of the subgenus *N. (Tubulostium)*, we had already mentioned and discussed the problem, that the differences and similarities in exterior tube morphologies do not well match the differences and similarities in number of tube wall layers and microstructures on subgenus level within the genus *Nogrobs*. A similar discrepancy exists also on genus level between the spiral representatives of *Nogrobs*, *Tectorotularia*, *Rotularia* and *Placostegus*.

When working on Jäger (2005), the gap in geological time between the geologically youngest obligately compact spiral *Nogrobs* (Oxfordian) and the geologically oldest *Tectorotularia* (Hauterivian) had still been large, and a phylogenetic connection was rather speculative. After recognizing that the Turonian species *Tubulostium discoideum* belongs to *Nogrobs* rather than to *Tectorotularia*, this gap in geological time has turned to an overlap reaching from the Hauterivian to the Turonian. If considering only the exterior morphology of the obligatorily tightly coiled spiral and neglecting the microstructure, a phylogenetic connection from the obligatory spiral Jurassic *Nogrobs (Tetralysis)* via Cretaceous *Nogrobs (Tubulostium)*

discoideum and/or Cretaceous *Tectorotularia* to Paleocene and Eocene *Tectorotularia* and *Rotularia* seems less speculative anymore.

Indeed, the spirals look very similar, and in a mind game, a *Nogrobs* (*Tetralysis*) spiral can easily be transformed into a *Tectorotularia* spiral and further into a discoidal spiral of *Rotularia spirulaea* (Lamarck, 1818): In addition to the four conspicuous longitudinal ridges characteristic for the genus *Nogrobs*, the attached tube portion as well as the periphery of the spiral may bear an additional fifth but often weaker median longitudinal ridge or rounded longitudinal convexity. If this fifth ridge is thought to be elevated and sharpened to become a keel and the four main longitudinal ridges lowered and smoothed but remain distinct, we get a *Tectorotularia* spiral. If the four longitudinal ridges are further lowered and smoothed so that they can only be indirectly recognized by a wide and very shallow depression in-between on the upper side and underside of the spiral, we get a *Rotularia spirulaea*. In case of *N. (Tetralysis) zekkarensis*, the *Tectorotularia*-like or even *Rotularia*-like aspect is even enhanced by diagentical compression, making the tubes thinner and more discoidal than they originally had been.

However, comparison of microstructures only support the geologically latest step of this mind game, from *Tectorotularia* to *Rotularia*. Instead, the following list of microstructures of the unfortunately only few hitherto studied obligatorily tightly coiled spiral species do not support the earlier, Jurassic and Cretaceous steps within the genus *Nogrobs* and from *Nogrobs* to *Tectorotularia*.

Nogrobs (Tetralysis) zekkarensis, late Pliensbachian to early Toarcian, this study: SPHP, SIOP.

Nogrobs (Tubulostium) discoideum Stoliczka, 1868 in Stoliczka, 1867–1868, Cenomanian or Turonian, Kupriyanova & Ippolitov (2015): SP, HG, SP.

Tectorotularia hexagona (Roemer, 1841 in Roemer, 1840–1841), Cenomanian or early Turonian, Rantuch et al. (2024): HAC, LF.

Rotularia spirulaea (Lamarck, 1818), Eocene, Vinn (2008); Elorza & Astibia (2017, 2018); Hassan-Vand et al. (2018): HAC, LF.

The tube walls of all four species only match by being multilayered (mostly two-layered, in a single species three-layered), in contrast to the generally most common unilayered tube wall in many other fossil and extant serpulid taxa. In spite of this, it can not be assumed that all

obligatorily spiral serpulid species, for unknown reason, must be two- or three-layered. The Late Jurassic obligatorily spiral species *Placostegus planorbiformis* (Münster, 1831 in Goldfuss, 1826–1844) (which is definitely not a rotulariid, because often the entire wide underside of its spiral is directly attached to a foreign substrate) is unilayered SP (Vinn & Furrer, 2008), just as is the case in optionally spiral *N. (Nogrobs)* tubes.

In contrast, *N. (Tetraserpula)*, *N. (Nogrobs)*, the Late Jurassic *Placostegus planorbiformis*, and recent species of the genera *Placostegus* Philippi, 1844 and *Vitreotubus* Zibrowius, 1979 are related to each other due to their microstructures (Kupriyanova & Ippolitov, 2015), and all belong to the Tribe Filopomatini.

Moreover, a revision of all *Tectorotularia*-like species, together with studies of their microstructures, may well make a few shiftings of species between genera *Rotularia*, *Tectorotularia* and spiral *Nogrobs* necessary.

***Annuloserpula* gen. nov.**

Dervatio nominis. A genus of the family Serpulidae characterized by many annuli (lat., plural of annulus = small ring), relating to the characteristic transverse rings.

Type species. *Annuloserpula etalensis* (Piette, 1856).

Diagnosis. The tube is medium-sized, consisting of a short attached and a very long free tube-portion, which may be straight, gently and regularly curved, or most often forms a wide open spiral. A high number of conspicuous, short and thin but high annular rings (peristomes, "annuli"), which may be arranged either very densely and regularly spaced or less densely and less regularly, are the most characteristic feature of this genus. The cross-section of the annuli as well as of tube between the annuli is circular.

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Stratigraphic range. Lower Jurassic, upper Hettangian to uppermost Pliensbachian; ? lowermost Toarcian.

Discussion. Jäger (1996) provided an overview over the type-species and a list of similarly shaped species, which include *A. strangulata* (Terquem, 1855), *A. nodifera* (Terquem & Piette, 1865), *A. mundula* (Dumortier, 1869), and *quenstedti* (O. Fraas); the latter is a manuscript name without stating a year, but figured by Quenstedt (1856 in Quenstedt, 1856–1858) from the "Turritellenplatte" of the Schurwald (a forest eastnortheast of Esslingen,

southwest Germany). Jäger (1996) remarked that this group is restricted to the Early Jurassic timespan reaching from late Hettangian to early Toarcian and needs a new genus name, which is introduced here. Tubes of the genus *Annuloserpula* occur in France, England, Wales, and Germany (for details, see below), and the present article proves its occurrence also in Morocco.

The similarly shaped Callovian – early Oxfordian genus *Genicularia* Quenstedt, 1856 in Quenstedt, 1856–1858 differs from *Annuloserpula* by its pentagonal cross-section.

In the Oxfordian – Kimmeridgian sponge/microbe reefs of southern Germany and adjacent countries, "*Serpula*" *cingulata* (Münster, 1831 in Goldfuss, 1826–1844) is often found attached to siliceous sponges. Also this species bears numerous conspicuous annular rings, just like the Early Jurassic *Annuloserpula*. However, "*Serpula*" *cingulata* differs by its long and irregularly curved or serpentine attached tube portion and its only short free tube portion. Moreover, both taxa are separated in geological time by more than the entire Middle Jurassic and occur in rather different palaeoenvironments. Therefore, we prefer not to assign "*Serpula*" *cingulata* to the genus *Annuloserpula*. Regenhardt (1961, p. 36) assigned this species to the genus *Josephella* and Ziegler (2006, p. 54) to *Genicularia* but also these suggestions are not convincing.

Vinn et al. (2008a) studied the microstructure of structurally well-preserved tube fragments of *A. etalensis* from the late Pliensbachian of eastern Germany. He found out that it is "purely aragonitic" and shows an "irregularly oriented prismatic structure", whereas a possibly recrystallized fragment of the same species from the late Sinemurian of southwest Germany shows a "homogeneous angular crystalline structure".

***Annuloserpula etalensis* (Piette, 1856)**

Fig. 5 D, D1-D2

1856 *Ancyloceras? etalensis* Piette. – Piette, p. 201, pl. 10, fig. 24.

1857 *Serpula Branoviensis* nov. sp. – Dumortier, pp. 15–16, pl. 7, fig. 4–8.

1858 *Serpula Etalensis* Piette sp. – Andler, p. 643.

1862 *Serpula Etalensis* – Terquem et Piette, pp. 379, 382.

1865 *Serpula etalensis* Piette, sp. – Terquem et Piette, p. 117, pl. 14, figs 6–9.

1867 *Serpula strangulata*, Terq. – Moore, pp. 473, 503, 532, 539, 559, pl. 16, fig. 32.

1867 *Serpula Etalensis* (Piette, spec.) – Dumortier, pp. 230–231, pl. 49, fig. 21, pl. 50, figs 3–4.

1869 *Serpula Etalensis* (Piette sp.) – Dumortier, pp. 162, 334–336, pl. 43, figs 8–12.

1870 *Serpula etalensis*, Piette. – Tate, p. 399.

1877 Beesley [article not available]

1878 *Ditrypa etalensis*, Dum. [sic!] – Beesley, p. 184.

1889 *Ditrypa etalensis* – Thompson, p. 258.

1889 *Ditrypa etalensis*, Piette. – Wilson & Crick, p. 342.

1925 *Serpula etalensis* Piette. – Dubar, p. 273.

1932 *Serpula* cfr. *etalensis* (Piette) Dum. sp. – Krumbeck, pp. 69, 70, 106, 116.

1935 *Serpula strangulata* Terqu. – Kuhn, p. 16.

1948 *Serpula branoviensis* Dum. – Kuhn, p. 101.

1995 Problematicum. – Hegele, p. 225, fig. top right.

1996 "*Serpula*" *etalensis* (Piette, 1856). – Jäger, pp. 38–40, 2 figs.

2008a '*Serpula*' *etalensis* (Piette, 1856) – Vinn et al., pp. 417–421, fig. 1A–G.

2014 *Serpula etalensis* (Piette, 1856). – Keupp et al., p. 243, fig. 2.

2015 *Serpula etalensis*. – Keupp & Schobert, p. 23, fig. 3.

Material. A single tube fragment from Zekkara, Morocco. This is the first known specimen of this species from outside Europe.

Stratigraphic Range. Lower Sinemurian – boundary between Pliensbachian to Toarcian; ? lowermost Toarcian.

Description. The tube fragment is very slightly curved, 8.6 mm long and measures 2.1 x 3.2 mm at the thinner end and 2.9 x 3.5 mm at the thicker end. The fragment possesses seven distinct transverse rings, with indistinct transversal striations between these rings. The size and exterior features match the description of Terquem & Piette (1865) who mentioned that the diameter of the tube attains between 2 and 4 mm. The lumen is circular.

Discussion. Originally, *Annuloserpula etalensis* was described as an ammonite *Ancyloceras*? *etalensis* by Piette (1856), found in the middle Lias at Étalle ("Étales"), Rimogne (both Département Ardennes), and Boust (Dépt. Moselle). Parsch (1956) listed *Annuloserpula*

etalensis with a question mark in his synonymy list of "*Serpula (Cycloserpula) cingulata* Münster in Goldfuss, 1831, a species which is common in the Oxfordian sponge/microbe reefs in southern Germany, but this is unlikely, because "*S. cingulata* stays smaller in tube diameter, is attached for most of its length, lived in a different environment and lived at a much younger geological time. Vinn et al. (2008a) revised this species and showed that it is a serpulid tube-worm because it is characterized by IOP (irregular oriented prismatic) microstructure.

Occurrences in France. Lower and upper Sinemurian, "*Ammonites bisulcatus*", "*Belemnites brevis*" and "*Belemnites acutus*" zones, Étalle ("Étalés"), Rimogne, Laval-Morency, Chilly (all Dépt. Ardennes) and Boust (Dépt. Moselle) (Piette, 1856; Terquem & Piette, 1862, 1865).

Upper Sinemurian, "*Ammonites oxynotus*" zone, Nolay, Sainte-Hélène, and Drevain, rare (Dumortier, 1867).

Lower Pliensbachian, "*Polymorphites jamesoni*" = *Uptonia jamesoni* zone, Saint-Sauveur (Dépt. Haute-Garonne), rare (Dubar, 1925).

Presumably upper Pliensbachian, lower part of "*Belemnites clavatus*" zone, Nolay and Lournand, rare (Dumortier, 1869).

Upper Pliensbachian or/and lower Toarcian, upper part of "*Belemnites clavatus*" zone, important fossil in the Charollais and Brionnais, very common around Semur and Saint-Christophe (both Dépt. Saône-et-Loire), Saint-Julien, Saint-Bonnet, Nolay, Sarry, Briant, Saint-Christophe, and Ligny (Dumortier, 1869).

Occurrences in Germany. Upper Hettangian, *Schotheimia angulata* zone, foreland of the Swabian Alb, southwestern Germany (Andler, 1858, p. 643).

Upper Sinemurian "Beta-Kalkbank", a small pit at the lowest point of the B27 motorway between the towns Hechingen and Bisingen, c. 60 km southwest of Stuttgart, southwestern Germany (Jäger, 1996; Johann Klaschka informed M.J. about this fossiliferous locality and the occurrence of *A. etalensis*).

Upper Sinemurian, *Oxynotoceras oxynotum* zone with *Bifericeras bifer*, Röckingen, southern Germany (Krumbeck, 1932).

Upper Pliensbachian, Barth 5/64 borehole TUG-1284 near Stralsund, northeastern Germany, (Vinn et al., 2008).

Upper Pliensbachian, motorway junction at Kirchheim/Teck (Hegele, 1995; Jäger, 1996).

Upper Pliensbachian, *Pleuroceras apyrenum* subzone, claypit at Buttenheim, southern Germany (Keupp et al., 2014; Keupp & Schobert, 2015).

Lower Toarcian (questionable, maybe rather uppermost Pliensbachian?), Franconia, southern Germany (Kuhn, 1948).

Occurrences in England and Wales. Upper Hettangian to lower Sinemurian, "*Ammonites angulatus*" and "*A. bucklandi*" zones, Stouts Hill (Gloucestershire), Camerton, Keynsham, and Munger Road quarry near Paulton (all Bath and North East Somerset), Bridgend and Southerndown (both south Wales) (Moore, 1867; all mis-determined as "*Serpula strangulata*, Terq.").

Lower Sinemurian, Aston Magna (Gloucestershire) (Tate, 1870).

Upper Sinemurian, "*Armatus* zone", Kings Sutton (Northamptonshire) and "Lias", Fenny Compton (Warwickshire) (Beesley, 1877; article not available, but mentioned by Beesley (1878) in a footnote).

Lower Pliensbachian, "*Capricornus* zone" = *Prodactylioceras davoei* zone, and upper Pliensbachian, *Amaltheus margaritatus* zone "*Margaritatus* Zone"), Chipping Norton Tunnel (Oxfordshire) (Beesley, 1878).

Boundary between uppermost Pliensbachian and lowermost Toarcian, "Transition Bed", which is a condensed layer at the of the Middle Lias, Northamptonshire (Thompson, 1889).

Upper Pliensbachian marlstones including the "Transition Bed" to the lowermost Toarcian, Tilton (Leicestershire) (Wilson & Crick, 1889).

Further occurrences of this species are listed in the BGS Palaeosaurus net pages: as *Ditrupa etalensis* Piette, Pliensbachian to Toarcian, Lightpill, Stroud, Gloucester; as *D. etalensis* Piette, Pliensbachian to Toarcian, Adderbury (Oxfordshire); as *Ditrupta* [sic!] *etalense* (Piette), Hettangian to Pliensbachian, Munger, Radstock (Somerset); as *Ditrupa etalense* (Piette), Hettangian to Pliensbachian, Aston Magna (Gloucestershire).

Occurrence in Morocco. Upper Pliensbachian and lower Toarcian, Zekkara (this article).

Other remains of serpulids or possible serpulids too badly preserved for safe determination

Remarks. Seven *Nogrobs* spirals are encrusted by very badly preserved remains of irregularly curved elongated objects. They differ from the small brown tube fillings described below by their larger diameter and their grey colour. Due to their badly compressed and corroded preservation, in five of the seven *Nogrobs* spirals it is even questionable if the encrusting objects are serpulid tubes at all. The encrusters of the other two *Nogrobs* spirals are probably tube fragments of serpulids, but their genus is uncertain.

One *Nogrobs* spiral is encrusted by two tubes, one of which is curved in one direction but does not form a tight spiral, and bears two keels located at its upper left and upper right edges. It may be interpreted as an aberrant (pathologic?) non-spiral tube of *Nogrobs* (*Tetralysis*) *zekkarensis*. If this interpretation is true, this would be the third *Nogrobs* spiral to which a smaller tube of the same species is attached.

Another tube forms a loop, and its upper side is broken off, except for a very short portion where a fragment of a single slightly undulating median keel is preserved. Due to its keel, this tube may belong to the genus *Propomatoceros* Ware, 1975.

Small brown tube fillings: *Josephella* Caullery & Mesnil, 1896?, or other polychaetes, or ichnofossils?

Figs 3B, 3E1, 3G1, 3J–J1, 4A1, 4C, 4D1, 4G, 4K, 4K2, 4L–L2, 5A–A3, 5B–B2, 5C–C2

Material. Many tube fillings attached to 31 spiral tubes of *Nogrobs* (*Tetralysis*) *zekkarensis*.

Description. The original tube wall is not preserved. Therefore it remains unknown, whether or not the tube's exterior surface originally bore any ornamentation. Only the dark brown filling of the tube's lumen is preserved. Its mineralogy was not studied, but the presumed original pyrite or marcasite later oxidized to limonite or other iron oxides/hydroxides. Generally, the diameter of these tube fillings is very small and increases only slowly, but varies considerably between specimens, pointing to several different kinds of organisms which originally built these tubes. Thirty-one per cent of the *N. (T.) zekkarensis* tubes are encrusted by these small brown tube fillings, varying between a single short fragment and a dense encrustation by many roughly parallel arranged tube fillings covering two thirds of the serpulid's upper side (Fig. 4L). Except for this *Nogrobs* specimen with parallel arranged tube

fillings, the tube fillings attached to all other *Nogrobs* specimens do not show any thigmotactic behaviour. Instead, they are irregularly curved or irregularly serpentine. Most but not all tube fillings have a smooth surface, indicating a smooth interior surface of the original tube. Most tube fillings encrust the *Nogrobs* spiral's upper surface or run along or across its periphery, but some are found on the spiral's underside.

In the studied material from Zekkara, the small brown tube fillings are found only on tubes of *N. (T.) zekkarensis*. Due to the low number of specimens of other invertebrate fossils, it cannot be decided whether or not these tube fillings are obligatorily restricted to *N. (T.) zekkarensis*.

Discussion. A few short straight or curved small brown tube fillings are located in the center of the spiral's underside and anteriorly continue into the first coil of the well-preserved *N. (T.) zekkarensis* spiral (Fig. 4D1, 4L1); they belong to the same individual.

If the small brown tube fillings match by diameter, but are not located close to the center of the spiral's underside or/and are not very long, then it may be possible that they represent the initial tube portions of other individuals of *N. (T.) zekkarensis* settling on a spiral of the same species, as is proven in the two specimens in which one small spiral is attached to a large spiral (Fig. 3G–G3). However, only few of the small brown tube fillings seem to be favourable candidates for such an interpretation, because they seem to be too thick or too long (e.g., Figs 4K, 5A, 5B).

Instead, it is assumed that the vast majority of the small brown tube fillings, especially those whose diameter is larger than the lumen at the onset of the spiral of *N. (T.) zekkarensis*, are the remains of unidentified invertebrates other than *Nogrobs (Tetralysis) zekkarensis*.

Although the tube fillings may resemble the tubes of the sabellid genus *Glomerula* Nielsen, 1931 by their small and only slowly increasing diameter and lack of any ornamentation, and although also in *Glomerula* the characteristic thigmotactic behaviour is not yet developed in juvenile tubes, the tube fillings do not belong to the genus *Glomerula*, because the vast majority of them display no convincing thigmotactic behaviour: no meanders with narrow hairpin-curves, no spirals, no irregular chaotic knots. Even the roughly parallel arrangement of several tube fillings attached to the specimen shown in Fig. 4L–L2 is not considered a convincing proof for the presence of the genus *Glomerula* at Zekkara.

Instead, the tube fillings may represent either a different serpulid genus with an aragonitic or very thin-walled and therefore not preserved tube wall, or a different polychaete family (maybe a sabellid other than *Glomerula*).

Among extant serpulids, similar small-sized, non-spiral, not ornamented or only poorly ornamented tubes occur in several genera. In palaeontological literature, such small tubes are mostly assigned to one of these extant genera, *Josephella* Caullery & Mesnil, 1896, although the fossil tubes usually do not allow proper differentiation from other small-sized serpulid genera. The fossil species *Josephella subanulata* Regenhardt, 1961 is known from the late Maastrichtian (Regenhardt, 1961) and from the early Cenomanian (Lommerzheim, 1979), whereas the affiliation of geologically still older *Josephella* tubes in older literature is even more uncertain. Also in case of the Early Jurassic tube fillings from Zekkara, the genus name *Josephella* should be used only with a question mark.

Moreover, it is well possible that a few of the "tube fillings" from Zekkara, especially those with a rough surface, are no true tube fillings at all, but ichnofossils: mineralized burrows of unknown organisms grazing microorganisms from the surface of *N. zekkarensis* tubes.

In practice it is often hardly possible to decide in detail, which tube filling specimen matches which of the above mentioned different interpretation best.

6. Conclusions

The tube-dwelling serpulid polychaete *Nogrobs* (*Tetralysis*) *zekkarensis* sp. nov., found in the uppermost Pliensbachian (*Pleuroceras spinatum* Zone) and lowermost Toarcian (*Dactylioceras tenuicostatum* Zone) at the locality Zekkara in the Oujda Mountains in northeastern Morocco is introduced, described and discussed. Tubes of this serpulid species were collected from marls and marly limestones that were deposited on a shallow siliciclastic ramp on the southwestern margin of the Tethys Ocean. The tubes possess a distinctive spiral morphology and a two-layered SPHP and SIOP microstructure, of which the SIOP microstructure was hitherto not known in the genus *Nogrobs*.

The obligatorily tightly spirally coiled tubes of this new *Nogrobs* species, together with the roughly equally old but non-spiral tubes of *Nogrobs* (*Tetraserpula*) *varicosa* (Behrendsen, 1891) from the upper Pliensbachian of Argentina, represent the two geologically oldest representatives of the species-rich and geologically long-living fossil genus *Nogrobs* de Montfort, 1808, which is characterized by the rounded quadratic cross-section of the tube, although several extant deep-water serpulids belonging to several different genera also possess very similar quadratic tubes.

Kupriyanova & Ippolitov (2015) provided a very comprehensive description of the extant deep-water serpulids possessing a more or less *Nogrobs*-like tube, including detailed morphologies and microstructures of the tubes and introduction of a new extant genus and several new extant species and new studies and images of the microstructures of several fossil *Nogrobs* tubes. Their studies proved the previous systematics of *Nogrobs*-like extant and fossil tubes, and especially the erroneous trial by Jäger (2005) to consider the extant genus *Spirodiscus* a junior synonym of the fossil genus *Nogrobs* de Montfort, 1808, to be too simple. Although the tubes of some of the extant species look indeed very similar to the tubes of some fossil *Nogrobs* species, they differ mainly by the tubes' microstructures. We agree with Kupriyanova & Ippolitov (2015) that very probably they are not closely related to any of the recent serpulid genera, and we agree that the genus *Nogrobs* should be restricted to fossil specimens. This decision is supported by a still more than 60 million years long gap in the fossil record between the geologically youngest fossil *Nogrobs* tubes found in the Maastrichtian or Danian and similarly-shaped tubes of Recent taxa. Kupriyanova & Ippolitov (2015) arranged the fossil *Nogrobs* species studied by them in three groups.

Moreover, the study of *Nogrobs (Tetralysis) zekkarensis* sp. nov. triggered a revision of a group of obligatorily spiral fossil species among the species-rich genus *Nogrobs* which Jäger (2005) originally had considered occasional iterative offshoots from a continuing non-spiral or only optionally spiral *Nogrobs* main line. But soon M. J. detected more and more obligatorily spiral *Nogrobs* species in the outcrops, in collections and in palaeontological literature, which made him doubt his iterative offshoot hypothesis. Instead, probably the obligatorily tightly coiled spiral *Nogrobs* species form a long-living continuous lineage, the subgenus *Nogrobs (Tetralysis)*.

All these relatively new data, together with an increasing number of microstructure data of fossil serpulid tubes, led to a revision of the fossil genus *Nogrobs*, which we subdivided into six subgenera, according to the following distinguishing features: (1) non-spiral, optionally spiral, obligatorily spiral or wide open spiral, (2) peristomes occurring occasionally and in normal size or occurring very frequently and in large, bulbous size, (3) number of tube wall layers, and (4) types of tube microstructure according to the scheme introduced by Vinn and co-workers.

Although no new subgenus name had to be introduced, most subgenera are now used in a more or less different extent and meaning than intended by their original authors. In three relatively species-poor of the six subgenera, *N. (Tetralysis)*, *N. (Tubulostium)* and *N.*

(*Tetraditrupa*), we mention all hitherto identified species, whereas in the other three relatively species-rich subgenera, *N. (Nogrobs)*, *N. (Tetraserpula)* and *N. (Glandifera)* this is not done, because in some nominal species a too low amount of available specimens, insufficient data or uncertainties about possible synonymies still hamper their safe assigning to a certain subgenus.

The two species-rich subgenera *N. (Nogrobs)* and *N. (Tetraserpula)* together match the combined "Group 1" and "Group 2" of Kupriyanova & Ippolitov (2015) relatively well, although in detail the species contents of each of both subgenera does not quite match the species contents of each of both "Groups". Most of the species of these two subgenera respectively "Groups" have a single-layered with SP or, when weathered, HG microstructure and probably are closely related to each other.

N. (Tetralysis) includes all the obligatorily spiral species sensu Jäger (2005) and also several additional species. Unfortunately, *N. (T.) zekkarensis* sp. nov. is the only species of its subgenus of which the microstructure is known; it is two-layered with microstructures. The SIOP microstructure is unique among all hitherto detected microstructures in the entire genus *Nogrobs*. It would be desirable to know also the microstructure of other species of *N. (Tetralysis)*, especially of the type-species *N. (T.) quadrangularis* (Lamarck, 1818), in order to decide if the combination SPHP/SIOP is characteristic for this subgenus, or if the species *N. (T.) zekkarensis* should be shifted to a new separate subgenus. Surprisingly, already the two geologically oldest *Nogrobs* species, the non-spiral *N. (Tetraserpula) varicosa* Behrendsen, 1891 and the obligatorily spiral *N. (Tetralysis) zekkarensis* sp. nov., both from the late Pliensbachian, look very different from each other. The separation between the two subgenera must be happened even earlier, but is not confirmed by fossils.

N. (Tubulostium) includes only its type-species *N. (T.) discoideum* Stoliczka, 1868 and is identical to "Group 3". It is unique among the entire genus *Nogrobs* by possessing a three-layered tube wall consisting of SP, HG and SP microstructure, whereas by its spiral exterior tube morphology it perfectly matches *N. (Tetralysis)* and the spiral tubes among *N. (Nogrobs)*. It may be speculated whether or not the intercalated HG layer could have been caused by local diagenetically alteration of the tube wall's interior. If so, then *N. (T.) discoideum* could easily be shifted to either the subgenus *N. (Nogrobs)* or to *N. (Tetralysis)*, but only if *N. (T.) zekkarensis* should get its own subgenus due to its unusual microstructure.

N. (Glandifera), originally introduced by Regenhardt, 1961 as a subgenus of *Genicularia* Quenstedt, 1858, is considered a subgenus of *Nogrobs*.

Similarly, also *N. (Tetraditrupa)*, originally introduced by Regenhardt, 1961 as a subgenus of *Ditrupa* Berkeley, 1835, is considered a subgenus of *Nogrobs*. A new species name, *Nogrobs (Tetraditrupa) folkestonensis* nom. nov., is introduced in order to replace its original name *Serpula rustica*, a junior homonym preoccupied by the same name of a different species. Although this species stands a little aside by its Cenomanian age and its hook-shaped tube with possibly diagenetically altered two-layered SPHP/HG microstructure from the Maastrichtian type-species *N. (T.) canteriata* (von Hagenow, 1840) with its loosely coiled, wide open spiral with unilayered SP microstructure, it is nevertheless considered an early species of the same subgenus.

Our scheme of six fossil subgenera combines both: the results of long experience with exterior tube morphology and new data of microstructure. Unfortunately, in a few of the fossil *Nogrobs* species, similarities or differences in number of tube layers and types microstructure do not match similarities or differences in tube shape and exterior morphology. For example, although the tubes of *Nogrobs (Tetralysis)*, *Nogrobs (Tubulostium)* and the "classical" rotulariid genus *Tectorotularia* look similar to each other exteriorly, these taxa are not closely related to each other, due to their rather different types of microstructure. A few uncertainties still remain, and future research may possibly lead to a few modifications of our scheme. Nevertheless, we believe that our scheme is a considerable step forward.

The rotulariid morphogenetic countdown program sensu Seilacher et al. (2008), originally described in some larger-sized spiral species of the genus *Rotularia* and similarly shaped genera, also matches most but not all of the smaller-sized tightly spirally coiled specimens of the genus *Nogrobs*. These *Nogrobs* spirals can well be added to the informal morphological group of "rotulariids", most of their genera bearing "...rotul..." in their names. However, rotulariids are definitively not a phylogenetical taxon in zoological nomenclature. In *N. (Tetralysis) zekkarensis*, 18 per cent of the spirals did not follow the rotulariid morphogenetic countdown program, but instead acted just like many other serpulids. Such a high percentage of deviants from the rotulariid program is known in only very few taxa of other rotulariids. In case of *N. (T.) zekkarensis*, its frequent deviation may be explained by its high geological age, which is roughly equal to the age of the oldest other rotulariids. Perhaps *N. (T.) zekkarensis* marks the still hesitant transition from the usual ontogeny displayed by most serpulids to the specialized rotulariid morphogenetic countdown program.

Moreover, the new genus name *Annuloserpula* is introduced for a group of established Early Jurassic serpulid species possessing plenty of annular peristomes. *A. etalensis*, the most common species of this genus, was hitherto known from France, England and Germany. A single characteristic tube fragment from Zekkara is the only known specimen of the genus *Annuloserpula* from outside of Europe.

Thirty-one per cent of the *N. (T.) zekkarensis* tubes are encrusted by the small brown tube fillings which are the remains of unidentified other invertebrates. It can only be speculated whether these may be remains of juvenile tubes of the same species, of the small-sized serpulid genus *Josephella*, of other tube-dwelling polychaetes, or of ichnofossils. Due to differences in diameter, presumably several kinds of invertebrates were involved.

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Captions

Table 1 Measurements and direction of coiling of 98 studied specimens (100 tubes) of *Nogrobs (Tetralysis) zekkarensis* sp. nov.

Fig. 1 Geographical and geological setting.

Fig. 2 Geological section at Zekkara (NE Morocco) encompassing the uppermost part of the Beni Hammad Formation (uppermost Pliensbachian) and the lowermost part of the Beni Amyir Formation (lowermost Toarcian), with two stratigraphic intervals where *Nogrobs (Tetralysis) zekkarensis* was found: above bed 23 at Zekkara B and above bed 18 at Zekkara A. Each white or grey scalebar equals 1 meter.

Fig. 3 *Nogrobs (Tetralysis) zekkarensis* sp. nov., Zekkara, Morocco. A–G, I–J. Upper sides (umbilical views). A1–G1, I1–J1. Undersides (apical views). A2–G2, H, I2–J2. Lateral views with frontal views to apertures. G3. Detail of aperture. A, B, E, G (large spiral) are dextrally coiled, C, D, F, G (small spiral), H, I, J are sinistrally coiled. B. A small tube (*Josephella* sp.?) is attached to a *Nogrobs* tube. G–G2. A small *Nogrobs* tube is attached to a large *Nogrobs* tube.

Fig. 4 *Nogrobs (Tetralysis) zekkarensis* sp. nov., Zekkara, Morocco. A–L. Upper sides (umbilical views). A1–L1. Undersides (apical views). A2–L2. Lateral views with frontal views to apertures. A–D, G–J, L are sinistrally coiled; E, F, K are dextrally coiled. K, L. One respectively many small brown tube fillings (*Josephella* sp.?) encrust the *Nogrobs* tubes.

Fig. 5 A–F. Several invertebrate fossils from Zekkara, Morocco. A–C. *Nogrobs (Tetralysis) zekkarensis* sp. nov. A1–C1. Undersides (apical views). A2–C2. Lateral views with frontal views to apertures. C3. Detail showing frontal view to aperture. A–C are sinistrally coiled. A–C, A1, A3, C1, C2. One respectively several small brown tube fillings (*Josephella* sp.?) encrust the *Nogrobs* tubes. A–C. Upper sides (umbilical views). D. *Annuloserpula etalensis* (Piette, 1856). D. Lateral view, D1–D2. Cross sections. E–E1 Gastropoda indet., lithified sediment (steinkern) fills the lumen of the dissolved shell), lateral views. F. Cidaroid echinoid indet., an incomplete interambulacral plate.

Fig. 6 *Nogrobs (Tetralysis) zekkarensis* sp. nov., Zekkara, Morocco. Microstructure in longitudinal sections of specimens shown in Fig. 3I and 3C. A, B. Overviews. A1, A2, A3, B1, B2, B3. Details showing inner and outer tube layers. The outer tube layer consists of large spherulitic crystals. The inner tube layer is poorly preserved and consists of irregularly oriented crystals.

Fig. 7 *Nogrobs (Tetralysis) zekkarensis* sp. nov., Zekkara, Morocco. Microstructure in transverse sections of specimens shown in Fig. 3I and 3C. A, B1. Overviews. A1, B. Details showing inner and outer tube layers. The outer tube layer consists of large spherulitic crystals which in transverse sections appear more or less circular. The inner tube layer consists of poorly preserved irregularly oriented crystals.

Fig. 8 *Nogrobs (Tetralysis) zekkarensis* sp. nov., Zekkara, Morocco. A, A1. Microstructure in longitudinal section, and A2, A3, A4 in transverse section, of specimen shown in Fig. 3J. A, A2 Overviews. A1, A3, A4. Details showing inner and outer tube layers. The outer tube layer consists of large spherulitic crystals which in transverse sections appear more or less circular. The inner tube layer consists of poorly preserved irregularly oriented crystals.

Fig. 9 *Nogrobs (Tetralysis) zekkarensis* sp. nov., Zekkara, Morocco. A, A1–A4. Microstructure in longitudinal section, and A5, A6 in transverse section, of specimens shown in Fig. 3F. A, A5 Overviews. A1–A4, A6. Details showing inner and outer tube layers. The outer tube layer consists of large spherulitic crystals which in upper left of A6 are arranged in several growth lamellae. The inner tube layer consists of poorly preserved irregularly oriented crystals.

Fig. 10 *Nogrobs (Tetralysis) zekkarensis* sp. nov., Zekkara, Morocco. Microstructure in transverse section of specimen shown in Fig. 3E. A. Overview. A1, A2. Details showing inner and outer tube layers; both layers are poorly preserved. The outer layer is recrystallized during diagenesis; the growth lamellae are almost invisible. It consists of large spherulitic crystals which in transverse sections appear more or less circular. The inner layer consists of large irregularly oriented crystals, which are dissolved and shorter toward the outer layer.

Fig. 11 *Nogrobs (Tetralysis) zekkarensis* sp. nov., Zekkara, Morocco. Microstructure in transverse sections of specimens shown in Figs 3J, 4B, 4C, 4F. A–D. Overviews. A1–D1. Details of inner and outer layers, spherulitic crystals are poorly preserved. D2. Detail of outer layer, crystals are irregularly oriented, growth lamellae are not preserved, inner layer consists of large crystals.