

Written in stone: history of serpulid polychaetes through time

ALEXEI P. IPPOLITOV^{1,*}, OLEV VINN², ELENA K. KUPRIYANOVA³ (<http://zoobank.org/urn:lsid:zoobank.org:author:D0BE23CD-F6C3-4FE8-AB09-EBD4B9A55D0B>) AND MANFRED JÄGER⁴

¹ Geological Institute of Russian Academy of Sciences, 7 Pyzhevski Lane, Moscow, Russia; (ippolitov.ap@gmail.com)

² Department of Geology, University of Tartu, Ravila 14A, 50411, Tartu, Estonia; (olev.vinn@ut.ee)

³ Australian Museum Research Institute, 6 College Street, Sydney, NSW 2010, Australia; (elena.kupriyanova@austmus.gov.au)

⁴ Lindenstraße 53, 72348 Rosenfeld, Germany; (langstein.jaeger@web.de)

* to whom correspondence and requests for reprints should be addressed. Email: ippolitov.ap@gmail.com

Abstract

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Although the fossil record of annelids in general is poor, calcareous tube-building Serpulidae are a notable exception. The “stumbling block” of understanding the serpulid fossil record is obtaining reliable taxonomic interpretations of fossil tubes based on morphology. Luckily, serpulid tubes demonstrate high variety of ultrastructures and nonuniform mineralogical composition, which can be used as new tools for decrypting the fossil record. Ancient Late Ediacaran (580–541 Ma) and Paleozoic (541–252 Ma) rocks contain diverse tubicolous fossils that have often been erroneously interpreted as annelids, and serpulids, in particular. Palaeozoic to Middle Jurassic coiled spirorbiform tubes, often referred to as *Spirorbis*, had been shown to be microconchids, a group of probable lophophorate affinity. The most ancient records of unequivocal serpulids date back to the Middle Triassic (~244 Ma) of the Mesozoic, and from the Earliest Jurassic (~200 Ma) fossil serpulids become common. From the latest Jurassic (~146 Ma) serpulids colonised hydrocarbon seep environments and possibly also penetrated the deep sea. Concerted efforts of paleontologists and zoologists are needed for further understanding of serpulid evolutionary history. The serpulid fossil record can become a valuable instrument for calibration of “molecular clocks” in polychaetes, which would allow dating not only divergence events in serpulids, but also in annelid groups that lack a representative fossil record.

Keywords

Annelida, Polychaeta, Serpulidae, biomineralisation, fossil record, tube ultrastructure, mineralogy

Introduction

Polychaetes are mostly soft-bodied animals with a very poor paleontological record. Imprints of soft-bodied animals are rare and only known from a limited number of localities with exceptional preservation (so called “Lagerstätten”). The most important among them are the Cambrian Burgess Shale (505 Ma; Conway Morris, 1979; Eibye-Jacobsen, 2004), the Devonian Hunsrück Slate (405 Ma; Briggs and Bartels, 2010), the Carboniferous Mazon Creek fauna (310 Ma; Fitzhugh et al., 1997), and the Cretaceous Hakel polychaete fauna (~95 Ma; Bracchi and Alessandrello, 2005). The oldest known annelid fossils are polychaetes from the Cambrian (Vinther et al., 2011) and the oldest known fossil polychaete is *Phragmochaeta canicularis* Conway Morris et Peel, 2008 from the Early Cambrian Sirius Passet (518 Ma) fauna.

In the paleontological record, polychaete fossils are dominated by biomineralised tubes and, sometimes, fossilised jaws, known

as scolecodonts (e.g. Hints and Eriksson, 2007). Although many polychaetes build muddy or mucous (Sabellidae), chitinous (e.g. Chaetopteridae, Siboglinidae), agglutinated (e.g. Pectinariidae, Sabellariidae) or calcareous tubes, only tubes made of calcium carbonate have good chances to be preserved. Of the three polychaete families known to build calcareous tubes (Serpulidae, Sabellidae, and Cirratulidae), serpulids are obligatory calcareous tube builders, whereas in cirratulids and sabellids calcareous tubes are restricted to a single genus in each family (Perkins, 1991; ten Hove and van den Hurk, 1993; Fischer et al., 1989; 2000; Vinn et al., 2008a; Vinn, 2009). Not surprisingly, serpulids have the best fossil record among all annelids, being represented mainly by tubes, and, to a lesser degree, by calcified opercula.

Serpulids are common on hard substrata in all marine habitats at all depths, being an important element of the encrusting biota in Recent seas. They are important fouling organisms and can also form reefs. Fossil serpulid tubes were first described over 300 years ago, in “Oryctografia Norica” by

the German doctor Johann Jakob Baier (1708) as “*Tubus vermicularis fossilis*”. Despite this, geologists and paleontologists traditionally pay little attention to the group, partly because of the perceived opinion of its small potential value in stratigraphy and reconstructing paleoenvironments. There are several large reviews of serpulid faunas of different geological periods (e.g. Rovereto, 1899; 1904; Brünnich Nielsen, 1931; Parsch, 1956; Schmidt, 1955; Lommerzheim, 1979; Jäger, 1983; 1993; 2005), but only few papers (e.g. Jäger 1983, 1993, 2005) discuss evolution and geological history of fossil serpulids. The only comprehensive overview of the entire serpulid fossil record in the Phanerozoic by Götz (1931), and a short summary by Regenhardt (1964) are now clearly outdated, and the most recent review (Vinn and Mutvei, 2009) focuses mainly on false serpulids from the Paleozoic.

The aims of the present paper are: 1) to outline the serpulid fossil record, including discussion of some serpulid-like tubicolous fossils; 2) to discuss the current state of knowledge of serpulid paleontology and 3) to indicate directions of future research in the evolutionary history of serpulids.

1. Current state of serpulid systematics and phylogeny

According to the most recent review of serpulid taxonomy (ten Hove and Kupriyanova, 2009), the family comprises 46 genera with about 350 extant species. This, however, does not include about 140 species from the nominal subfamily Spirorbinae, arranged in 24 genera (Ippolitov and Rhzavsky, 2014). Serpulidae Rafinesque, 1815 was not subdivided into subfamilies until Chamberlin (1919) established the subfamily Spirorbinae for small-sized serpulids having tubes coiled into flat spirals. Later Rioja (1923) placed hypothetically primitive species with a pinnulated operculum-bearing radiole or without operculum into the subfamily Filograninae. Pillai (1970) elevated Spirorbinae to the family Spirorbidae, which was widely accepted until phylogenetic data, both based on morphology and molecular analyses (e.g. Kupriyanova, 2003; Kupriyanova et al., 2006; Lehrke et al., 2007) indicated that spirorbins are nested inside Serpulidae. Thus, the family status of Spirorbinae is not justified because recognition of Spirorbidae would make Serpulidae *sensu stricto* a paraphyletic group. All phylogenetic molecular analyses indicate that neither traditional Serpulinae, nor Filograninae are monophyletic and that spirorbins are close to “filogranin” taxa (Kupriyanova et al., 2006; 2009; Lehrke et al., 2007; Kupriyanova and Nishi, 2010), with the result that the traditional subfamilies were abandoned. The analyses inferred two major clades (tentatively termed A and B) within Serpulidae (fig. 1). Clade A comprises two subclades: clade AI, the “*Serpula*-group” (with the genera *Serpula*, *Crucigera*, *Hydroides*), and clade AII, the “*Spirobranchus*-group” (with, amongst others, the genera *Spirobranchus*, *Ficopomatus* and *Ditrupa*). Clade B included clade BII (the monophyletic subfamily Spirorbinae) as sister group to clade BI, the “*Protula*-group” (with amongst others the genera *Protis*, *Protula* and *Vermiliopsis*). Relationships within clade AI were further briefly studied by Kupriyanova et al. (2008). No molecular spirorbin phylogeny is currently available, but Macdonald (2003) proposed a hypothesis based on morphological data.

2. Decrypting the serpulid fossil record: where we are

2.1. The stumbling block in fossil record interpretation

The main problem of serpulid paleontological record is obtaining reliable taxonomic interpretations of fossil tubes. Starting with Rovereto (1899; 1904) for the Cenozoic and Regenhardt (1961) and all subsequent authors for the Mesozoic, attempts were made to determine fossil tubes according to the classification used for Recent species (e.g. Lommerzheim, 1979; 1981; Jäger, 1983; 1993; 2005; Radwańska, 1994a; 2004; Ippolitov, 2007a; 2007b; Jäger and Schubert, 2008; Schlögl et al., 2008; Vinn and Wilson, 2010). However, classification of extant serpulids is based on body and chaetal characters, while little attention is paid to the tube morphology. While a tube is important for protection, it is not integrated with the animal body, and thus, does not constitute a genuine exoskeleton (Regenhardt, 1964; Weedon, 1994; Seilacher et al., 2008). Adaptive evolution of tubes is relatively independent of that of the soft tissue, resulting in relatively weak correlations between tube and body characters used by zoologists for classification of Recent forms. This probably explains why polychaete tubes, unlike mollusc shells, have not become very important for taxonomy. Some Recent genera have very distinct tubes (e.g. *Janita*, *Vitreotubus*, *Neomicrorbis*, *Placostegus*, *Ditrupa*) easily recognizable in fossil state (see section 2.2). In others (e.g. *Bathypermilia*, part of *Filogranula*, *Semivermilia*, *Pseudovermilia*, *Pyrgopolon*, *Spiraserpula*), tube morphology is important for species distinction, but reliable generic attribution based on tubes alone is difficult due to high intra-generic variability. Moreover, tubes of some speciose genera often show little or no interspecific variability (*Spirobranchus*, *Serpula*, and *Hydroides*) or have a very simple tube morphology (e.g. *Apomatus/Protula*, *Hyalopomatus*), making their recognition in the fossil state problematic. Most species of the largest genus *Hydroides* comprising around 100 extant species have uniform tubes with a flattened upper surface, sometimes with two or three indistinct keels.

Such genera that are “problematic” from the paleontological point of view comprise about 55% of the Recent non-spirorbin serpulids (Table 1). In Spirorbinae the situation is even worse, as normally no Recent genera, except for a very distinct questionable spirorbin *Neomicrorbis* and the peculiar fossil genus *Bipygmaeus*, can be confidently determined by tube morphology alone. Reasonably confident determinations of fossil spirorbins are based mainly on opercula associated with tubes (Lommerzheim, 1981; Jäger, 1993; 2005). However, because preservation of opercula is uncommon, determinations by tubes inevitably remains the main means of study of fossil spirorbins.

Paleontologists are restricted in their interpretations to “easily recognisable” genera. Other fossil species are tentatively classified within known Recent genera, assigned to exclusively “fossil” genera, or conventionally treated as “*Serpula*?” (Lommerzheim, 1979; Jäger, 1993; 2005). As a result, zoologists are skeptical about most generic affinities proposed by paleontologists based on tubes. This leads to a paradoxical situation when despite diverse and abundant fossils, zoologists lack reliable paleontological data for understanding the

Table 1. Recent serpulid genera and their fossil record. The list of Recent non-spirorbin genera follows ten Hove and Kupriyanova (2009) data with modifications, the list of Recent spirorbin genera and species number is after Ippolitov and Rzhavsky (2014: Tab. 1). Dating of the most ancient finds does not reflect origin time as due to the scarcity of fossil record most taxa are probably older than indicated. The number of fossil species for each genus is approximate, as most of fossil species described as “*Serpula*” in older publications need to be revised. Absolute ages here and in the text are provided according to the official site of the International Commission of Stratigraphy www.stratigraphy.org/GSSP/index.html, accessed 10-12-2013. Designations: *genera with fossil type species; **some extant species recognised also as fossils in sub-Recent (Pliocene-Holocene) sediments; †taxa originally used in paleontological literature only (extinct genera).

Genus (including most common synonyms and subgenera)	Number of extant species	Number of fossil species	Most ancient fossil finds and their age	Tube characters allowing recognition in fossil state
SABELLIDAE				
<i>Glomerula</i> * Brünnich Nielsen, 1931 = <i>Calcisabella</i> Perkins, 1991, =† <i>Cycloserpula</i> Parsch, 1956, =† <i>Omasaria</i> Regenhardt, 1961	1	7+	Late Carboniferous (323-304 Ma; present paper) or Late Hettangian (200 Ma; Jäger, 2005)	glomerate coiling; very slow expansion; absence of basal cementing flanges
NON-SPIRORBIN SERPULIDAE				
<i>Apomatus</i> Philippi, 1844	7	-	-	not recognised
<i>Bathyditrupa</i> Kupriyanova, 1993a	1	?	?Late Pliensbachian (~185 Ma; Behrendsen, 1891);?Late Albian (~105 Ma; Jäger, 2005)	unattached tusk-shaped tubes with quadrangular cross-section. Maybe synonym of † <i>Nogrobs</i> (<i>Tetraditrupa</i>) (see Jäger, 2005) or † <i>Nogrobs</i> (<i>Tetraserpula</i>) (see Ippolitov, 2007a).
<i>Bathyvermilia</i> Zibrowius, 1973	5	1?	??Late Sinemurian (“ <i>Serpula</i> ” <i>etalensis</i> (Piette, 1856); ~194 Ma)	long free anterior part with characteristic frequent peristomes
<i>Chitinopoma</i> Levinsen, 1884	3-4	-	-	not recognised
<i>Chitinopomoides</i> Benham, 1927	1	-	-	not recognised
<i>Crucigera</i> Benedict, 1887	5	-	-	not recognised
<i>Dasynema</i> de Saint-Joseph, 1894	1	-	-	not recognised
<i>Ditrupa</i> Berkeley, 1835 =† <i>Acerrotrupa</i> Yu et Wang, 1981, =† <i>Sinoditrupa</i> Yu et Wang, 1981	2	1+	Danian (65 Ma; Jäger, 1993)	unattached tusk-shaped tubes with circular cross-section
<i>Ficopomatus</i> Southern, 1921	5	-	-	not recognised.
<i>Filograna</i> Berkeley, 1835	1	5+	Late Anisian (244 Ma; Senowbary-Daryan et al., 2007)	pseudocolonial; small-sized; individual tubes packed in branching bundles. Indistinguishable from <i>Salmacina</i>
<i>Filigranella</i> Ben-Eliahu et Dafni, 1979	1(3?)	-	-	not recognised
<i>Filigranula</i> Langerhans, 1884 ?=† <i>Flucticularia</i> Regenhardt, 1961	6	6**	late Early Toarcian (~180 Ma; Jäger, unpubl.; Ippolitov, 2007a)	sculpture; size; aperture with spines
<i>Floriprotis</i> Uchida, 1978	1	-	-	not recognised
<i>Galeolaria</i> de Lamarck, 1818	2	1	Cenomanian (100 Ma; Lommerzheim, 1979)	sculpture (massive median bicarinate keel), cross-section
<i>Hyalopomatus</i> Marenzeller, 1878	11-12	-**	-	not recognised
<i>Hydroides</i> Gunnerus, 1768	89	?**	?Middle Paleocene (~60 Ma; Lommerzheim, 1981); or Middle Miocene (~15 Ma; Schmidt, 1955)	flattened upper side, usually bordered by keels, coiling tendency
<i>Janita</i> de Saint-Joseph, 1894	1	-**	?Cenomanian (100 Ma; Lommerzheim, 1979); or ?Badenian (15 Ma; Radwańska, 1994a)	not recognised confidently

Genus (including most common synonyms and subgenera)	Number of extant species	Number of fossil species	Most ancient fossil finds and their age	Tube characters allowing recognition in fossil state
<i>Josephella</i> Caullery et Mesnil, 1896	1	2	?earliest Cenomanian (100 Ma; Lommerzheim, 1979)	size, very slow expansion
<i>Laminatubus</i> ten Hove et Zibrowius, 1986	1	-	-	not recognized
<i>Marifugia</i> Absolon et Hrabě, 1930	1	-**	Pliocene/earliest Pleistocene (2.5-3.6 Ma; Bosák et al., 2004)	the only extant species found in fossil state
<i>Metavermlia</i> Bush, 1905 subgen.: † <i>Vepreculina</i> Regenhardt, 1961	14	7+	Late Rhaetian (205 Ma; Jäger, 2005); or Late Callovian (165 Ma; Ippolitov, 2007a)	sculpture, size, growth rate
<i>Microprotula</i> Uchida, 1978	1	-	-	not recognized
<i>Neovermlia</i> Day, 1961 =† <i>Proliserpula</i> Regenhardt, 1961	6	3+**	Late Oxfordian (158 Ma; Radwańska, 2004)	size, sculpture, attachment structures morphology
<i>Nogrobs</i> * de Montfort, 1808 = <i>Spirodiscus</i> Fauvel, 1909, =† <i>Ditrupula</i> Brünnich Nielsen, 1931, ?=† <i>Glandifera</i> Regenhardt, 1961, ?=† <i>Tubulostium</i> Stoliczka, 1868; subgen.: (?)† <i>Tetraditrupa</i> Regenhardt, 1961; (?)† <i>Tetraserpula</i> Parsch, 1956 [Interrelations between all subgenera remain uncertain]	1	10+	Late Pliensbachian (~185 Ma; see Jäger, 2005) – non-spiral forms of subgenus <i>Tetraserpula</i> ; Late Toarcian (~176 Ma; Jäger, 2005) – spiral forms of <i>Nogrobs s. str.</i>	spiral coiling, quadrangular cross-section
<i>Omphalopomopsis</i> de Saint-Joseph, 1894	1	-	-	not recognised
<i>Paraprotis</i> Uchida, 1978	1(2?)	-	-	not recognised
<i>Paumotella</i> Chamberlin, 1919	1	-	-	not recognised
<i>Placostegus</i> Philippi, 1844 =† <i>Eoplacostegus</i> Regenhardt, 1961	7	7+	Late Oxfordian (158 Ma; Radwańska, 2004)	cross-section, aperture with spines, size, growth mode
<i>Pomatostegus</i> Schmarda, 1861	3	-	-	not recognised
<i>Protis</i> Ehlers, 1887	6-7	-	-	not recognised
<i>Protula</i> Risso, 1826 = <i>Membranopsis</i> Bush, 1910; subgen.: † <i>Longitubus</i> Howell, 1943	?24	3+**	Early Albian (~113 Ma; see Jäger, 2005)	medium to large-sized tubes, often growing upwards from the substrate; no sculpture
<i>Pseudochitinopoma</i> Zibrowius, 1969	2	2	Early Oxfordian (163 Ma; Ippolitov, unpubl.)	size, well-developed transverse sculpture
<i>Pseudovermlia</i> Bush, 1907	10	2?	?Cenomanian (100 Ma; Lommerzheim, 1979); or ?Burdigalian (20 Ma; Jäger and Schneider, 2009)	size, sculpture
<i>Pyrgopolon</i> * de Montfort, 1808 = <i>Sclerostyla</i> Mørch, 1863, =† <i>Falcula</i> Conrad, 1870, =† <i>Hexaserpula</i> Parsch, 1956, =† <i>Hepteris</i> Regenhardt, 1961; subgen.: † <i>Hamulus</i> Morton, 1834; † <i>Turbinia</i> Michelin, 1845 (=† <i>Pyrgopolopsis</i> Rovereto, 1904); † <i>Ornatoporta</i> Gardner, 1916; † <i>Septenaria</i> Regenhardt, 1961	3	15+	Barremian (128 Ma; Jäger, 2011)	tube size, expansion rate; growth mode; sculpture

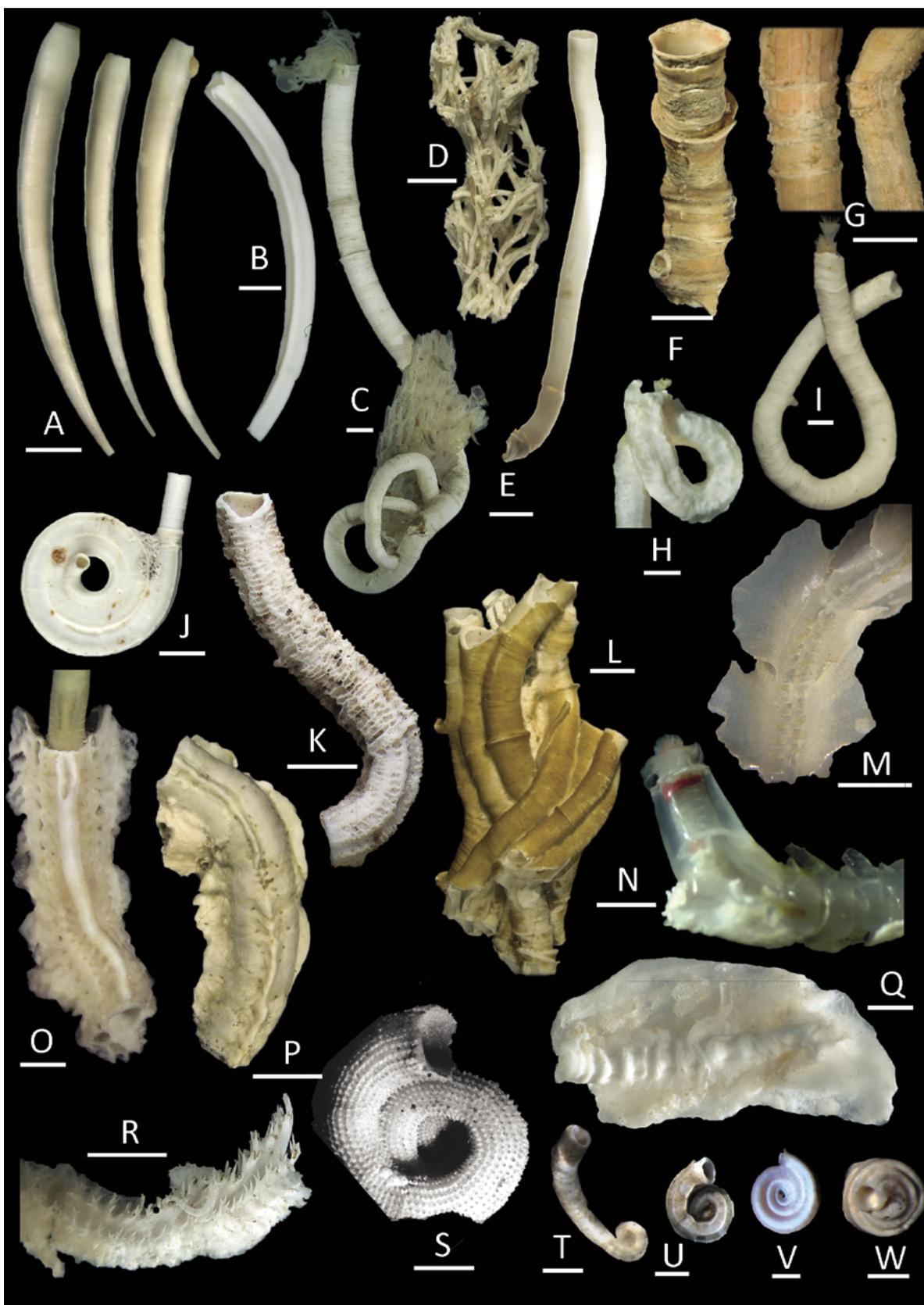
Genus (including most common synonyms and subgenera)	Number of extant species	Number of fossil species	Most ancient fossil finds and their age	Tube characters allowing recognition in fossil state
<i>Rhodopsis</i> Bush, 1905	2	-	-	not recognised
<i>Salmacina</i> Claparède, 1870	11	?	?	indistinguishable from <i>Filograna</i>
<i>Semivermilia</i> ten Hove, 1975	8	?1	?Badenian (15 Ma; Radwańska, 1994a)	not recognised confidently
<i>Serpula</i> Linnaeus, 1758 (?) subgen.: † <i>Cementula</i> Brünnich Nielsen, 1931	29	?**	?Cenomanian (100 Ma; Jäger, 2005); Paleogene (~66 Ma) to Recent	most fossil species are described under this generic name. True <i>Serpula</i> ("s. str.") determined by two/three keeled tubes. Morphological specification is too poor to allow confident recognition, so precise number of fossil species is not clear now.
<i>Spiraserpula</i> * Regenhardt, 1961	18	6+	Late Callovian (164 Ma; Ippolitov, 2007b)	coiling type, ITS
<i>Spirobranchus</i> de Blainville, 1818 = <i>Pomatoceros</i> Philippi, 1844, = <i>Pomatoleois</i> Pixell, 1913	26+	2+**	?Cenomanian (100 Ma; Lommerzheim, 1981, by opercula); Middle Paleocene (~60 Ma; Lommerzheim, 1981)	large size; subtriangular section, opercular morphology
<i>Tanturia</i> Ben-Eliahu, 1976	1	-	-	not recognised
<i>Vermiliopsis</i> de Saint-Joseph, 1894 =† <i>Peraserpula</i> Regenhardt, 1961	13-19	4+	Late Callovian (164 Ma; Vinn and Wilson, 2010)	trumpet-shaped peristomes, sculpture, fast growth
<i>Vitreotubus</i> Zibrowius, 1979	1	-.**	-	not recognised
SPIROBINAЕ				
<i>Amplicaria</i> Knight-Jones, 1984	1	-	-	not recognised
<i>Anomalorbis</i> Vine, 1972	1	-	-	not recognised
<i>Bushiella</i> Knight-Jones, 1973	13(14?)	-	-	not recognised
<i>Circeis</i> de Saint-Joseph, 1894	6	3	Middle Paleocene (~60 Ma; Lommerzheim, 1981)	some species described by opercula with good confidence; tubes – by coiling direction; sculpture; with poor confidence
<i>Crozetospira</i> Rzhavsky, 1997	1	-	-	not recognised
<i>Eulaeospira</i> Pillai, 1970	2	1	??Cenomanian (100 Ma; Lommerzheim, 1979)	low confidence
<i>Helicosiphon</i> Gravier, 1907	1	-	-	not recognised
<i>Janua</i> de Saint-Joseph, 1894	1	3**	??Cenomanian (100 Ma; Lommerzheim, 1979); Middle Paleocene (~60 Ma; Lommerzheim, 1981)	some species described after opercula; some based on tubes, with low confidence
<i>Knightjonesia</i> Pillai, 2009	1	-	-	not recognised
<i>Leodora</i> de Saint-Joseph, 1894	1	-	-	not recognised
<i>Metalaeospira</i> Pillai, 1970	4	2	??Cenomanian (100 Ma; Lommerzheim, 1979) or Middle Paleocene (~60 Ma; Lommerzheim, 1981)	low confidence for ancient Paleocene species determined by opercula

Genus (including most common synonyms and subgenera)	Number of extant species	Number of fossil species	Most ancient fossil finds and their age	Tube characters allowing recognition in fossil state
<i>Neodexiospira</i> Pillai, 1970	10(11?)	5+	?Late Barremian (~126 Ma; Jäger, 2011), Maastrichtian (72 Ma)	operculum; tube sculpture, coiling direction; relatively good confidence for most ancient species
<i>Nidificaria</i> Knight-Jones, 1984	8	-	-	not recognised
<i>Paradexiospira</i> Caullery et Mesnil, 1897	3(4?)	-	-	not recognised
<i>Paralaeospira</i> Caullery et Mesnil, 1897	10	1	Middle Paleocene (~60 Ma; Lommerzheim, 1981)	operculum morphology, coiling direction, sculpture
<i>Pillaiospira</i> Knight-Jones, 1973	3	-	-	not recognised
<i>Pileolaria</i> Claparède, 1868	21(22?)	?**	?Late Barremian (~126 Ma; Jäger, 2011)	low confidence
<i>Protolaeospira</i> Pixell, 1912	12	-.**	-	not recognised
<i>Prototeodora</i> Pillai, 1970	4	-	-	not recognised
<i>Romanchella</i> Caullery et Mesnil, 1897	8	-	-	not recognised
<i>Simplaria</i> Knight-Jones, 1984	3	-	-	not recognised
<i>Spirorbis</i> Daudin, 1800	15	?**	??Cenomanian (100 Ma; Lommerzheim, 1979)	most of fossil material described in older publications is conventionally placed under this name
<i>Vinearina</i> Knight-Jones, 1984	3	-	-	not recognised
GENERA OF UNCERTAIN NATURE (DOUBTFUL SPIRORBINAE)				
<i>Neomicrorbis</i> * Rovereto, 1903 =† <i>Granorbis</i> Regenhardt, 1961; =† <i>Spirorbula</i> Brünnich Nielsen, 1931	1	7+	?Late Bathonian (~167 Ma; Jäger, 2005); Late Berriasian (~142 Ma; Ippolitov, unpubl.)	coiling to both directions, sculpture, large size

(Ehlers, 1908), *S. israelitica* Amoureux, 1976, and *Pyrgopolon differens* (Augener, 1922)), are secondary free-living on soft substrate as adults, while larvae attach to smallest objects. Among fossils similar free-lying tubes are known in such genera as *Tetraserpula*, *Tetraditrupa*, *Tritiditrupa*, *Pentaditrupa*, and *Nogrobs*, as well as in large number of highly diversified spirally coiled forms (*Rotularia*-shaped genera, *Conorca*, *Orthoconorca*).

Tube shape and coiling. General tube shape in most genera is undetermined, resulting in a variety of straight, irregularly twisted or coiled tubes within a genus or even species. Some, however, have a determined tube shape, e.g. tusk-shaped *Ditrupa*, *Bathyditrupa* and all spirally coiled taxa (fig. 2A, B, J, S-W). *Spiraserpula*, known both as Recent and fossil, tends to alternate spirally coiled and irregularly curved tube segments. Coiling mode (spirals attached to substrate or growing over each other) and direction (clockwise only, anticlockwise only, or both) are the most important characters for both extant and extinct forms. Obligatory trochospiral

coiling, where coiling direction can be both clockwise and anti-clockwise within a species, is characteristic only of some fossil genera such as *Conorca*, *Protectoconorca*, *Orthoconorca*, and *Rotularia*-shaped genera (Regenhardt, 1961; Jäger, 1983; 1993). The proportion of tubes coiled in each direction can be either constant within a species or vary intraspecifically for material of slightly different geological ages (Jäger, 1983: Tab. 3-5). There is also a tendency to have one coiling direction strongly dominant (e.g. in some *Orthoconorca*, *Protectoconorca* and *Rotularia*). Spirorbins (fig. 2S-W) are an example of mostly attached spiral tubes coiled in a certain direction within most genera and species. The most remarkable exception is the problematic *Neomicrorbis* (fig. 2S), having tubes coiled equally in both directions in all species. Among indeterminately coiled tubes, sometimes there are coiling tendencies allowing generic attribution. For example, *Hydroides* species often form wide rounded loops (fig. 2H) and so do fossil *Mucroserpula* and, less often, Recent *Serpula*.



Sculpture (=ornament) and cross-section. Along with coiling mode, external sculpture is the most important character for tube identification. In cases when tubes lack pronounced sculpture (*Apomatus*, *Hyalopomatus*, *Protula* - fig. 2C, E), identification of fossils becomes problematic. The tube sculpture typically consists of longitudinal keels (up to 9) or rows of denticles, and transverse ridges and peristomes of varying complexity (fig. 2G, H, J-S, U, W). Keels modify the external cross-section making it (sub)triangular (fig. 2O, P) or multi-angular (fig. 2K, R), and the cross-section is the most robust character allowing generic recognition in fossil state. Transverse peristomes indicate growth stops and can be rare and irregularly spaced (fig. 2L), or almost regularly spaced (e.g. in *Pseudochitinopoma*, fig. 2Q). Sculpture can also be represented by regular pits (e.g. in *Pseudomicrorbis*, *Metavermlia*, fig. 2K) and alveoli (perforations, fig. 2O), which are usually species-specific rather than characteristic of genera.

Sculpture and tube cross section can change in ontogeny and during the transition to growth away from the substrate. In the latter case cross-section tends to become circular, while longitudinal sculpture disappears and peristomes become more frequent (fig. 2F). Thus, free tube fragments of most genera can hardly be identified with confidence, however, in some taxa (e.g. fossil members of *Vermiliopsis* and "*Filigranula*") sculpture is well-developed in free fragments as well, and in some taxa (*Pyrgopolon* (*Septenaria*)) keels become even more numerous than in the attached part. Several Recent genera (e.g. *Janita*, *Pseudochitinopoma*, *Vitreotubus*, fig. 2R, Q, M, respectively) can be easily recognised by sculpture only; all others show some interspecific variability, however, the limited extent of this variability usually justifies generic attributions.

Internal tube structures. The lumen of serpulid tubes is circular and smooth, but members of genus *Spiraserpula* have unique internal tube structures (ITS), such as longitudinal keels and crests of often fragile appearance inside the lumen (Pillai,

1993; Pillai and ten Hove, 1994; ten Hove and Kupriyanova, 2009). Although *Spiraserpula* seems to be a genus well-recognisable by tube coiling mode, differences in ITS morphology make species recognition a lot easier. Internal tube structures are also known for calcareous sabellids of the genus *Glomerula*, where it was found in some fossil species of Cretaceous-Paleogene age (see Jäger, 1993, 2005; fig. 8A).

Attachment structures. The area of tube attachment is often widened to form basal flanges running along tube sides (e.g. *Pseudovermlia*, *Spirobranchus*; fig. 2P). When these flanges are continuously hollow (fig. 7H) or subdivided by septae inside (fig. 8P), they are referred to as tubulae (Hedley, 1958: fig. 9; Jäger, 1983: 11, text-fig. 2; Ippolitov, 2007a, b), and probably help the animal to widen and thus to strengthen the attachment area, without requiring too much calcareous material. The frequency of septae inside tubulae has been used as one of justifications for synonymy of the fossil genus *Proliserpula* with Recent *Neovermlia* (Jäger, 1993; 2005).

Tabulae. Some serpulids from clades AI and AII may build inside the tube lumen transverse septae (tabulae) that partition the oldest tube parts as a response to posterior tube damage (ten Hove and Kupriyanova, 2009). Although tabulae are sometimes mentioned by paleontologists (e.g. Müller, 1963; 1970; Nestler, 1963; Ziegler and Michalík, 1980; Ziegler, 1984), their morphology, frequency and variability have not been studied well enough to be useful for classification.

Wall transparency. Tubes of most serpulids can be either opaque or porcellaneous, (i.e. with an internal opaque and external hyaline layer), but *Placostegus*, *Vitreotubus* (fig. 2N, M, respectively), and some spirorbins (e.g. *Neomicrorbis*, fig. 2S) have completely transparent (hyaline) tubes that can be recognised in the fossilised state. Transparency is determined by certain tube ultrastructure (see below).

Figure 2. Morphological diversity of Recent serpulids. A–R: non-spirorbin serpulids: A – *Ditrupa arietina* (O. F. Müller, 1776), unattached tusk-shaped tubes with circular cross-section. B – *Bathyditrupa hovei* Kupriyanova, 1993a, unattached tusk-shaped tube with quadrangular cross-section (after Kupriyanova et al., 2011: 47, fig. 2E). C – *Apomatus globifer* Théel, 1878, simple tube without sculpture. D – pseudocolony of *Filigrana* sp. tubes. E – *Hyalopomatus bififormis* (Hartman, 1960), simple tube without sculpture (after Kupriyanova and Nishi, 2010: 62, fig. 5a). F – orange tube of *Serpula vermicularis* Linnaeus, 1758, distal unattached part with peristomes. G – same, attached tube parts with multiple low keels. H – *Hydroides albiceps* (Grube, 1870) tube with flattened upper surface bordered by a pair of keels. I – *Hydroides norvegicus* Gunnerus, 1768, tube without keels, with wavy growth lines. J – *Nogrobs grimaldii* (Fauvel, 1909), unattached spirally coiled tube, quadrangular in cross-section (after Kupriyanova and Nishi, 2011: 2, fig. 1C). K – *Metavermlia arctica* Kupriyanova, 1993b, tube with characteristic combination of transverse and longitudinal sculptural elements resulting in "honey-comb" structure. L – *Ficopomatus enigmaticus* (Fauvel, 1923), aggregation of tubes with irregularly spaced peristomes. M – *Vitreotubus digeronimoi* Zibrowius, 1979, transparent tube with very characteristic flat wide paired keels. N – *Placostegus* sp., transparent tube (after ten Hove and Kupriyanova, 2009: 8, fig. 1F). O – *Spirobranchus polytrema* (Philippi, 1844), tube with single keel and alveoles. P – *Spirobranchus taeniatus* (de Lamarck, 1818), simple tube with single smooth keel and peripheral flanges. Q – *Pseudochitinopoma beneliahuae* Kupriyanova et al., 2012, completely attached tube with transverse ridges (after Kupriyanova et al., 2012: 63, fig. 3A). R – *Janita fimbriata* (delle Chiaje, 1822), tube with very characteristic sculpture. S–W: Spirorbinae: S – *Neomicrorbis azoricus* Zibrowius, 1972, coiled attached tube with numerous keels of denticles (after ten Hove and Kupriyanova, 2009: 65, fig. 29C). T – *Bushiella* (*Bushiella*) *evoluta* (Bush, 1905), clockwise coiled tube with planospiral initial whorls and evolved distal part. U – *Bushiella* (*Jugaria*) *kofiadii* Rzhavsky, 1988, clockwise coiled tube with distinct keels. V – *Circeis armoricana* de Saint-Joseph, 1894, anticlockwise coiled planospiral tube. W – *Paradexiospira vitrea* (Fabricius, 1780), anticlockwise coiled vitreous tube. A, C, D, F–I, K, L, O, P – photo E. Wong, E, M, Q – photo E. Kupriyanova, B, J – photo E. Nishi, T–W – photo A. Rzhavsky, S – photo R. Bastida-Zavala, R – photo A. Ravara, N – photo G. Rouse. Scale: A – 1 mm, B – 0.5 mm, C – 1 mm, D – 2 mm, E – 0.5 mm, F, G – 5 mm, H, I, J, K – 1 mm, L – 1 mm, M – 2 mm, N–P – 1 mm, Q – 0.5 mm, R – 1 mm, S – 2 mm, T–W – 1 mm.

Opercula. Several serpulid genera (*Spirobranchus*, *Pyrgopolon*, except for fossil subgenus *Pyrgopolon* (*Septenaria*), *Neomicrorbis* and all spirorbins) have fully or partially calcified opercula that fossilise well and are characteristic enough for distinguishing genera and species. Linking fossil tubes and opercula is often problematic as they are usually found separately (but see Cupedo, 1980a, b; Jäger, 2005), resulting even in generic taxa based on opercula only (e.g. Lommerzheim, 1979; 1981). Opercula of *Bathyvermilia*, a Recent genus having thin calcified opercular endplates, are not known in the fossil record. The literature on fossil opercula can be found in full in Radwańska (1994b) and Gatto and Radwańska (2000).

Size. At least two Recent serpulid genera, *Rhodopsis* and *Josephella*, are characterised by minute tubes with diameter not exceeding 0.2 mm, which was used as an argument for attributing minute fossil tubes to *Josephella* (Regenhardt, 1961; Bałuk and Radwański, 1997). In all other genera interspecific variability of tube size is more or less clearly defined, making this character useful for understanding the fossil tube affinity.

All the characters mentioned above are used while determining fossil tubes. Although determination may not be very precise, a combination of characters usually allows making a qualified guess regarding at least the group of closely related Recent genera, “Formenkreis” *sensu* Lommerzheim (1979), where a fossil species belongs. Morphology is used not only for descriptions of fossil species and genera, but also for inferring phylogenetic relationships among those taxa (e.g. Jäger, 1983; 1993; 2005).

In some striking cases taxa originally described by paleontologists by tubes were later found or recognised among Recent serpulids by zoologists. One example of such “living fossils” is the fossil *Neomicrorbis* that was discovered as a bathyal *N. azoricus* Zibrowius, 1972 and recognised by size, coiling, and characteristic sculpture (fig. 2S). Other examples include *Spiraserpula* recognised by ITS found both in fossil and extant taxa (Pillai, 1993; Pillai and ten Hove, 1994) and characteristically coiled calcareous sabellid *Glomerula* known to paleontologists from the early 19th century (Jäger, 2005; Ippolitov, 2007a), but discovered in Recent fauna only recently (Perkins, 1991). Recent *Spirodiscus* (fig. 2J) with distinct spirally coiled quadrangular tubes was synonymised with fossil genus *Nogrobs* (Jäger, 2005; ten Hove and Kupriyanova, 2009) having very similar tubes, and Recent *Sclerostyla* was considered a synonym of fossil *Pyrgopolon* (Jäger, 1993; 2005) based on tube shape, size, sculpture, and very characteristic calcified opercula (Wrigley, 1951; Cupedo, 1980a, b).

2.3. Tube ultrastructures: a new tool in serpulid systematics?

Studies over the last three decades revealed extensive ultrastructural diversity in serpulid tube walls (e.g. Bohné Havas, 1981; Bubel et al., 1983; Bandel, 1986; ten Hove and Zibrowius, 1986; Zibrowius and ten Hove, 1987; Nishi, 1993; Sanfilippo, 1998a, b; 2001; Vinn, 2005; 2007; 2008; Vinn et al., 2008b, d). Vinn et al. (2008b) recognised four main groups of tube ultrastructures in serpulids according to orientation of calcium carbonate crystals: 1) isotropic structures (the crystallisation axis lacks a uniform orientation, fig. 3A-E); 2)

semi-oriented structures (the crystallisation axis has semi-uniform orientation, fig. 3F, G); 3) oriented prismatic structures (the crystallisation axis has a uniform orientation and is continuous through successive growth increments, fig. 3H, I, M-O); and 4) oriented complex structures (the crystallisation axis of the crystals has a uniform orientation that is not continuous through successive growth increments, fig. 3J-L). In total, 13 distinct ultrastructures (Vinn et al., 2008b, d) are currently recognised in Recent serpulids (fig. 3, 4).

These 13 types can be arranged into several (up to 4) tube layers, though the majority of species have single-layered tubes. Vinn et al. (2008b) examined 44 species belonging to 36 genera and showed that 47% of studied species possess a unique combination (ultrastructural types and their arrangement into layers) of tube characters. Most advanced and highly ordered types of structures are difficult to explain from the point of the classic for serpulids “granular secreting” model (Neff, 1971), so a matrix-mediated model of biomineralisation was proposed (Vinn et al., 2009).

Ultrastructures of Recent tubes may show inter-specific variability (Vinn, 2007; Ippolitov and Rzhavsky, 2008) and can even have a more or less clear adaptive significance (Sanfilippo, 1996; Vinn and Kupriyanova, 2011), but intra-generic variability of ultrastructures is poorly understood. The idea that generic affiliation of fossils can be evaluated using tube ultrastructures was first proposed by Sanfilippo (1998b). The ultrastructural investigation into fossil tubes has recently commenced (e.g. Sanfilippo, 1998a; 1999; Vinn, 2005; 2007; 2008; Vinn and Furrer, 2008; Vinn et al., 2012) and has already helped to prove the serpulid nature of fossils in some doubtful cases (Vinn et al., 2008c; Taylor, 2014).

Ultrastructures can potentially be used to distinguish serpulid taxa and even to verify linking fossils with recent taxa (Kupriyanova and Ippolitov, 2012) and thus, they may be crucially important for further interpretation of the fossil record and understanding serpulid evolution. However, the ultrastructural method is not widely used to estimate the systematic position of Recent and fossil tubes for two reasons. First, ultrastructural variability within Recent genera is insufficiently studied for any meaningful comparison with fossils. Second, fossil material is often diagenetically altered (i.e. original mineralogy, crystal shapes and arrangement may be changed during the sediment to rock transformation); although direct comparisons are still possible, they are restricted to well-preserved fossil material (fig. 5D-I).

Comparison of ultrastructural variation with molecular phylogenies (e.g. Kupriyanova and Nishi, 2010) reveals a striking difference in the complexity of tube ultrastructures between the two major clades. The complex oriented structures and the oriented prismatic structures restricted to the clade A (Vinn et al., 2008b; Vinn and Kupriyanova, 2011: fig. 1) seem to be derived from isotropic structures that are considered to be plesiomorphic (Vinn, 2013c). However, oriented prismatic structures are also known for spirorbins (Ippolitov and Rzhavsky, 2008) nested inside clade B that predominantly has isotropic structures, thus suggesting an evolutionarily independent origin. In both clade A (Vinn and Kupriyanova, 2011) and in spirorbins (Ippolitov and Rzhavsky, 2008)

Table 2. Main “fossil” serpulid genera still not recognised in Recent fauna. Uncommon genera, taxa of doubtful validity, and taxa erroneously described as serpulids (e.g. numerous Paleozoic genera listed in Ziegler, 2006) are not included. For designations see Table 1.

Fossil genera and most common synonyms	Number of species	Known stratigraphic range	Comments
NON-SPIRORBIN SERPULIDS			
† <i>Austrorotularia</i> Macellari, 1984	8	Kimmeridgian to Maastrichtian (157-66 Ma)	originally described as a subgenus of † <i>Rotularia</i> , but likely a separate lineage
† <i>Cementula</i> Brünnich Nielsen, 1931	10+	?Late Pliensbachian to ?Late Burdigalian (184-17 Ma)	included species partly may be related to <i>Serpula/Hydroides</i> , partly to <i>Spiraserpula</i> with reduced ITS, and partly to sabellid <i>Glomerula</i> . In paleontological literature also as subgenus of <i>Serpula</i> (see Jäger and Schneider, 2009).
† <i>Conorca</i> Regenhardt, 1961	5	?Cenomanian, Turonian to Maastrichtian (?100, 92-66 Ma)	
† <i>Corynotrypoides</i> Bizzarini et Braga, 1994	1	Carnian (237-227 Ma)	originally described as cyclostome bryozoan, serpulid affinities proposed by Taylor (2014)
† <i>Cycloplacostegus</i> Jäger, 2005	2	?Late Turonian, Early Santonian to Early Maastrichtian (?91, 86-71 Ma)	
† <i>Dorsoserpula</i> Parsch, 1956	6+	Middle Oxfordian to latest Maastrichtian (160-66 Ma)	
† <i>Genicularia</i> Quenstedt, 1856	1+	Early Oxfordian (163 Ma)	
† <i>Jereminella</i> Lugeon, 1919	1	Maastrichtian (72-66 Ma)	doubtful validity, poorly studied genus
† <i>Laqueoserpula</i> Lommerzheim, 1979	5+	Late Oxfordian to latest Maastrichtian (159-66 Ma)	doubtful status, may be related to <i>Filogramula</i> , <i>Metavermilina</i> or other genera
† <i>Martina</i> Ziegler, 1984	1+	Early Turonian (93 Ma; Ziegler, 1984)	<i>nomen dubium</i>
† <i>Mucroserpula</i> Regenhardt, 1961	6+	?Late Pliensbachian (Jäger and Schubert, 2008); Bajocian to Maastrichtian (?184, 170-66 Ma)	large-sized representatives from the Pliensbachian may belong to † <i>Propomatoceros</i>
† <i>Octogonella</i> Ziegler, 2006	1	Middle Danian (64 Ma)	doubtful validity, may be a synonym of <i>Pyrgopolon</i>
† <i>Orthoconorca</i> Jäger, 1983	7+	Late Albian to Late Danian (~105-~62 Ma)	
† <i>Paliurus</i> Gabb, 1876	2	Cenomanian to Eocene (100-34 Ma)	doubtful validity, revision needed
† <i>Pannoserpula</i> Jäger et al., 2001	3	Middle Oxfordian to Late Kimmeridgian (161-152 Ma)	
† <i>Parsimonia</i> Regenhardt, 1961	5+	Late Volgian to Middle Santonian, ?Campanian to Maastrichtian (~147-85 Ma, ?80-66 Ma)	partly may be a synonym of <i>Serpula</i>
† <i>Pentaditrupe</i> Regenhardt, 1961	4+	Hettangian to Danian (201-62 Ma; Jäger 2005)	may be a synonym or subgenus of † <i>Genicularia</i>

Fossil genera and most common synonyms	Number of species	Known stratigraphic range	Comments
† <i>Propomatoceros</i> Ware, 1975	24+	Pliensbachian to Turonian (190~89 Ma)	some species included in the genus may be referred to <i>Serpula</i> and <i>Spirobranchus</i> . Upper time limit is uncertain, as Cretaceous species listed by Ippolitov (2007b) need revision
† <i>Protectoconorca</i> Jäger, 1983	2	Cenomanian to Maastrichtian (100-66 Ma)	
† <i>Rotularia</i> Defrance, 1827a =† <i>Spirulaea</i> Bronn, 1827	20+	Danian to Priabonian (66-34 Ma)	all subgenera, classically treated under this genus (e.g., Regenhardt, 1961; Jäger, 1993) are considered as separate genera in the present paper
† <i>Rotulispira</i> Chipionkar et Tapaswi, 1973b =† <i>Praerotularia</i> Lommerzheim, 1979	20+	Hauterivian to ?Maastrichtian (133-?66 Ma)	
† <i>Ruxingella</i> Stiller, 2000	1	Late Anisian (244 Ma)	questionable validity, as no comparison with other fossil and Recent taxa provided
† <i>Sarcinella</i> Regenhardt, 1961	1	Middle Jurassic to Early Campanian (~174-80 Ma; Jäger, 2005)	
† <i>Tectorotularia</i> Regenhardt, 1961	10+	Hauterivian to Maastichtian (133-66 Ma)	doubtful validity, partly (including type species) may belong to † <i>Tubulostium</i> Stoliczka, 1868. Originally † <i>Tectorotularia</i> was described as a subgenus of † <i>Rotularia</i> , but likely a separate lineage
† <i>Triditrupa</i> Regenhardt, 1961	1	Cenomanian (100-94 Ma)	originally described as a subgenus of <i>Ditrupa</i> , but likely a separate lineage. Doubtful status, maybe a subgenus of <i>Pyrgopolon</i> (Jäger, 1993, 2005).
† <i>Tubulostium</i> Stoliczka, 1868 ?=† <i>Tectorotularia</i> Regenhardt, 1961	2	Albian to Turonian (113-90 Ma)	doubtful validity, may be a synonym of <i>Nogrobs</i> de Montfort, 1808 (<i>s. str.</i>)
† <i>Weixiserpula</i> Stiller, 2000	1	Late Anisian (244 Ma)	questionable validity, as no comparison with other fossil and Recent taxa provided
SPIRORBINAE			
† <i>Bipygmaeus</i> Regenhardt, 1961	2	Early Cenomanian to Middle Danian (100-63 Ma)	
† <i>Cubiculovinea</i> Lommerzheim, 1981	1	Middle Paleocene (62-59 Ma)	genus description based on opercula only
† <i>Ornatovinea</i> Lommerzheim, 1979	1	Earliest Cenomanian (~100 Ma)	genus description based on opercula only
DOUBTFUL SPIRORBINAE			
† <i>Pseudomicrorbis</i> Jäger, 2011	1	Late Berriasian to Barremian (~142~125 Ma)	

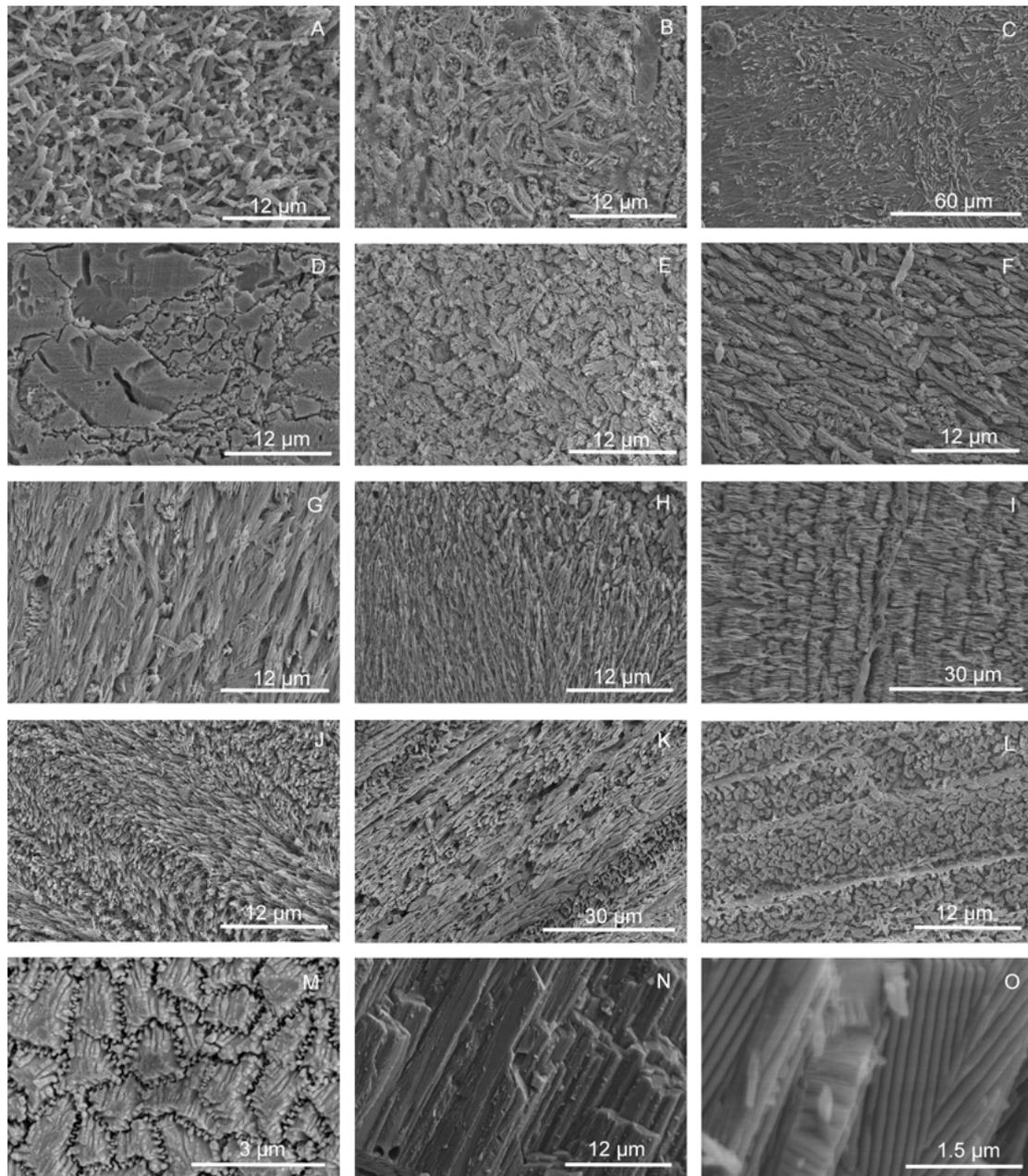


Figure 3. Ultrastructural diversity of Recent serpulid tubes. A-E: isotropic structures: A – *Serpula crenata* Ehlers, 1908, inner tube layer, cross section of irregularly oriented prismatic structure (IOP), B – *Pseudovermilia madracicola* ten Hove, 1989, cross section of spherulitic irregularly oriented prismatic structure (SIOP) (after Vinn et al., 2008b: fig. 2A), C – *Neovermilia falcigera* (Roule, 1898), cross section of irregularly oriented platy structure (IOPL), D – *Laminatubus alvini* ten Hove et Zibrowius, 1986, cross section of homogeneous angular crystal structure (HAC), E – *Pomatostegus stellatus* (Abildgaard, 1789), cross section of homogeneous rounded crystal structure (HRC) (after Vinn et al., 2008b: fig. 3E), F, G: semi-oriented structures: F – *Protula diomedea* Benedict, 1887, cross section of semi-ordered irregularly oriented prismatic structure (SOIOP) (after Vinn, 2007: fig. 5.5), G – *Pyrgopolon ctenactis* Mörch, 1863, outer tube layer, cross section of semi-ordered spherulitic irregularly oriented prismatic structure (SOSIOP) (after Vinn, 2007: fig. 7.4), H, I and M-O: oriented prismatic structures: H – *Spiraserpula caribensis* Pillai et ten Hove, 1994, outer tube layer, longitudinal section of spherulitic prismatic structure (SPHP) (after Vinn, 2007: fig. 6.5), I – *Vitreotubus digeronimoi* Zibrowius, 1979, longitudinal section of simple prismatic structure (SP) (after Vinn et al., 2008b: fig. 5B, enlarged), J-L: oriented complex structures: J – *Hydroides dianthus* Verrill, 1873, third layer from outside, longitudinal section of lamello-fibrillar structure (LF) (after Vinn, 2008: fig. 4.5), K – *Floriprotis sabiuraensis* Uchida, 1978, inner layer, cross section of spherulitic lamello-fibrillar structure (SLF), L – *Spirobranchus giganteus* (Pallas, 1766), outer layer, longitudinal section of ordered fibrillar structure (OF) (after Vinn et al., 2008b: fig. 6B), M-O – *Ditrupa arietina* (O. F. Müller, 1776), regularly ridged prismatic structure (RRP): M – tube external surface, etched with 1% acetic acid for 30 sec (after Vinn et al., 2008d: fig. 3F), N – external tube layer, longitudinal section, O – lateral surface of a RRP structure prism with ridges (after Vinn et al., 2008d: fig. 4A).

oriented prismatic structures tend to form dense outer tube layer near the surface of the wall. Unilayered tubes with prismatic structure of the only layer are transparent (Ippolitov and Rzhavsky, 2008; Vinn et al., 2008b) because of parallel orientation of optical axes in crystals.

2.4. Tube mineral composition: new cues for serpulid evolution

Tubes of serpulids consist of calcite, aragonite, or a mixture of both modifications of calcium carbonate (Bornhold and Milliman, 1973; Vinn et al., 2008b) interspersed with an organic mucopolysaccharide matrix. The first comprehensive overview of serpulid tube mineralogy by Bornhold and Milliman (1973) provides data for over 100 specimens belonging to 24 species of 11 genera. The study found only limited correlations of tube mineralogical composition with environmental factors and with classification. However, data on mineralogical composition have been used to test the generic affiliation of serpulid tubes (Ferrero et al., 2005) and to distinguish species within a single genus (e.g. Bornhold and Milliman, 1973; followed by ten Hove, 1974: 47).

Calcite and aragonite are rarely present in almost equal quantities within one tube, and calcite-aragonite ratio may significantly vary not only among species, but also within a species and even within a single tube during the ontogeny (Bornhold and Milliman, 1973). Vinn et al. (2008b) found some correlations between mineralogy and ultrastructural types, showing that lamello-fibrillar ultrastructure, mainly known for clade A, is exclusively calcitic. Similarly, the simple prismatic ultrastructural type is clearly correlated with calcite mineralogy.

When mapped to existing phylogeny, aragonitic mineralogy is predominantly associated with the “filogranin” non-spirorbin clade BI having simple un-oriented structures, while calcitic mineralogy is more typical for clade A showing complex ultrastructures (Vinn, 2012). Aragonitic irregularly oriented prismatic structure (fig. 3A, 4A) appears to be plesiomorphic for serpulids (Vinn and Kupriyanova, 2011), while complex oriented calcitic structures are far more advanced. Vinn (2012) hypothesised that calcite is favoured by the serpulid biomineralisation system for producing complex structures. In contrast, within molluscs aragonite has a greater variety of complex structures as compared to that of calcite (Carter et al., 1990). Recently Smith et al. (2013) also showed that clade AI (“*Serpula*-group”) tends to have mixed mineralogy with dominating calcite, and clade AII (“*Spirobranchus*-group”) tends to have fully calcitic mineralogy, sometimes with little aragonite. Again no clear correlations with environmental factors were found.

According to the hypothesis by Vinn and Mutvei (2009), supported by Smith et al. (2013), ocean chemistry was the dominant factor controlling the evolution of serpulid tube mineralogy over geological time periods with differing conditions favouring the precipitation of a certain mineral (so-called “calcitic” and “aragonitic” seas, see Stanley, 2006). According to this idea, plesiomorphic serpulids of clade BI tend to have aragonitic mineralogy because they originated and diverged in aragonitic seas of the Triassic period, while more advanced calcitic serpulids of clade A mainly evolved during the Jurassic-Cretaceous time, which was the epoch of calcitic seas.

2.5. Organic component of tubes: will biochemistry meet paleontology?

The only approach complementing ultrastructural and mineralogical studies is histochemical investigation of the organic tube component as suggested by ten Hove and van den Hurk (1993) and Gatto and Radwańska (2000). This organic component is represented by an inner organic membrane lining the lumen and an organic matrix inside the tube walls. The inner organic membrane is found in all serpulids (Nishi, 1993; Vinn, 2011) and may play an important role for the biomineralisation process (Tanur et al., 2010), but this needs further clarification (Vinn, 2011). The organic matrix of the tube wall should be preserved in fossil serpulid tubes, as it does in mollusc shells. The tube matrix seems to be organised in thin sheets running parallel to accretion surfaces (Vinn et al., 2008b), but such organisation was observed only in some taxa within clade A (Vinn, 2013b). Tanur et al. (2010) found that most of the soluble organic tube matrix of a Recent species *Hydroides dianthus* (Verill, 1873) is composed of carboxylated and sulfated polysaccharides, whereas proteins form a minor component. No data on other species are available and further studies are needed to determine usability and potential of this method for paleontology.

3. An outline of serpulid evolution as revealed by fossils

3.1. False serpulids: tubular fossils below the Precambrian-Cambrian boundary (~541 Ma)

During so-called “Cambrian explosion”, an episode in the Earth history that took place about 541 Ma, most major fossil invertebrate groups suddenly appeared in paleontological record within a short time interval, often having developed mineral structures within or around the body.

Many tubular fossils of problematic affinity appeared already during the preceding Late Ediacaran (~577-541 Ma). They include chitinous tubes of sabelliditids, often considered to be the ancestors of Recent Siboglinidae, and calcified tubular problematics *Cloudina*, *Sinotubulites* (Chen et al., 2008), as well as unusual forms with triradial symmetry, such as *Anabarites* (Kouchinsky et al., 2009). Many of these tubular fossils have been attributed to annelids in general and serpulids in particular (e.g. Yochelson, 1971; Glaessner, 1976; Chen et al., 1981; Bandel, 1986), but their true biological affinities are usually unresolved. The major function of mineralised tubes was probably protection against predation (Bengston, 2002), but physiological adaptation to changing ocean chemistry and the opportunity to grow larger were also proposed (e.g. Bengston, 2004: 69-70).

Cloudina (fig. 6A), the most famous tube-building metazoan common in deposits of the terminal Neoproterozoic Ediacaran Period (549-541 Ma), has often been affiliated with serpulids (Germes, 1972; Glaessner, 1976; Hua et al., 2005). Tube morphology and microgranular ultrastructure (fig. 5A) suggest that *Cloudina* is not closely related to any Recent calcareous polychaetes (serpulids, sabellids or cirratulids) (Vinn and Zatoń, 2012a). The type of asexual reproduction and presence of a closed tube base in *Cloudina* is more compatible

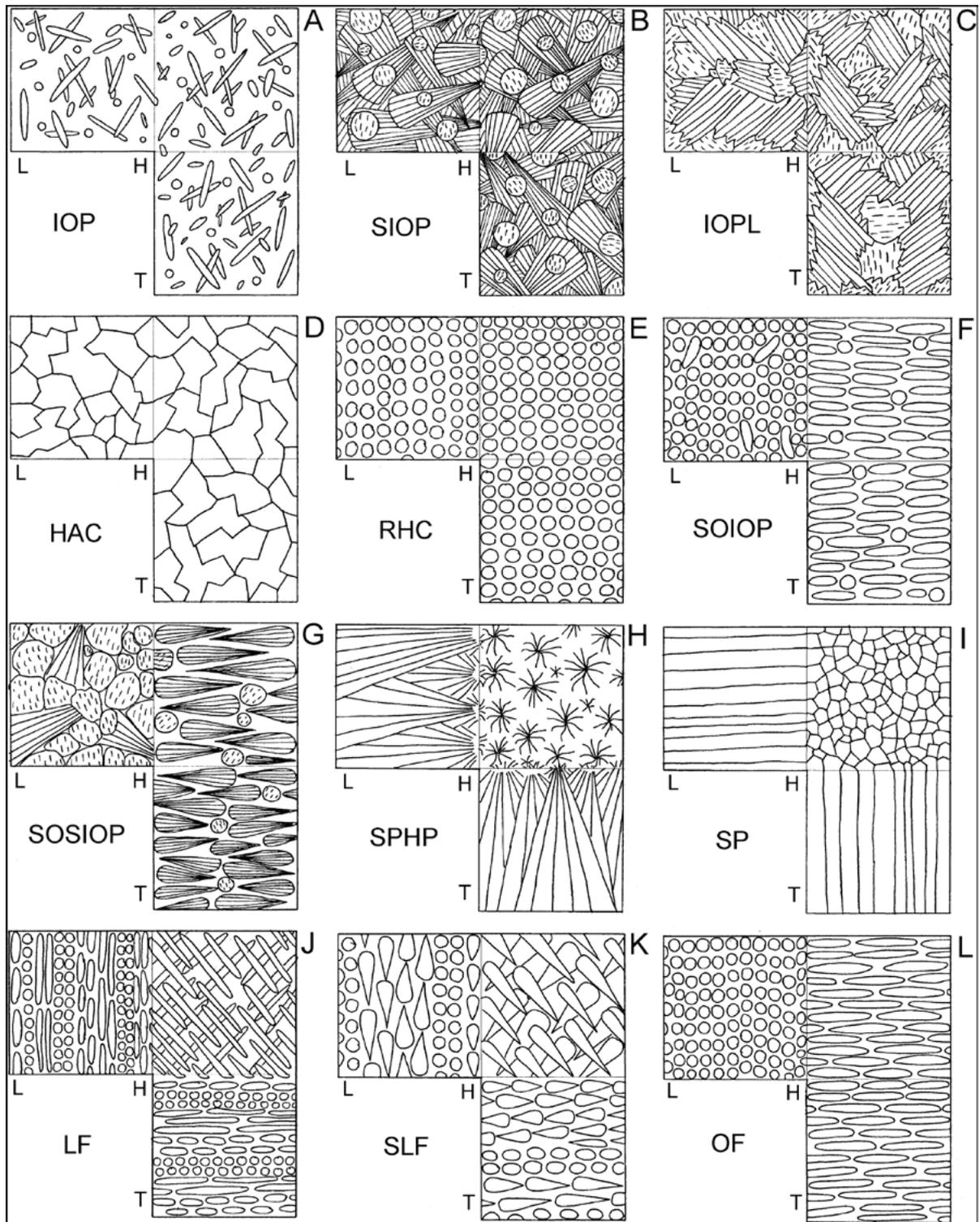


Figure 4. Schematic presentation of serpulid tube ultrastructures (from Vinn et al., 2008b). A – irregularly oriented prismatic (IOP) structure. B – spherulitic irregularly oriented prismatic (SIOP) structure. C – irregularly oriented platy (IOPL) structure. D – homogeneous angular crystal (HAC) structure. E – rounded homogeneous crystal (RHC) structure. F – semi-ordered irregularly oriented prismatic (SOIOP) structure. G – semi-ordered spherulitic irregularly oriented prismatic (SOSIOP) structure. H – spherulitic prismatic (SPHP) structure. I – simple prismatic (SP) structure. J – lamello-fibrillar (LF) structure. K – spherulitic lamello-fibrillar (SLF) structure. L – ordered fibrillar (OF) structure. Regularly ridged prismatic structure (RRP, see fig. 3 M-O) is similar to SP structure. Abbreviations: H: horizontal section; L: longitudinal section; T: transverse section.

with the hypothesis of an animal of cnidarian grade (Hua et al., 2005; Vinn and Zatoń, 2012a; Zhuravlev et al., 2012).

3.2. Paleozoic (541-252 Ma) tubular problematic taxa

Paleozoic rocks, especially of Early Cambrian age (~540 Ma), contain tubular fossils of uncertain affinities, some of which are carbonate (e.g. *Coleolella*), and others are phosphatic (*Hyolithellus*, *Sphenothallus*) or even siliceous (*Platysolenites*). Among Paleozoic fossils, two common and diverse fossil groups, Cornulitida and Microconchida, have traditionally been described as serpulids. Including them in the serpulid fossil record resulted in a long-held controversy regarding the geological age of calcareous polychaetes and in wrong interpretations of evolutionary patterns within the Serpulidae by both zoologists (e.g. Pillai, 1970; Knight-Jones, 1981) and paleontologists (Jäger, 1993: 101).

Cornulitids (fig. 6B) are mostly small (2-5 mm, although some species could reach 25 mm in tube diameter) calcareous

tubular fossils ranging from the Middle Ordovician to the Carboniferous (470-300 Ma) and found in normal marine settings. They have been affiliated with annelids due to the tubular shape of their shells. Similar to modern serpulids, cornulitids were presumably suspension feeders and common encrusters on Paleozoic hard substrates. Their biological affinities have long been debated, but they could represent stem group of phoronids (Taylor et al., 2010). Recent analysis by Vinn and Zatoń (2012b) places them with confidence within the Lophotrochozoa.

Microconchids (fig. 6C) are a *Spirorbis*-like extinct group of lophophorates ranging from the Late Ordovician to the Middle Jurassic (458-164 Ma) that inhabited all aquatic environments from hypersaline to freshwater (Zatoń et al., 2012). Due to their small size (usually <1 mm, up to 2 mm in coil diameter) and obligatory spirally coiled calcareous tubes, for decades microconchids were treated as spirorbins (e.g. Goldfuss, 1831; Zittel, 1880; Malaquin, 1904; Howell, 1962;

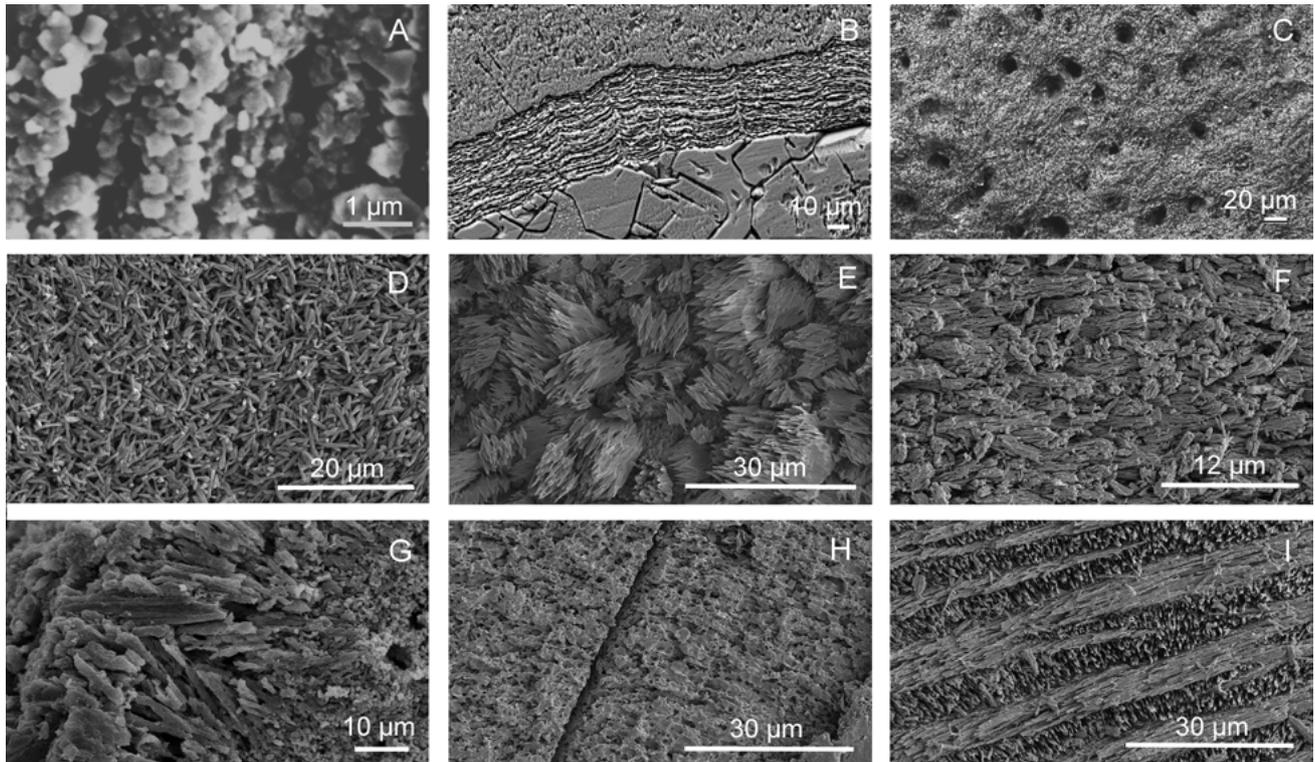


Figure 5. Ultrastructural diversity of fossil serpulids and some typical “pseudoserpulids”. A-C: ultrastructures of most characteristic pseudoserpulids: A – *Cloudina sinensis* Zhang et al. in Ding et al., 1992, showing microgranular structure; Late Ediacaran (549-542 Ma), China (after Feng et al., 2003: fig. 1b). B – microconchoid *Palaeoconchus tenuis* (Sowerby in Murchison, 1839), Silurian (Wenlockian; 433-427 Ma), England (after Vinn, 2006: fig. 4). C – microconchoid *Punctaconchus ampliporus* Vinn et Taylor, 2007, surface showing pores; Middle Jurassic (Bathonian, 168-166 Ma), U.K. (after Vinn and Taylor, 2007: fig. A₂). D-I: ultrastructures of fossil serpulids: D – ‘*Serpula*’ *etalensis* (Piette, 1856), longitudinal section of irregularly oriented prismatic structure (IOP); Early Jurassic, Late Pliensbachian (~185 Ma), eastern Germany (after Vinn et al., 2008c: fig. 1D). E – *Rotularia spirulaea* (Lamarck, 1818), longitudinal section of homogeneous angular crystal structure? (HAC); Eocene (56-34 Ma) of Doss Trento, Northern Italy. F – *Protula* sp., cross section of semi-ordered irregularly oriented prismatic structure (SOIOP); Tongrian, Late Eocene (~35 Ma), Latdorf, North Germany (after Vinn, 2007: fig. 3.1, detail). G – *Propomatoceros* sp., outer tube layer, spherulitic prismatic structure (SPHP); Middle Volgian (~148 Ma), Samara region, Russia. H – *Placostegus polymorphus* Rovereto, 1895, cross section of simple prismatic structure (SP); Badenian (~15 Ma), Miocene, Ehrenhausen, Styria, Austria (after Vinn, 2007: fig. 1.5, detail). I – *Spiraserpula* sp., oblique section of lamello-fibrillar structure (LF); Badenian (~15 Ma), Miocene, Nussdorf, Vienna, Austria (after Vinn, 2007: fig. 4.5).

Regenhardt, 1964; Pillai, 1970; Lommerzheim, 1979; 1981; Jäger, 1983; 1993). Burchette and Riding (1977) who analysed microconchid morphology and tube ultrastructure, were the first to justify doubts about their annelid affinities and interpreted them as gastropods. The microconchid microlamellar tube wall (fig. 5B) with small pores (fig. 5C) is incompatible with known serpulid ultrastructural diversity,

and currently microconchids are interpreted as extinct tentaculitoids (Weedon, 1991; Taylor and Vinn, 2006).

None of the reports of Paleozoic serpulids, starting from Cambrian and Ordovician (e.g. Dalvé, 1948; Clausen and Álvaro, 2002) and continued by Devonian (e.g. Sandberger and Sandberger, 1856) records, show the presence of unequivocal serpulid tube characters (such as, for example, a

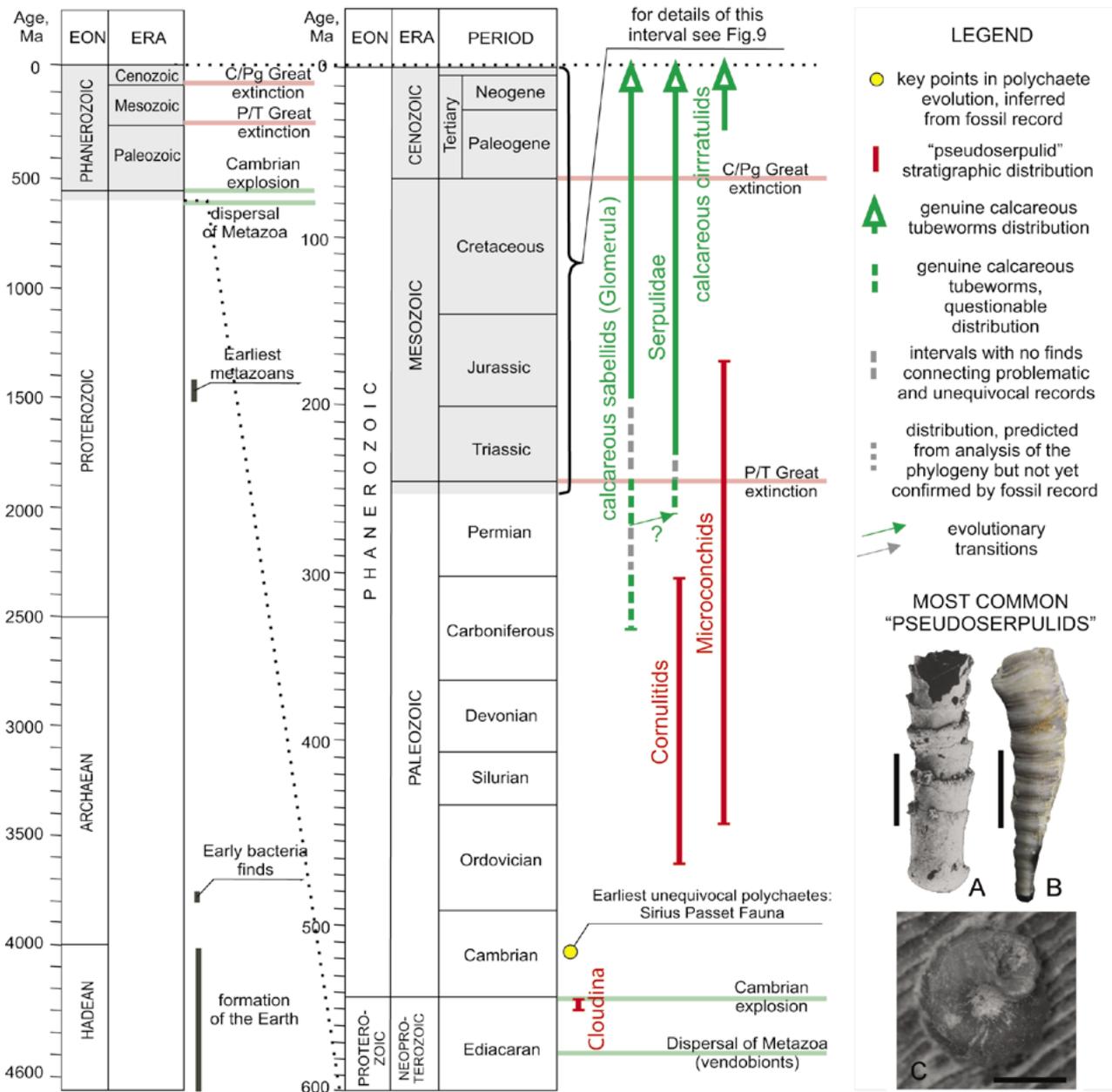


Figure 6. Outline of geological history of calcareous polychaetes and some convergent tube-dwelling taxa (“pseudoserpulids”) during the Phanerozoic. A – *Cloudina hartmannae* Germs, 1972, SEM, Late Ediacaran (549-542 Ma), China (after Hua et al., 2005: fig. 1A). B – *Cornulites* sp., Early Ordovician (485-470 Ma), Estonia (after Vinn, 2013a: fig. 8). C – microconchoid *Palaeoconchus tenuis* (Sowerby in Murchison, 1839), Silurian (Wenlockian; 433-427 Ma), England (after Vinn, 2006: fig. 4). Scale: A – 3 mm, B – 0.5 mm, C – 1 mm.

median keel or tubules). Many of these finds still should be re-investigated to check their annelid affinity. The most confusing records of numerous Paleozoic serpulid genera are provided in the overview by Ziegler (2006), who treated almost all existing tubular fossils as serpulids. There is no reason to support such an opinion.

3.3. Possible calcareous tubeworms of the Late Paleozoic

Some Late Carboniferous to Permian records of calcareous tubes likely belong to the sabellid genus *Glomerula* judging by their slowly growing tubes with characteristic glomerate coiling. The most ancient among them are the Late Carboniferous (323-304 Ma) “tubeworms” (Hoare et al., 2002, fig. 1.1-1.7) and probably also species described as “*Serpula*” spp. by Stuckenber (1905). Younger finds of the same type are Late Permian (265-254 Ma) fossils from Australia described as *Serpula testatrix* Etheridge, 1892. All these finds are characterised by the tube diameter of only about 0.25 mm, while younger Mesozoic *Glomerula* tubes (fig. 7C-E) can reach up to 4-5 mm in diameter, and tubes of the only known Recent species *G. piloseta* (Perkins, 1991) have diameters about 0.5 mm. Sabellids seem to have a primitive biomineralisation system compared to that of serpulids (Vinn and Mutvei, 2009), and thus their earlier representatives may be interpreted as common ancestors of calcified sabellids and serpulids.

More or less coeval are Late Permian finds of attached tubes that do not show typical glomerate coiling and, therefore, may potentially represent true serpulids (e.g. some figured specimens of “*Serpula pusilla* Geinitz, 1848”, “*Vermilia*” *obscura* King, 1850 and maybe “*Serpulites*” from Australia (Guppy et al., 1951)). Such fossils were also reported from Lithuania by Suveizdis (1963). Due to small size of these fossils, similar to that of above-mentioned sabellids, details of

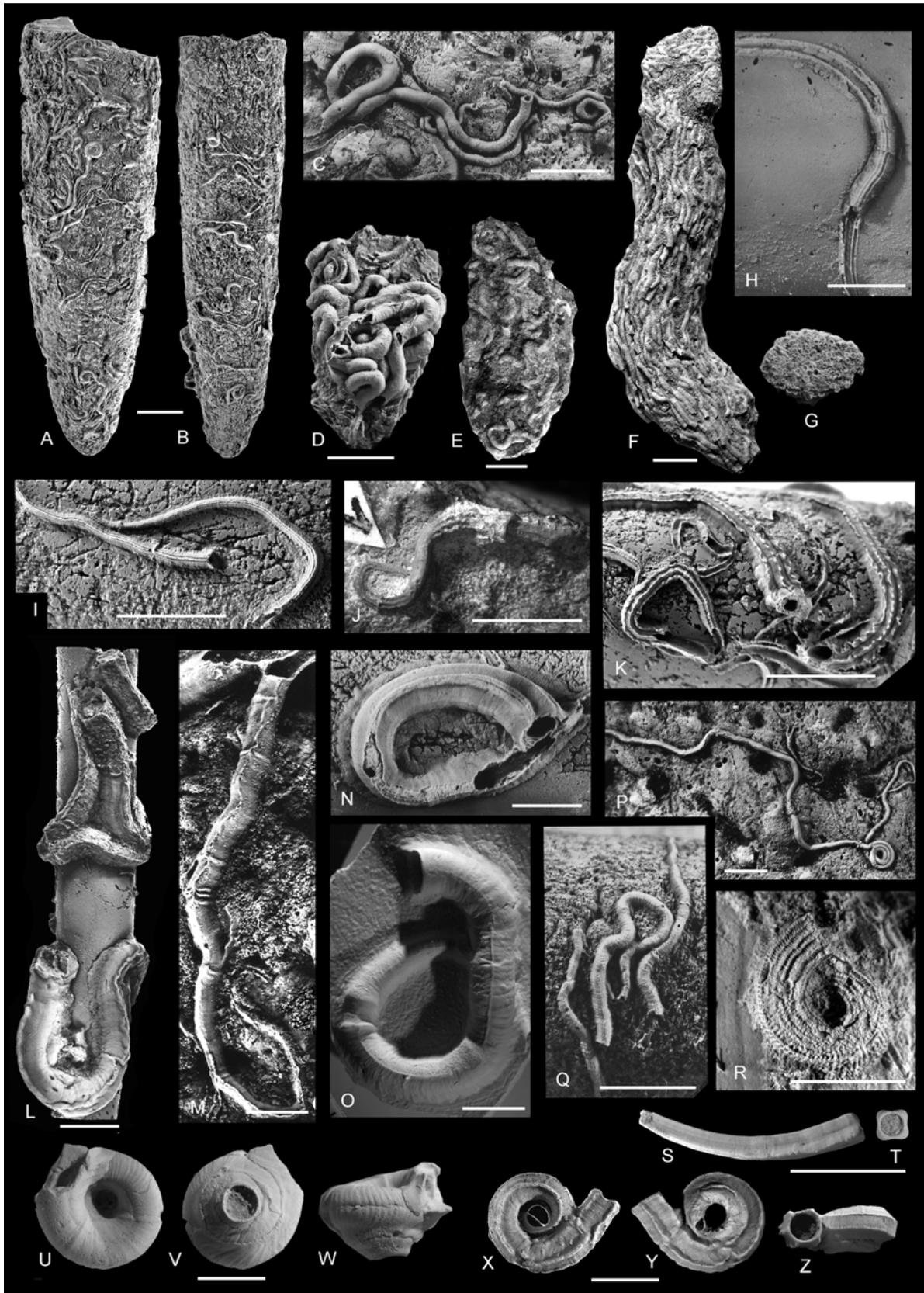
their morphology are unclear from old descriptions and figures, so their potentially serpulid nature is yet to be re-investigated.

3.4. Earliest records of genuine serpulids

Serpulids seem to rise soon after the Permian-Triassic boundary, famous for being the largest extinction event in geological history. Adequately preserved fossils of first unequivocal serpulids from the Middle Triassic (Late Anisian, ~244 Ma) of China are represented by strange tiny tubes lacking any sculpture or having an indistinct single median keel. They were described within two new genera as *Weixiserpula weixi* Stiller, 2000 and *Ruxingella lianjiangensis* Stiller, 2000. Exactly of the same age (Late Anisian; ~244 Ma) are the first unequivocal finds of small pseudocolonial tubes described as *Filograna minor* by Senowbary-Daryan et al. (2007) from Turkey, and a diversified community described by Assmann (1937) from Upper Silesia (Western Poland). The latter, besides *Filograna* morphotype, includes large-sized tubes, some of which have longitudinal sculpture and some show a tendency to build aggregations. Slightly younger (Ladinian; ~242-237 Ma) are records of tubes from South Europe with more or less prominent single median keels (Flügel et al., 1984: 186, Pl. 26, fig. 9).

During the Late Triassic serpulids became widely distributed along the northern and southern margins of the Tethys Ocean. Fossil tubes morphologically similar to Recent morphotypes are known from Indonesia (Jaworski, 1915) and Europe (Münster, 1841; Ziegler and Michalík, 1980; Jadoul et al., 2005, fig. 4c). Some of them are large-sized forms, with tube diameters up to 5-6 mm, but mostly unsculptured. Numerous records of small tube bundles from the Late Triassic sediments of Southern Europe and Turkey (Schmidt and von Pia, 1935; Senowbari-Daryan and Link, 2005) comparable to those of Recent *Filograna* (fig. 2D, 7F-G) indicate wide dispersal of this genus during the

Figure 7. Morphological diversity of Jurassic and Cretaceous (mainly Early Cretaceous) tube-dwelling polychaetes. A, B – fossil serpulid communities encrusting belemnite rostra, PIN 5071/100 and 5071/101, respectively; Middle Oxfordian (161 Ma), Kostroma region, Russia. C-E: calcareous sabellids: C – *Glomerula flaccida* (Goldfuss, 1831), PIN 5071/2, Late Callovian (163.5 Ma), Moscow region, Russia (after Ippolitov, 2007a: Pl. 7, fig. 2); D – *Glomerula gordialis* (von Schlotheim, 1820) with characteristic glomerate coiling, PIN 5071/102, Middle or Late Oxfordian (161-158 Ma), Mordovia region, Russia; E – *Glomerula* cf. *plexus* (J. de C. Sowerby, 1829), pseudocolonial form, PIN 5071/106; Middle Volgian (150 Ma), Samara region, Russia. F-J: possible members of serpulid clade BI: F-G – *Filograna socialis* (Goldfuss, 1831), pseudocolonial form, PIN 5071/109; Middle Volgian (150 Ma), Orenburg region, Russia; H – *Metavermilia goldfussi* Ippolitov, 2007a, PIN 5071/15, Late Callovian (163.5 Ma), Moscow region, Russia (after Ippolitov, 2007a: Pl. 7, fig. 15); I – *Metavermilia striatissima* (Fürsich, Palmer et Goodyear, 1994), PIN 5071/134(1, 2), Late Oxfordian (159 Ma), Kostroma region, Russia; J – *Vermiliopsis negevensis* Vinn et Wilson, 2010, TUG 1372-2, Late Callovian (~164 Ma), Israel (after Vinn and Wilson, 2010: fig. 6.2). K-O – possible members of serpulid clade AII: K – “*Filogranula*” *runcinata* (J. de C. Sowerby, 1829), PIN 5071/112(1, 2), Middle Oxfordian (161 Ma), Kostroma region, Russia; L – *Propomatoceros lumbricalis* (von Schlotheim, 1820), No. 5071/24-28, Late Callovian (163.5 Ma), Moscow region, Russia (after Ippolitov, 2007b: Pl. 12, fig. 3); M – the same, PIN 5071/36, same age and locality (after Ippolitov, 2007b: Pl. 12, fig. 7); N – *Mucroserpula tricarinata* (J. de C. Sowerby, 1829), PIN 5071/19, Late Callovian (163.5 Ma), Moscow region, Russia (after Ippolitov, 2007b: Pl. 12, fig. 2); O – *Neovermilia ampullacea* (J. de C. Sowerby, 1829), PIN 5204/9, ?Turonian (94-89 Ma), Bryansk region, Russia. P-Q: probable members of serpulid clade AI: P – *Spiraserpula oligospiralis* Ippolitov, 2007b, PIN 5071/50 (holotype), Late Callovian (163.5 Ma), Moscow region, Russia (after Ippolitov, 2007b: Pl. 12, fig. 11); Q – “*Serpula*” sp. nov., PIN 5071/136 (1, 2, 3), Late Oxfordian (~158 Ma), Kostroma region, Russia. R-Z: clade uncertain: R – *Pseudomicrorbis* cf. *pseudomicrorbis* Jäger, 2011, problematic taxon interpreted as close to plesiomorphic spirorbins, PIN 5071/150, Late Berriassian (~141 Ma), Crimea, Ukraine; S-T: *Nogrobs* (*Tetraserpula*) *barremicus* (Sasonova, 1958), PIN 5071/151, Late Barremian (~126 Ma), Saratov region, Russia; U-W: *Rotulispira damesii* (Noetling, 1885), clockwise coiling, PIN 5204/13, Cenomanian (100-94 Ma), Orel region, Russia: U – view from upper side, V – view from lower (attachment) side, W – lateral view; X-Z: *Tectorotularia* cf. *polygonalis* (J. de C. Sowerby, 1829), PIN 5204/6, Aptian (125-113 Ma), Atyrau region, Kazakhstan: X – view from upper side, Y – view from the attachment side, Z – lateral view. Material is deposited in the Paleontological Institute of Russian Academy of Sciences (PIN) and the Natural History Museum, Geological Museum, University of Tartu, Estonia (TUG). Scale: A-C – 10 mm, D-K – 5 mm, L, M – 10 mm, N-Z – 5 mm.



Late Triassic epoch. The Late Triassic (Carnian) genus *Corynotrypoides*, characterized by tiny quickly branching tubes forming procumbent pseudocolonies and originally described as bryozoan (see Taylor, 2014), seems too be reasonably close to *Filograna*. At least some of the Triassic serpulids were members of reef communities, and some of them were even reef-forming organisms (e.g. Braga and Lopez-Lopez, 1989).

In total, only about 10 species are known from the Late Triassic (e.g. Ziegler and Michalík, 1980; Senowbari-Daryan and Link, 2005; Senowbari-Daryan et al., 2007), but due to the relatively small size of tubes, Triassic fossil diversity is poorly studied. Morphological diversity of this period includes several characteristic types similar to Recent forms, suggesting that at least some extant genera have their evolutionary roots in the Triassic. The presence of *Filograna*-

like fossils indicates that not only clade B was already separated from clade A by this time, but inside clade BI the *Protis-Filograna* clade had already diverged from the *Chitinopoma-Protula-Metavermilia-Vermiliopsis* clade by the end of the Triassic (fig. 9). Probable members of the latter group are small triangular to pentangular tubes described as “*Serpula* spec. indet.” by Jaworski (1915). Interestingly, in the earliest known *Filograna* (*F. minor* Senowbari-Daryan et al., 2007) from the Middle Triassic, tubes of individual specimens are not yet densely connected to each other, while in Late Triassic species the integration of individuals is more prominent (see Senowbari-Daryan and Link, 2005). This may mean that early evolution of the *Filograna/Salmacina* clade and its divergence from other serpulids occurred shortly before the Middle Triassic.

Figure 8. Morphological diversity of Mesozoic (Late Cretaceous) and earliest Cenozoic tube-dwelling polychaetes. A, B: calcareous sabellid *Glomerula serpentina* (Goldfuss, 1831): A – cross-section, showing trilobate lumen, GPI HH 4402, latest Maastrichtian (~66 Ma), Maastricht region, Netherlands (after Jäger, 2005: Pl. 1, fig. 6); B – specimen with characteristic meandrous coiling, GPI HH 2556, Early Maastrichtian (~71 Ma), Lower Saxony, Germany (after Jäger, 1983: Pl. 2, fig. 2). C-F: possible members of clade BI: C, D – “*Filigranula*” *cincta* (Goldfuss, 1831): C – BGR/NLFB kma 324, Late Maastrichtian (~70 Ma), Lower Saxony, Germany (after Jäger, 1983: Pl. 8, fig. 10); D – SCMh 782, Coniacian (~88 Ma), Helgoland Island, Schleswig-Holstein, Germany (after Jäger, 1991: Pl. 5, fig. 1a). E – *Metavermilia* (*Vepreculina*) *minor* Jäger, 1983, holotype, BGR/NLFB kca 46, Early Campanian (~80 Ma), Lower Saxony, Germany (after Jäger, 1983: Pl. 9, fig. 8b). F – *Vermiliopsis fluctuata* (J. de C. Sowerby, 1829), BGR/NLFB kma 321, Early Maastrichtian (~70 Ma), Lower Saxony, Germany (after Jäger, 1983: Pl. 8, fig. 2a). G-U – possible members of AII clade: G, H – *Dorsoserpula wegneri* (Jäger, 1983); G – aperture with “Nebenröhre”, additional tube of uncertain nature, GPI GÖ 843-4, Campanian or Early Maastrichtian (~83-72 Ma), Lower Saxony, Germany (after Jäger, 1983: Pl. 4, fig. 5); H – holotype, characteristic coiling mode around crinoid stem object, BGR/NLFB ksa 15, Late Santonian (~84 Ma), Lower Saxony, Germany (after Jäger, 1983: Pl. 4, fig. 1a); I – *Neovermilia ampullacea* (J. de C. Sowerby, 1829), SCMh 885, Turonian or Coniacian (~94-86 Ma), Helgoland Island, Schleswig-Holstein, Germany (after Jäger, 1991: Pl. 1, fig. 4c); J – *Parsimonia parsimonia* Regenhardt, 1961, spirally coiled modification, GPI GÖ 843-3, Middle Santonian (~85 Ma), Lower Saxony, Germany (after Jäger, 1983: Pl. 3, fig. 4a); K, L – *Pyrgopolon* (*Septenaria*) *macropus* (J. de C. Sowerby, 1829), GPI HH 2577, Early Maastrichtian (~71 Ma), Rügen Island, Mecklenburg-Western Pomerania, Germany (after Jäger, 1983: Pl. 10, fig. 8b,d); M, N – *Pyrgopolon* (*Hamulus*) *sexangularis* (Münster in Goldfuss, 1831), GPI GÖ 843-8, Late Campanian (~74 Ma), Lower Saxony, Germany (after Jäger, 1983: Pl. 11, fig. 11d, a); O, P – *Pyrgopolon* (*Pyrgopolon*) *mosae mosae* de Montfort, 1808; O – GPI HH 4427, latest Maastrichtian (~66 Ma), Maastricht region, Netherlands (after Jäger, 2005: Pl. 7, fig. 3); P – base of broken tube showing tubulae, NHMM 2001 101, Late Maastrichtian (~67 Ma), Maastricht region, Netherlands (after Jäger, 2005: Pl. 7, fig. 1); Q-R – operculum of *Pyrgopolon* (*Pyrgopolon*) *mosae cipliana* (de Ryckholt, 1852), from private collection, Late Maastrichtian (~68 Ma), Maastricht region, Netherlands (after Jäger, 2005: Pl. 7, fig. 7b,a); S – *Pyrgopolon* (*Pyrgopolon*) *regia regia* Regenhardt, 1961, NHMM JJ 882b, Late Maastrichtian (~68 Ma), Belgium (after Jäger, 2005: Pl. 8, fig. 6b); T – *Pyrgopolon* (*Septenaria*) *polyforata* (Jäger, 1983, BGR/NLFB kma 335, Early Maastrichtian (~70 Ma), Lower Saxony, Germany (after Jäger, 1983: Pl. 10, fig. 11); U – *Ditrupe schlotheimi* (Rosenkrantz, 1920), NHMM 1992200-2, Early Danian (~66-65 Ma), Belgium (after Jäger, 1993: Pl. 4, fig. 2). V-W: questionable members of clade AII: V – *Pentaditrupe subtorquata* (Münster in Goldfuss, 1831), BGR/NLFB kma 309, Early Maastrichtian (~71 Ma), Lower Saxony, Germany (after Jäger, 1983: Pl. 7, fig. 2); W – *Nogrobs* (*Tetraditrupe*) *canteriata* (von Hagenow, 1840), GPI BN 2 GPI Bo M. Jäger, Early Maastrichtian (~71 Ma), Rügen Island, Mecklenburg-Western Pomerania, Germany (after Jäger, 1983: Pl. 7, fig. 10). X-HI: clade uncertain, taxa with obligatory spiral coiling: X-Y – *Conorca trochiformis* (von Hagenow, 1840), GPI HH 2588, Early Maastrichtian (~72 Ma), Schleswig-Holstein, Germany (after Jäger, 1983: Pl. 13, fig. 8a, b); Z – *Cycloplacostegus pusillus* (J. de C. Sowerby, 1844), GPI HH 2582, latest Campanian (~73 Ma), Schleswig-Holstein, Germany (after Jäger, 1983: Pl. 12, fig. 11); AB-BC – *Protectoconorca senonensis* Jäger, 1983, holotype, GPI HH 2609, Middle Santonian (85 Ma), Lower Saxony, Germany (after Jäger, 1983: Pl. 16, fig. 2a,b); CD – *Rotularia tobar gracilis* Jäger, 1993, holotype, NHMM 1992201-1, Early Danian (~66-65 Ma), Belgium (after Jäger, 1993: Pl. 5, fig. 1); DE – *Orthoconorca turricula* (d’Eichwald, 1865), GPI HH 2593, Early Maastrichtian (~72 Ma), Schleswig-Holstein, Germany (after Jäger, 1983: Pl. 14, fig. 3); EF – *Neomicrorbis crenatostratus subrugosus* (Münster in Goldfuss, 1831), lectotype, GPI BN 5 GPI Bo M. Jäger; Late Campanian (~73 Ma), North Rhine-Westphalia, Germany (after Jäger, 1983: Pl. 15, fig. 9a); FG-HI: *Neomicrorbis crenatostratus crenatostratus* (Münster in Goldfuss, 1831): FG – BGR/NLFB (G), Nr. kma 351, Early Maastrichtian (~71 Ma), Lower Saxony, Germany (after Jäger, 1983: Pl. 15, fig. 2a); GH-HI – operculum, GPI HH 2604, Early Campanian (~83 Ma), Schleswig-Holstein, Germany (after Jäger, 1983: Pl. 15, fig. 6b,a). IJ-KL: genuine spirorbins: IJ – *Bipygmaeus pygmaeus* (von Hagenow, 1840), GPI HH 4434, latest Maastrichtian (~66 Ma), Maastricht region, Netherlands (after Jäger, 2005: Pl. 8, fig. 13a); JK-KL – *Neodexiospira palaeoforaminosa* Jäger, 2005, latest Maastrichtian (~66 Ma), Maastricht region, Netherlands: JK – GPI HH 4437 (after Jäger, 2005: Pl. 8, fig. 17); KL – GPI HH 4438 (after Jäger, 2005: Pl. 8, fig. 18b). Material is deposited in the Geologisch-Paläontologisches Institut und Museum der Universität Hamburg (GPI HH), Geozentrum Hannover (formerly: Bundesanstalt für Geowissenschaften und Rohstoffe/Niedersächsisches Landesamt für Bodenforschung, Hannover) (BGR/NLFB), Geowissenschaftliches Zentrum der Universität Göttingen (formerly: Geologisch-Paläontologisches Universitäts-Institut, Göttingen) (GPI GÖ); Naturhistorisch Museum Maastricht (NHMM); Steinmann-Institut für Geologie, Mineralogie und Paläontologie der Universität Bonn (formerly: Geologisch-Paläontologisches Universitäts-Institut), Bonn (GPI BN); Stühmer collection in the Museum Helgoland (SCMH). Scale: A – 0.5 mm, B-H, K-S, U, V, X-Z, CD-KL – 1 mm, I, J, T, W, AB, BC – 5 mm.



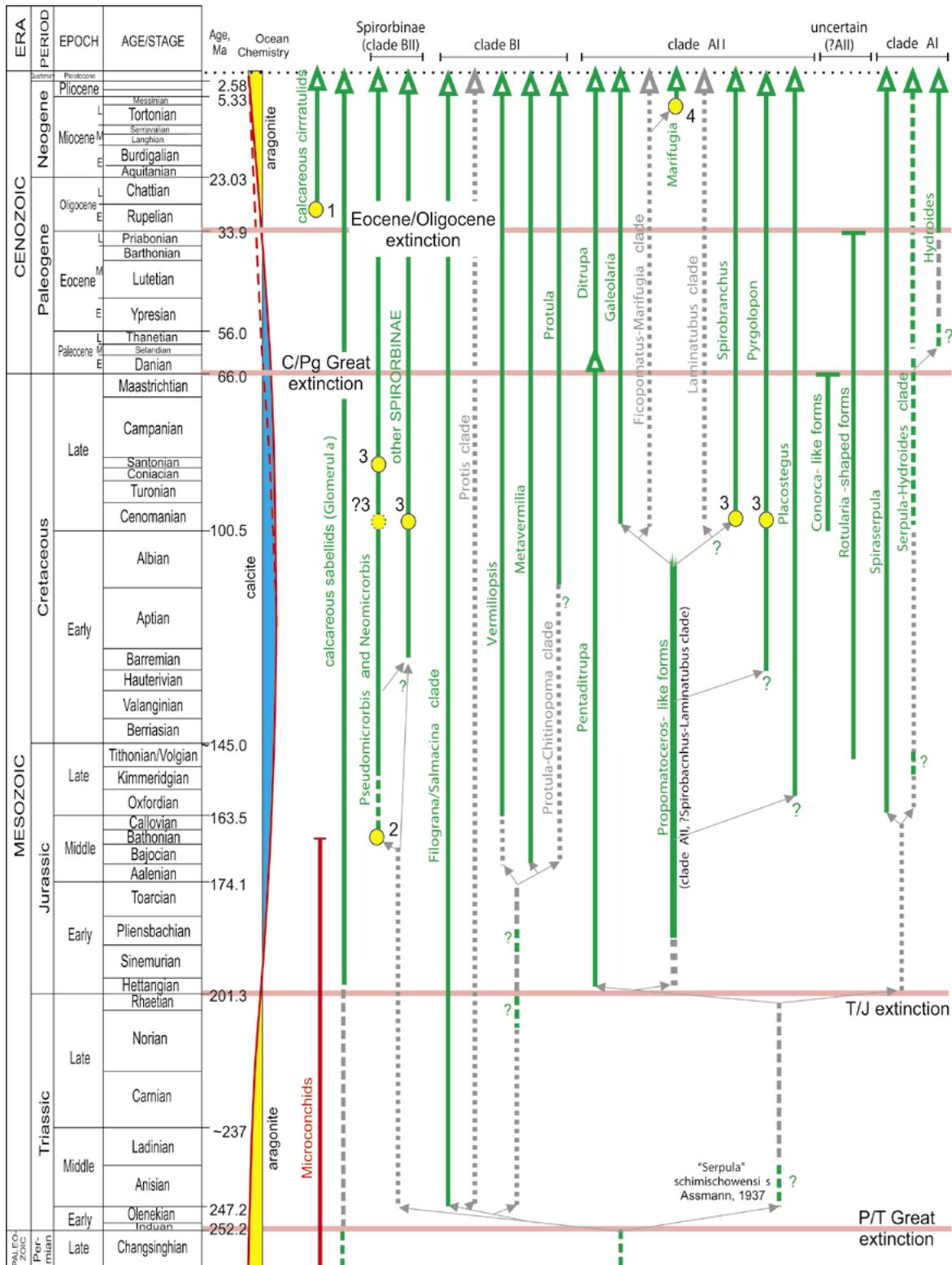


Figure 9. Geological history of calcareous tube-building polychaetes in Mesozoic and Cenozoic suggested by fossil record. Only the most common serpulid genera and those from the phylogenetic tree (fig. 1) are included. For legend see Figure 6. Major events: 1 – most ancient finds of cirratulids with calcified tubes; 2 – the youngest possible position of “coiling point” in spirorbins; 3 – first finds of calcified opercula in several serpulid lineages; 4 – penetration of serpulids to freshwater cave habitat.

Whether triangular tubes with single keels on the upper side (e.g. “*Propomatoceros*” *slavicus* Ziegler and Michalik, 1980) and large-sized tubes with round cross-section (“*Serpula*” *constrictor* Winkler, 1861 *sensu* Jaworski, 1915) from Indonesia are representatives of clade A or clade BI is uncertain. “*Serpula*” *schimischowensis* Assmann, 1937, characterised by large tubes with one or two indistinct keels, is probably the only Triassic species that can be confidently interpreted as a member of clade A (either AI or AII). However, most Triassic finds cannot be attributed to any particular clade.

In conclusion, serpulids did not seem to play a significant role in Middle Triassic ecosystems, and their wide diversification and world-wide dispersal began during the Late Triassic to the Early Jurassic (237–174 Ma). Calcareous tubes first appeared in sabellids and serpulids either in the Late Paleozoic or during the Triassic as an adaptation to predation pressure and evolved in rapidly changing post-Permian/Triassic extinction ecosystems. The main evolutionary trends suggested by Triassic finds are size diversification that resulted in appearance of large tubes, including irregularly coiled attached ones, and wide dispersal of pseudocolonial forms. However, all known Triassic serpulid localities are restricted to the margins of the warm Tethys Ocean that extended sub-latitudeally from South Europe to Indonesia.

3.5. Jurassic (201–145 Ma) diversification epoch

Serpulid faunas of the Jurassic are relatively well studied. Taxonomical reviews describing morphological variety of fossil tubes are mostly based on European material (Parsch, 1956; Ippolitov, 2007a, b; Jäger and Schubert, 2008) with most species known since the 19th century (e.g. Goldfuss, 1831).

The Triassic/Jurassic boundary is characterised by the large extinction event, but its influence on serpulid biota has not been studied. In the Early Jurassic (201–174 Ma) new serpulid morphotypes include larger sculptured subtriangular to sub-pentangular attached tubes with prominent median keels (genus *Propomatoceros*) and free-lying pentagonal tubes (genus *Pentaditrupa*; see Jäger, 2005; Jäger and Schubert, 2008). During the Early Jurassic epoch, serpulids, including *Filograna*-like forms (Aberhan, 1992) seem to disperse from Europe to South America (Behrendsen, 1891; Biese, 1961). The most ancient finds of free-lying tetragonal serpulids of the genus *Nogrobs* are known from South America (Behrendsen, 1891) and dated by Late Pliensbachian (~185 Ma), while finds of this genus in Europe are somewhat younger (Late Toarcian; ~176 Ma; Jäger, 2005). During the Early Jurassic, serpulids also first dispersed to temperate waters of Northern Hemisphere, appearing in North Siberia (Ippolitov, unpubl.; Kirina, 1976: 98). In Canada diversified Boreal serpulid communities are known starting from the Middle Jurassic (Bathonian/Callovian boundary, ~166 Ma; Parsch, 1961).

During the Middle-Late Jurassic (174–145 Ma) the total number of known serpulids increased up to about 150 nominal species (Parsch, 1956; Ippolitov, 2007a, b; 2010), but the exact number is uncertain because many taxa are in need of revision. This was the time of remarkable radiation in Mesozoic (Ippolitov, 2010), which included the appearance of most important serpulid morphotypes, such as forms with multiple keels and spiral tubes (Ippolitov, 2010; also fig. 7). The earliest

representatives of many extant genera (e.g. *Vermiliopsis*, *Nogrobs*, *Metavermlia*, *Spiraserpula*) can be recognised with confidence in the Jurassic (Jäger, 1983; 1993; 2005; Ippolitov, 2007a, b; 2010; Vinn and Wilson, 2010).

Comparison of the fossil record of this age with the molecular phylogeny of Recent taxa (fig. 1) shows that Middle Jurassic fossil faunas already contain members of all three major clades, and even smaller clades, including some extant genera, can be recognised (fig. 9). Clade BI is represented by numerous small to medium-sized tubes with several keels classified as *Vermiliopsis* and *Metavermlia*. The first members of these genera are confidently traced from the Middle Jurassic (*Metavermlia goldfussi* Ippolitov, 2007a and *Vermiliopsis negevensis* Vinn et Wilson, 2010) starting from the Bajocian (~170 Ma). There are earlier records of *Metavermlia*-like tubes from the Late Triassic (Rhaetian; 208.5–201 Ma) and Pliensbachian (191–183 Ma) (Jäger, 2005: 148), but because these finds remain undescribed, they are considered here as members of *Metavermlia-Vermiliopsis* clade (fig. 9) or its stem group. During the Late Jurassic the morphogroup *Metavermlia-Vermiliopsis* (fig. 7H–J) was represented by numerous species (Goldfuss, 1831; Parsch, 1956), suggesting that all main divergence events in the *Chitinopoma-Protula-Metavermlia-Vermiliopsis* clade happened before the end of the Jurassic. However, unequivocal members of the *Protula-Chitinopoma* clade were still not present in the Jurassic, probably indicating that divergence within this branch took place later. Another member of clade BI, *Filograna/Salmacina* (fig. 7F, G) was common in the Jurassic continuing from the Triassic. Non-attached and variously curved tubes were widely spread in the Early Jurassic (Jäger, 1993). Some of them, e.g. “*Serpula*” *etalensis* (Piette, 1856), have tubes with round cross-sections and numerous peristomes, thus resembling free anterior parts of Recent deep-sea *Bathyvermlia* (ten Hove, pers. comm. 2014) belonging to clade BI. The affinity of “*Serpula*” *etalensis* with this clade is supported by simple unilayered wall with irregularly oriented prismatic (IOP) (Vinn et al., 2008c) structure, which is characteristic for members of clade BI.

Clade AI is represented in the Jurassic by *Spiraserpula*. The most ancient probable member of this genus is *Spiraserpula oligospiralis* Ippolitov, 2007b (fig. 7P) from the Middle-Upper Jurassic boundary (Late Callovian/Early Oxfordian; 163.5 Ma), which has characteristic tube coiling, but no ITS typical for younger (Cretaceous to Recent) members of the genus. There are numerous doubtful records of this genus and related *Cementula* from the Early-Middle Jurassic (see Jäger, 1993; Ippolitov, 2007b; Jäger and Schubert, 2008) and even Triassic (Ziegler and Michalik, 1980). Because all these pre-Callovian tubes do not have typical subtriangular cross-sections with median keel extending into a spine over the aperture, these records may belong either to the representatives of the calcareous sabellid *Glomerula* (that tends to have spirally coiled tubes as juveniles) or to a yet undescribed genus. The presence of well-defined *Spiraserpula* in Middle-Late Jurassic indicates that true representatives of the *Serpula-Hydroides* clade must have already existed at that time, but most fossil species can hardly be placed within these

genera. The probable exception is Late Jurassic (Tithonian, ~150 Ma) *Serpula coacervata* Blumenbach, 1803, which is similar in morphology to some Recent *Serpula* species and also produced tube aggregations (ten Hove and van den Hurk, 1993). Another possible clade AI member of Late Oxfordian age (~158 Ma), belonging to still undescribed species, can be seen in fig. 7Q.

Clade AII is represented by the well-recognizable genus *Placostegus* traced from the Late Oxfordian (~158 Ma: *Placostegus conchophylus* Radwańska, 2004). Like Recent forms, fossil *Placostegus* spp. already had transparent tubes (Ippolitov, unpubl.) Other transparent tubes of the same age are usually classified as *Filogramula* (fig. 7K) (see Ippolitov, 2007a) and are known from the latest Early Jurassic and Middle Jurassic (“*Serpula tricristata*” Goldfuss, 1831: Early Toarian to earliest Aalenian, ~180–174 Ma). Given that tube transparency is produced by simple prismatic (SP) structure (Vinn et al., 2008b) and that all non-spirorbin Recent species having this structure are members of clade AII (Vinn and Kupriyanova, 2011), fossil transparent tubes can be interpreted as belonging to members of clade AII, probably related to the *Placostegus* and *Vitreotubus*. Data on tube ultrastructures of some fossil species with quadrangular tubes (Vinn and Furrer, 2008; Vinn et al., 2012) show that such tubes also have SP structure, thus confirming attribution of such tubes to clade AII. Another possible member of the clade AII is *Neovermilia* (fig. 7O) that, like *Placostegus*, is known from the Late Oxfordian (Radwańska, 2004).

The *Ditrupe-Pseudochitinopoma* group is another subclade within clade AII with possible roots in the Jurassic period. Small tubes with characteristic more or less regular transverse ridges and circular cross-section, closely resembling Recent *Pseudochitinopoma beneliahuae* Kupriyanova et al., 2012, are known from the Late Callovian or Early Oxfordian (~164–163 Ma; Ippolitov, unpubl.) of Crimea. Although representatives of true *Ditrupe* appear only after the Cretaceous-Paleogene boundary (Jäger, 1993 and fig. 8U), from the beginning of the Early Jurassic (Hettangian; ~200 Ma) there are records of *Pentaditrupe* (Jäger and Schubert, 2008), a genus with free-lying pentagonal tubes considered as a likely direct ancestor of *Ditrupe* (see Jäger, 1993: 92; Jäger and Schubert, 2008: 56).

Numerous fossils having large sub-triangular tubes with pronounced median keels appear during the Early Jurassic. They are classified within the exclusively “fossil” genus *Propomatoceros* (fig. 7L, M) and related *Mucroserpula* (Ippolitov, 2007b; Jäger and Schubert, 2008). Tube ultrastructures of *Propomatoceros* show a dense outer layer (*sensu* Vinn and Kupriyanova, 2011) formed by spherulitic prismatic structure (SPHP; fig. 5G), typical for clade A. Despite the striking morphological similarity of these tubes to Recent *Spirobranchus*, fossil *Propomatoceros* seem to lack opercular calcification, therefore, its attribution to any of Recent genera is not justified (Ippolitov, 2007b). Jurassic *Propomatoceros* appears to be a member of *Laminatubus-Spirobranchus* clade (fig. 1) or a stem group including common ancestors of *Laminatubus-Spirobranchus* and *Galeolaria-Ficopomatus-Marifugia* clades.

In addition to the morphotypes well-represented in Recent biota, large spirally coiled tubes adapted for settlement on small objects with subsequent transition to free-lying on soft substrates originated during the Jurassic (Jäger, 1993). Such tubes became an essential component of serpulid faunas in late Mesozoic (Cretaceous) seas. It seems that during the Jurassic such a morphotype has appeared at least twice: in the Early Jurassic (*Nogrobs s. str.* with tetragonal tubes) and in the Late Jurassic (Kimmeridgian; ~155 Ma) of Austral Realm (*Austrorotularia* with three-keeled tubes). The phylogenetic position of these genera is uncertain. Fossil *Nogrobs* seems to be a member of clade AII according to its transparent tube with simple prismatic (SP) structure (Kupriyanova and Ippolitov, 2012). However, Recent members of the genus, *Nogrobs grimaldii* (Fauvel, 1909), have opaque tubes (*ibid.*), which makes matching of Recent and fossil forms doubtful. Tubes of *Austrorotularia* by their size and type of sculpture are comparable with those of Recent *Spirobranchus*, thus, *Austrorotularia* is likely to belong to clade AII as well. Although Jäger (1993: 86–87) suggested an evolutionary transition from *Nogrobs* to *Austrorotularia* and other genera formerly included in *Rotularia* as subgenera (see Regenhardt, 1961; Jäger, 1993), the tube sculptures in all these taxa are too different, suggesting that coiling in all these taxa could have evolved independently within clade A. Comparative ultrastructural study of all former *Rotularia* subgenera is still pending, but at least one genus, *Rotularia sensu stricto* from the Paleogene, shows distinct advanced lamello-fibrillar (LF) structure in the tube wall (Vinn, 2008), which is quite difficult to connect with simple prismatic structure of *Nogrobs*.

To conclude, although Jurassic was the epoch of rapid diversification of serpulids and their world-wide dispersal, subtropical latitudinal Tethys Ocean remained the main centre of dispersal throughout the entire Jurassic.

3.6. Cretaceous (145–66 Ma): further diversification

During the Cretaceous period (145–66 Ma) the number of nominal species increased to over 200 (e.g. Jäger, 1983; 1993; 2005; Ippolitov, 2010). The Cretaceous serpulid fauna is relatively well-studied (Brünnich Nielsen, 1931; Regenhardt, 1961; Chiplonkar and Tapaswi, 1973a, b; Lommerzheim, 1979; Jäger, 1983; 1993; 2005; Ziegler, 1984; Koči, 2009; 2012 and many more papers) and was subject to elaborate classification of fossil tubes under Recent generic names. However, the serpulid fossil record of the Early Cretaceous epoch (145–100 Ma) is still very fragmentary, with large unstudied gaps, while the Late Cretaceous epoch (100–66 Ma) is probably the best-studied time interval in serpulid evolutionary history, characterised by a very continuous fossil record.

Excluding scarce data scattered over older publications (e.g. Regenhardt, 1961, who redescribed, amongst others, some Early Cretaceous serpulids and introduced several new taxa), there are only three comprehensive investigations analysing serpulid faunas of the Early Cretaceous. The generic composition of the serpulid community from the Hauterivian (~132 Ma) of South America (Garberoglio and Lazo, 2011; Luci et al., 2013) looks basically similar to that of the Jurassic. The only innovation is the abundance of coiled *Neomicrorbis*/

Pseudomicrorbis that were extremely rare in the Jurassic. The fauna of Barremian age (~128 Ma) described by Jäger (2011) from South-Eastern France differs from Late Jurassic serpulid biota and resembles that of the Late Cretaceous. Besides *Neomicrorbis* (fig. 8EF-HI) and its possible ancestor *Pseudomicrorbis* (fig. 7R), it includes diversified spirorbins as well as large tubes of *Pyrgopolon* (fig. 8K-T) and characteristic small *Vepreculina* (treated as subgenus of *Metavermilina* by Jäger, 1993; 2005; 2011; see fig. 8E), both unknown in the Jurassic. The younger Early Aptian (~125-120 Ma) fauna from England (Ware, 1975), however, again resembles the Jurassic one, as no genera such as *Neomicrorbis* and *Pyrgopolon* were present. This is probably because the territory of England was part of the cold-water Boreal realm, while the major serpulid diversification took place in the warmer Tethyan Realm. Also, because this community inhabited sponges as a substrate, direct comparisons with communities found on other substrates are not really confident. The early Cretaceous was also the time of wide divergence of *Rotularia*-like coiled serpulids, represented now by *Austrorotularia*, *Tubulostium* (both in Southern Hemisphere only), *Rotulispira* and *Tectorotularia*.

The Late Cretaceous was the time when warm epicontinental seas characterised by high rates of carbonate sedimentation occupied large areas in Europe. Serpulid evolution of this time has been described in detail by Jäger (2005: 210-212). The main changes in the serpulid biota include diversification of species within older genera and shifts of dominant genera. Because of the carbonaceous mud floor of Late Cretaceous European seas, this time period was dominated by forms quickly starting to grow upwards, such as the large *Pyrgopolon*, and free-lying forms like *Pentaditrupe* (fig. 8V) and *Nogrobs* (*Tetraditrupe*) (fig. 8W) that did not need much space to attach their initial tubes. Some *Pyrgopolon* species, such as hexagonal members of the subgenus *Hamulus* (fig. 8M-N), adapted to a new lifestyle by modifying their tube sculpture into a peculiar “snow shoe” shape *sensu* Savazzi (1995), which allowed animals to live free on the surface of a muddy substrate (see discussion of “*Serpula*” *alata* in Savazzi (1995; 1999)). The deficit of hard substrates probably also explains appearance of numerous genera with spiral tubes that cannot be attributed to any Recent genus (e.g. *Conorca*, *Orthoconorca*, and *Protectoconorca*, see fig. 8X, Y, AB, BC, DE) as well as diversification of *Placostegus*-like taxa normally growing upwards from the substrate (fig. 8Z). On the contrary, large spiral *Rotularia*-shaped forms, the common element of serpulid biota during the Early Cretaceous and earliest Late Cretaceous (Cenomanian; 100-94 Ma), almost disappeared in European communities starting from the base of Turonian (~94 Ma), probably being displaced by *Conorca*-like forms (Jäger, 1993). However, in epicontinental seas of former Gondwana continent in the Southern Hemisphere during the Mesozoic, coiled free-lying forms remained the dominant morphotype during the entire Late Cretaceous epoch (e.g. see Tapaswi, 1988 for India and Macellari, 1983 for Antarctica).

Large tubes having pronounced median keels (clade AII) and mostly attached to the substrate (*Propomatoceros*-like forms) became less common in the Cretaceous than they were in the Jurassic. Finds of *Spirobranchus*-like opercula (Lommerzheim, 1979) starting from the earliest Late

Cretaceous (Cenomanian; 100 Ma) indicate that this clade probably diverged from the *Laminatubus* lineage before that time. However, because *Spirobranchus* is hardly distinguishable from Jurassic *Propomatoceros* by tube morphology, further studies are needed to date this transition.

Starting from the end of Early Cretaceous (Early Albian; ~110 Ma; Jäger, 2005), records of large unsculptured *Protula*-like tubes (clade BI) become common. However the origin of this genus should be hypothesised cautiously because simple unsculptured tubes of *Protula* are hardly recognisable among fossils of Early Cretaceous and Jurassic. *Protula*-like tubes are common in the Albian and Cenomanian (100-94 Ma), but almost completely disappear in shallow-water European seas starting from Turonian and up to the end of Late Cretaceous (94-66 Ma). The first representatives of another BI member, characteristic tiny-sized serpulid genus *Josephella*, are known from the Late Cretaceous of Europe (Regenhardt, 1961; Jäger, 2005).

During the Cretaceous, opercular calcification appeared in several independent lineages (*Neomicrorbis* and other Spirorbinae (fig. 8GH-HI); *Spirobranchus-Galeolaria* clade and *Pyrgopolon* (fig. 8Q, R)) (Wade, 1922; Avnimelech, 1941; Lommerzheim, 1979; Cupedo, 1980a, b; Jäger, 1983; 2005), supposedly improving protection against predators.

3.7. The rise of Spirorbinae

The earliest spirorbins, represented by characteristic large-sized *Neomicrorbis* tubes (up to 6-7 mm in diameter) bearing numerous longitudinal rows of tiny tubercles appear to be of Early Cretaceous age (?Early Hauterivian, ~132 Ma, Luci et al., 2013; Late Barremian, ~126 Ma, Jäger, 2011; Late Berriassian, ~141 Ma, Ippolitov, unpubl.). Undescribed finds mentioned by Jäger (2005) from the Middle Jurassic (Late Bathonian; ~166 Ma) also seem to belong to *Neomicrorbis* (Jäger, unpubl.). It is unclear whether the Late Jurassic (?Middle Kimmeridgian, ~154 Ma) “*Spirorbis clathratus*” Étallon, 1862 *sensu* von Alth, 1882 belongs to *Neomicrorbis* or to the closely related *Pseudomicrorbis* (fig. 7R). The latter genus is similar to *Neomicrorbis*, but its tube sculpture is represented by rows of very small pits, not tubercles, and the initial tube is straight. For the latter character *Pseudomicrorbis* was originally placed outside Spirorbinae (Jäger, 2011), however, in Recent Spirorbinae the initial tube is also straight or just slightly curved (Rzhavsky, pers. comm., 2013; Malaquin, 1904: fig. 1; Okuda, 1946: Pl. 26, fig. 16; ten Hove, 1994: 66). Whether *Pseudomicrorbis* belongs within or outside Spirorbinae depends on a formal definition of spirorbins, but *Pseudomicrorbis* is clearly closely related to *Neomicrorbis*. The only known Recent species of this group, *Neomicrorbis azoricus*, combines characters typical for spirorbins and non-spirorbin serpulids, so its attribution to spirorbins is uncertain (ten Hove and Kupriyanova, 2009: 66; Rzhavsky, pers. comm.).

Abundant undisputable spirorbins similar to extant forms appear from the middle of the Early Cretaceous (Late Barremian, ~126 Ma, Jäger, 2011). These finds are represented by anticlockwise coiled sculptured species questionably referred to *Neodexiospira* (mentioned as “*Janua* (*Dexiospira*)?”), and clockwise coiled unsculptured tubes described as *Pileolaria*? spp.

From the latest Cretaceous (~66 Ma) spirorbins, again attributed to *Pileolaria?* and *Neodexiospira* (fig. 8JK-KL), the latter with good confidence due to characteristic sculpture and preserved opercula associated with tubes (Jäger, 2005), together with exclusively fossil genus *Bipygmaeus* (fig. 8IJ), became common among encrusters (e.g. Jäger, 1983; 1993; 2005). Younger Early Paleogene (62-59 Ma) communities (Lommerzheim, 1981) already contain diversified spirorbins.

The intensive radiation of Spirorbinae can be attributed to their small size, short generation time, and compact spiral tubes allowing them to quickly colonise flexible and ephemeral substrates, such as macroalgae and seagrass blades, and thus, to compete for settlement sites in the highly productive and densely populated upper subtidal zone (Ippolitov, 2010). Spirorbinae were not the only Mesozoic serpulids adapted to settlement on algae, also some larger forms twisted over algal blades. Other Mesozoic serpulids that experimented with coiling were *Rotularia*-shaped forms (*Austrorotularia*, *Rotulispira*, *Tectorotularia*, *Tubulostium*) and *Nogrobs sensu stricto* with large planospiral tubes adapted to soft sediments, as well as small *Conorca*-like tubes (*Conorca*, *Orthoconorca*, *Protectoconorca*) often coiled in high turret-like spirals. The latter forms probably disappeared due to being outcompeted by Spirorbinae.

The origin of Spirorbinae is still a challenge for paleontologists because fossil data do not agree with molecular phylogenies. As pseudocolonial serpulids representing the *FiligranalSalmacina* clade are common in the Middle and Late Triassic, the spirorbin lineage that apparently diverged early within “filigranin” clade BI (fig. 1) should have appeared even earlier, far from the Late Jurassic to Early Cretaceous age postulated by paleontological data. But the divergence point does not necessarily coincide with the “coiling point”, which possibly occurred later in this lineage (fig. 9).

3.8. Cenozoic (66 Ma) to Recent: the rise of Recent serpulid fauna

The serpulids seem to cross the Cretaceous-Paleogene boundary (66 Ma) without any drastic losses, even though this boundary is famous for its extinction event killing numerous other marine groups and the dinosaurs. A detailed study of the Maastrichtian-Danian boundary interval (around 66 Ma) by Jäger (1993) has shown no drastic changes in serpulid faunas around the boundary. However, reshaping of post-crisis marine ecosystems of the early Cenozoic might have indirectly triggered further radiation of serpulid biota. At least some genera seem to completely disappear during the latest Cretaceous (Table 2; see also Jäger, 1993), but whether this is a true extinction pattern or an artifact of our poor knowledge of the Early Cenozoic serpulid faunas, remains unclear.

The number of serpulid species increased in the Paleogene (66-23 Ma), but the fauna of this period is relatively poorly studied. Paleogene serpulid diversity was studied by Brünnich Nielsen (1931), who described a fauna of mostly attached serpulids from the Danian (mostly Middle Danian; ~64-63 Ma) of Denmark. His data show that faunas of Paleogene are comparable to those of Late Cretaceous age, as many genera and dominating morphotypes (*Neomicrorbis*, *Pyrgopolon*, *Spirobranchus*-like forms, *Protula*) remain common.

Starting from Danian there was a remarkable come-back of coiled forms (represented now by *Rotularia sensu stricto*), which continued throughout the entire Paleocene and Eocene (66-34 Ma; Jäger, 1993; Wrigley, 1951). At least in some fossil communities of the Middle Paleocene (62-59 Ma), spirorbin diversity is similar to that of non-spirorbin serpulids, indicating their intensive diversification (e.g. Lommerzheim, 1981).

The influential, but clearly outdated monograph on serpulid faunas of the Cenozoic including Eocene (56-34 Ma) and Oligocene (34-23 Ma) epochs by Rovereto (1904) treats materials from Western Europe and Italy. In general, serpulid fauna of this age resembles that described by Brünnich Nielsen (1931) from the Paleocene. Rovereto (1904: Pl.3, fig. 3) figures at least one remarkable loop-coiled species of Eocene age (56-34 Ma) that closely resembles Recent *Hydroides*, the genus not known from older Mesozoic sediments. Gradual expansion of free-lying *Ditrupa* in Europe started from the earliest Paleogene and peaked in the Eocene (~56-34 Ma). Also, during the Eocene *Pyrgopolon* tubes that can be traced back to the Cretaceous, but are remarkably smaller, became common and diverse at least in some regions (Wrigley, 1951).

The Eocene/Oligocene boundary, the largest extinction event in the Cenozoic, was also an important time in serpulid evolution (Jäger, 2005: 211). Some taxa that once flourished in Mesozoic seas have gradually lost their dominance in the calcareous tubeworm communities by this time. The most remarkable example is the calcified sabellid *Glomerula*, traced up to the end of Eocene (34 Ma) and nowadays known as a single species endemic to the Great Barrier Reef. Other examples include free-lying coiled *Rotularia*, which completely disappeared by the end of Eocene (34 Ma; Jäger, 1993: 88) and problematic *Neomicrorbis*, still present in Recent seas as a single bathyal relict species (Zibrowius, 1972; ten Hove and Kupriyanova, 2009).

To summarise, during the entire Paleogene period there were no drastic evolutionary experiments with tube shape and coiling comparing with the Mesozoic, but there were obvious shifts in dominance of serpulid communities. However, the most ancient calcareous tubes of cirratulids are known from the late Oligocene (~25 Ma) in North America (Fischer et al., 1989; 2000), suggesting that cirratulids acquired tube calcification quite late and independently from serpulids and sabellids (Vinn and Mutvei, 2009).

Serpulid communities of the younger Cenozoic (Neogene period; 23-2.6 Ma) are very similar to those found in Recent seas. Several hundreds of fossil serpulid species have been described from the Neogene (e.g. Rovereto, 1899; 1904; Schmidt, 1950; 1951; 1955; Radwańska, 1994a). The important new element compared to Mesozoic faunas is the wide dispersal of the *Hydroides* morphotype (slowly growing tubes with flattened upper side and loop-coiling tendency). *Hydroides* probably had appeared during the early Paleogene (e.g. Lommerzheim, 1981) or Eocene (Rovereto, 1904) and became common starting from the Neogene (Rovereto, 1899; 1904; Schmidt, 1950; 1951; 1955; Radwańska, 1994a).

During the latest Cenozoic serpulids colonised freshwater cave habitats. The most ancient fossilised tubes of the only known Recent freshwater species *Marifugia cavatica* Absolon

and Hrabě, 1930 were discovered in a collapsed cave in Slovenia are dated around the Late Pliocene/earliest Pleistocene (2.5–3.6 Ma; Bosák et al., 2004). Molecular data of Kupriyanova et al. (2009) suggest that penetration into non-marine waters appeared once in the evolution of Serpulidae. The transition of *Marifugia* to a subterranean environment likely has occurred via ancestral marine shallow-water to intertidal or estuarine species (like extant *Ficopomatus*) that evolved the necessary adaptations to withstand low salinity and then penetrated freshwater caves via surface lakes (Kupriyanova et al., 2009). The age of serpulid penetration of brackish water is uncertain as there is no reliable fossil record of the brackish-water genus *Ficopomatus*. Two Cenozoic species described by Schmidt (1951) as “*Mercierella*”, a junior synonym of *Ficopomatus*, are unlikely to belong to this genus (ten Hove and Weerdenburg, 1978: 101), and the Late Jurassic *Mercierella(?) dacica* Dragastan, 1966 is not a serpulid, but most likely a calcareous alga (*ibid.*).

Given that representatives of clade AI (“*Serpula*-group”) have the most diverse and complex tube ultrastructures (Vinn et al., 2008b) and considering its intensive radiation during the Cenozoic, it is likely that the main ultrastructural diversification of serpulid tubes, which resulted in appearance of highly ordered ultrastructures, also took place at that time. This may partly explain why Mesozoic, especially Jurassic, serpulids do not show such ultrastructural diversity (e.g. Vinn and Furrer, 2008) as seen in Recent forms. On the contrary, ultrastructural diversity of Cenozoic material looks to be close to that of Recent taxa (Vinn, 2007). Species-level radiation within extant genera of serpulid clade AII (“*Spirobranchus*-group”) also could have happened largely during the Cenozoic, while most genera seem to be of Mesozoic origin.

Recent diversity, which counts around 500 species, is not necessary indicative of intensive diversification in evolution of Serpulidae during Pleistocene-Holocene (2.6 Ma to Recent). Because the fossil record is never as well-known as Recent diversity, comparing Recent richness with generalised numbers for large time intervals covering millions of years is speculative. Numerous Recent species identifiable by their tube morphology and geographic distribution have been recognised in Pliocene-Holocene sediments (Table 1) (e.g. Di Geronimo and Sanfilippo, 1992).

3.9. Calcareous sabellids: rise and fall during the Mesozoic-Cenozoic

Calcified sabellids of the genus *Glomerula* appeared during the Late Paleozoic (Late Carboniferous, see above) or Early Jurassic (Late Hettangian; 200 Ma) and flourished in Mesozoic shallow seas producing numerous species (Jäger, 2005: Table 1), which were amongst the most common encrusters in Mesozoic shallow-water serpulid communities all over the world, often constituting up to 50% of total number of tubes. They were so common that six out of seven known Mesozoic sabellid species were described already in the early 19th century by pioneers of paleontology (von Schlotheim, 1820; Defrance, 1827b; J. de C. Sowerby, 1829; Goldfuss, 1831). Besides typical forms, the diversity of fossil Mesozoic *Glomerula* includes pseudocolonial species appearing as large

irregular glomerates of interweaving tubes (fig. 7E), and species with strange internal tube structures making the lumen cross-section triradial (Jäger, 1983; 1993; 2005; see fig. 8A). Late Cretaceous sabellids demonstrate “balls-of-wool” tube coiling with no visible attachment areas, probably indicating a transition to the “rolling stone” lifestyle (Savazzi, 1999). Gradual decrease in abundance of calcareous sabellids relative to that of serpulids during the subsequent Cenozoic suggests that more advanced biomineralisation system acquired by serpulids allowed greater evolutionary plasticity of coiling and growth modes, thus giving serpulids competitive advantage over sabellids. The most crucial competitor for sabellids was probably *Hydroides*, which spread widely over shallow-water environments when calcareous sabellids declined. However, precise timing of this change is unclear because during the Oligocene (34–23 Ma) neither *Hydroides*, nor *Glomerula* seem to be common.

3.10. “False serpulids” of the Cenozoic: a fossil record bias

As in the Paleozoic, the outline of Cenozoic serpulid history is somewhat disturbed by numerous records of false serpulids as well as some true serpulids described as belonging to different fossil groups. Two examples are tusk-shaped scaphopods, which are often confused with serpulid genus *Ditrupa*, and vermetid gastropods, which have irregularly coiled shells with complex sculpture comparable to that of *Spirobranchus* tubes. Shells of both these mollusc groups are frequently confused with serpulid tubes in older zoological publications and even in current zoological practice (ten Hove, 1994). Therefore, numerous fossils described as “*Dentalium*” or “*Ditrupa*” in older publications need to be re-investigated (as e.g. done by Palmer, 2001). Scaphopods are an ancient group first appearing in the Paleozoic, while tusk-shaped serpulid worms with circular cross-section (*Ditrupa*) appear only in the latest Mesozoic. This means that for most of the Mesozoic the tusk-shaped serpulids are easily distinguishable from scaphopods by multiangular cross-sections of the tube. Confusion of serpulids with vermetids (e.g. part of species in Zelinskaja, 1962) is typical mainly for the material from Paleogene and Neogene periods, when irregularly coiled gastropods became common. There are also few records of problematic fossils from the Cenozoic, e.g. phosphatic tubes from the Paleogene of Chile described as serpulid *Semiserpula chilensis* by Wetzel (1957). Because phosphate mineralogy is unknown for Recent serpulids, the affinity of these irregularly loop-coiled tubes remains unclear.

3.11. Serpulid reefs and sediments

In Recent ecosystems, serpulid tubes contribute to sediment and reef formation (reviewed by ten Hove and van den Hurk, 1993 and Ferrero et al., 2005). *Serpula vermicularis* Linnaeus, 1758 and *Galeolaria hystrix* Mörch, 1863 build reefs in temperate seas with normal salinity (ten Hove and van den Hurk, 1993), while extensive reefs of *F. enigmaticus* (Fauvel, 1923) are found in brackish-water subtropical locations around the world (Dittmann et al., 2009). Tubes of free-lying Recent *Ditrupa* form shell banks (density up to 1000 ind. m⁻²) on continental shelves in temperate to tropical seas all over the

world (ten Hove and van den Hurk, 1993), and *D. arietina* (O. F. Müller, 1776) significantly contributes to calcite sediment production in temperate seas (Medernach et al., 2000). Both serpulid reefs and banks produced by free-lying forms are known in the fossil record.

The “serpulid” reefs from Paleozoic sediments were formed not by true annelids, but by tentaculitoids, the group closely related to lophophorates (Vinn and Mutvei, 2009). The earliest true serpulid build-ups are known from the Late Triassic (Norian) of Europe (ten Hove and van den Hurk, 1993; Berra and Jadoul, 1996; Cirilli et al., 1999), around the Triassic-Liassic boundary in Spain (Braga and López-López, 1989), and Middle Jurassic of Southeastern Spain (Navarro et al., 2008). They became common in the Late Jurassic–Early Cretaceous (Regenhardt, 1964; Palma and Angelieri, 1992; ten Hove and van den Hurk, 1993; Kiessling et al., 2006). “*Serpula*” *coacervata* Blumenbach, 1803 tube fragments form a considerable portion of the rock mass around the Jurassic/Cretaceous boundary in north Germany (ten Hove and van den Hurk, 1993), probably being restricted to brackish water environments, the formation of such rocks may be explained by wave erosion of some build-ups. In younger Cenozoic rocks serpulid build-ups are described from the Early Eocene deposits of India (Ghosh, 1987), Miocene and Pliocene of Spain (ten Hove and van den Hurk, 1993), and Miocene (23–5 Ma) of the southern part of Eastern Europe (south Poland, Ukraine, Moldova). Miocene deposits of Eastern Europe contain especially numerous spirorbin and serpulid build-ups (Pisera, 1996; Górka et al., 2012), and the mass occurrence of serpulid build-ups is explained by enormously high water alkalinity in isolated water basins of the Paratethys (Górka et al., 2012). The diversity of serpulids constituting these reefs has not been studied, and at least some of these “serpulids” can be vermetid gastropods (see section 3.10). Sub-recent records of serpulid reefs include those from the Mid-Holocene of Argentina (Ferrero et al., 2005) and the Holocene of California (Howell et al., 1937).

Fossil banks of free-lying serpulids are known from the latest Early Jurassic (Late Toarcian; 176 Ma) of England, Middle Jurassic of Germany and France (Jäger, unpubl.); Middle Jurassic (Bathonian; ~167 Ma and Late Callovian; ~164 Ma) in Crimea (Ippolitov, unpubl.). In all listed cases banks are formed by mass occurrence of tetragonal spirally coiled *Nogrobs s. str.* tubes. Banks formed by tusk-shaped *Ditrupa*, similar to those known from Recent seas, become common from earliest Paleogene (Danian; 66 Ma) onwards in Europe (Jäger, unpubl.), and are also described from the Early Miocene (~20 Ma) of Taiwan (Cheng, 1974).

Both banks and carbonate build-ups in fossil state result in carbonate rocks consisting mainly of serpulid tubes with some matrix, called “serpulit” (alternatively, “serpula limestone” or “spirorbis limestone”) by geologists.

3.12. Serpulids in deep-sea chemosynthetic communities

Serpulids apparently colonised seeps during the Jurassic: their first appearance in such environments is recorded from the latest Volgian (~146 Ma) of Svalbard (Vinn et al., in press). Fossil (Early Cretaceous) serpulid communities from methane seeps are characterised by low species diversity and mostly

low abundance (Vinn et al., 2013). Hydrocarbon seep serpulids belong to several genera only (Vinn et al., 2013 and in press), and in the majority of fossil seeps only a single species was found. This pattern resembles that of molluscs from vents and seeps (Kiel, 2010a, 2010b). Unlike many gastropods and bivalves at vents and seeps that are restricted to these environments, serpulids are ‘colonists’ (Olu et al., 1996a): taxa from the surrounding sea floor that opportunistically invade seeps and vents because of the high abundance of organic matter. The fact that both serpulids and molluscs started colonising the seep environment shortly after their first appearance in the geological record supports the hypothesis that the seep faunas share evolutionary traits with the deep-sea fauna in general (Kiel and Little, 2006).

Similar to serpulids of fossil seeps, most serpulids at modern vents (ten Hove and Zibrowius, 1986; Kupriyanova et al., 2010) and seeps (Olu et al., 1996a, 1996b) also show low diversity. Seep serpulid abundance is high relative to the surrounding seafloor, but low to moderate compared to that of molluscs or siboglinid tubeworms that typically dominate these ecosystems (Vinn et al., 2013).

4. Conclusions and future studies: where to go next

Because studies of fossil serpulid tubes have no well-established stratigraphical, paleoecological or biogeographical application in palaeontology, the end result is that relatively little attention has been traditionally paid to the fossil record of this group. Concerted efforts of both palaeontologists and zoologists are required to advance our understanding of serpulid evolutionary history. Palaeontologists need to provide fossil material from poorly studied stratigraphical intervals (especially re-evaluation of problematic Late Paleozoic tubicolous fossils, the Early Cretaceous gap, and review of the Cenozoic fauna) and from poorly studied geographical regions (mainly outside Europe). New robust phylogenies with greater taxon coverage and integrating new molecular and morphological data from all serpulid genera are expected from zoologists. Further ultrastructural, mineralogical and histochemical studies of both Recent and fossil tubes are needed for reliable linking of fossils to Recent taxa.

Examination of genetic differences between closely related taxa allowing the estimation of a divergence time based on a known rate of accumulation of neutral genetic differences, known as molecular clock. No attempts have been made to age the Serpulidae based on genetic data, even though main diversification events can be roughly dated by the fossil record. This fossil record can provide an invaluable tool for calibration of molecular clocks not only in serpulids, but by extrapolation also in other annelid groups that lack a fossil record.

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