Ultrastructure of the Jurassic serpulid tubes – phylogenetic and paleoecological implications

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The ultrastructural diversity of the Middle and Late Jurassic serpulid tubes from the Polish Basin has been investigated. The inspection of 12 taxa representing the two major serpulid clades allowed for the identification of three ultrastructure kinds – irregularly oriented prismatic structure (IOP), spherulitic prismatic structure (SPHP), and simple prismatic structure (SP). Six of the studied species are single-layered and six species possess two distinct layers. Ultrastructural diversity corresponds to certain serpulid clades. The members of Filograninae have single-layered tube walls composed of possibly plesiomorphic, irregularly oriented prismatic structure (IOP). Two-layered tubes occur solely within the clade Serpulinae, where the external, denser layer is built of either the ordered spherulitic (SPHP) or simple prismatic microstructure (SP), and the internal layer is composed of irregularly oriented prismatic structure (IOP). Apart from phylogenetic signals provided by the tube ultrastructure, it can be used in analyzing paleoecological aspects of tube-dwelling polychaetes. Compared to the more primitive, irregularly oriented microstructures of Filograninae, the regularly oriented microstructures of Serpulinae need a higher level of biological control over biomineralization. The advent of the dense outer protective layer (DOL) in serpulids, as well as the general increase in ultrastructure diversity, was likely a result of the evolutionary importance of the tubes for serpulids, enhanced also by the intensified predation during the Mesozoic Marine Revolution. Such diversity of the tube ultrastructural fabrics allowed for maximizing functionality by utilizing a variety of morphogenetic programs. The biomineralization system of serpulids remains more complex compared to other tube-dwelling polychaetes. Physiologically more expensive tube formation allows for mechanical strengthening of the tube by building robust, strongly ornamented tubes and firm attachment to the substrate. Contrary to sabellids, which perform a fugitive strategy, an increased tube durability allows serpulids a competitive advantage over other encrusters.

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12 **Abstract**

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14 Polish Basin has been investigated. The inspection of 12 taxa representing the two major serpulid

15 clades allowed for the identification of three ultrastructure kinds – irregularly oriented prismatic

16 structure (IOP), spherulitic prismatic structure (SPHP), and simple prismatic structure (SP). Six

17 of the studied species are single-layered and six species possess two distinct layers.

18 Ultrastructural diversity corresponds to certain serpulid clades. The members of Filograninae

19 have single-layered tube walls composed of possibly plesiomorphic, irregularly oriented

20 prismatic structure (IOP). Two-layered tubes occur solely within the clade Serpulinae, where the

21 external, denser layer is built of either the ordered spherulitic (SPHP) or simple prismatic

22 microstructure (SP), and the internal layer is composed of irregularly oriented prismatic structure

23 (IOP). Apart from phylogenetic signals provided by the tube ultrastructure, it can be used in

24 analyzing paleoecological aspects of tube-dwelling polychaetes. Compared to the more

25 primitive, irregularly oriented microstructures of Filograninae, the regularly oriented

26 microstructures of Serpulinae need a higher level of biological control over biomineralization.

27   The advent of the dense outer protective layer (DOL) in serpulids, as well as the general increase

28   in ultrastructure diversity, was likely a result of the evolutionary importance of the tubes for

29   serpulids, enhanced also by the intensified predation during the Mesozoic Marine Revolution.

30   Such diversity of the tube ultrastructural fabrics allowed for maximizing functionality by

31   utilizing a variety of morphogenetic programs. The biomineralization system of serpulids

32   remains more complex compared to other tube-dwelling polychaetes. Physiologically more

33   expensive tube formation allows for mechanical strengthening of the tube by building robust,

34   strongly ornamented tubes and firm attachment to the substrate. Contrary to sabellids, which

35   perform a fugitive strategy, an increased tube durability allows serpulids a competitive advantage

36   over other encrusters.

38   **Introduction**

39   Numerous polychaete families produce habitation tubes (Rouse and Pleijel, 2001).

40   Tubicolous polychaetes may either agglutinate exogenous material, such as sand particles and

41   shell fragments, using a proteinaceous cement to form a tube (e.g., Stewart et al., 2004; Zhao et

42   al., 2005; Fournier, Etienne and Le Cam, 2010; Vinn and Luque, 2013) or produce secretions by

43   themselves utilizing a variety of glands (e.g., Hausen, 2005; Tanur et al., 2010). Secreted tubes

44   may be composed of organic substances, such as proteins and polysaccharides (e.g., Barnes,

45   1965; Chamoy et al., 2001; Nishi and Rouse, 2013), and mineral substances such as calcium

46   carbonate (Weedon, 1994; Fischer, Pernet and Reitner, 2000; Vinn et al., 2008). Amongst tube-

47   dwelling polychaetes producing hard, mineralized exoskeletons are the families Sabellidae,

48   Cirratulidae, and Serpulidae. Whereas calcareous sabellids (Perkins, 1991; Vinn, ten Hove and

49   Mutvei, 2008; Słowiński, Banasik and Vinn, 2023) and cirratulids (Reish, 1952; Fischer, Oliver

50   and Reitner, 1989; Fischer, Pernet and Reitner, 2000; Taylor et al., 2010; Kočí et al., 2021) are

51   restricted to one (*Glomerula*) and two genera (*Dodecaceria*, *Diplochaetetes*) in each family

52   respectively, only serpulids dwell exclusively in tubes composed of calcium carbonate (Vinn et

53   al., 2008).

54   Thus, having a hard, mineralized exoskeleton, serpulids are the most abundant

55   polychaetes in the fossil record, appearing as far back as the Middle Permian (Sanfilippo et al.,

56   2017; 2018). However, their hard parts are not strictly related to the organism's soft body and

57   form only a habitation tube serving, among others, for protection against predators (e.g., Morton

58   and Harper, 2009; Klompmaker, 2012). Although tubes' taxonomic usefulness is not without

59   validity, as many genera possess easily recognizable tubes, which are diagnostic displaying

60   different longitudinal and transverse elements (see e.g., Ippolitov et al., 2014), homeomorphy is

61   still a common feature in serpulid tube morphology (e.g., Kupriyanova and Ippolitov, 2015) due

62   to convergence and high ecophenotypic plasticity. This leads to certain discrepancies between

63   paleontological and biological classification, the latter of which is based solely on the molecular

64   data, soft parts, and their reciprocal relationships (Kupriyanova, Macdonald and Rouse, 2006; ten

65   Hove and Kupriyanova, 2009). Moreover, it makes the linkage of contemporary species with

66   their ancestors difficult due to the lack of fully reliable taxonomic tools.

67   Serpulid tubes can be composed of up to four layers; however, most of them are single-

68   layered (Vinn et al., 2008). They exhibit different ultrastructural fabrics, depending on how

69   calcium carbonate crystals are arranged and oriented (see Vinn et al., 2008). During the

70   progressing expansion of the tube, an animal secretes consecutive growth lamellae, which

71   correspond to a single growth episode. Such lamellae may be either straight, perpendicular to the

72   direction of growth (e.g., Bałuk and Radwański, 1997) or much more frequently chevron-shaped

73   (see Weedon, 1994). Serpulid ultrastructures may provide phylogenetic signals in the case of

74   Jurassic taxa but also serve as a record of the physiological changes of the worm during its entire

75   lifespan, providing important ecological signatures that may be successfully implemented in

76   paleoecological analyses. Moreover, serpulid tubes may exhibit additional skeletal structures

77   such as tubulae, alveolar structures, or internal tube structures, helping in unraveling their true

78   systematics (e.g., Pillai, 1993; Pillai and ten Hove, 1994; Jäger, 2005).

79   Recent studies have proven a tube microstructure to be a useful tool in deciphering the

80   true affinity of fossil serpulid (e.g., Bornhold and Milliman, 1973; Vinn, ten Hove and Mutvei,

81   2008; Vinn and Kupriyanova, 2011; Kupriyanova and Ippolitov, 2012; Vinn, 2013; Buckman,

82   2020; Buckman and Harries, 2020), and other calcareous tube-dwelling polychaete species

83   (Vinn, ten Hove and Mutvei, 2008; Taylor et al., 2010; Słowiński, Banasik and Vinn, 2023).

84   Anyhow, the majority of them were conducted based on single species, and/or single specimens.

85   In the present study, we performed a microstructural investigation of the Jurassic serpulid

86   tubes based on the representatives of the two main serpulid clades according to the newest

87   systematics (Kupriyanova, ten Hove and Rouse, 2023). We provide paleoecological implications

88   of different microstructures and consequently biomineralization system and highlight some

89   phylogenetic signals and evolutionary patterns of distinct microstructures.

90

91   **Material and its provenance**

92   The examined fossils consist of 47 specimens of serpulids representing 12 taxa (table 1).

93   The studied material has been selected from an ample collection (see Słowiński et al., 2020;

94   2022) concerning the well-preserved specimens, which allowed for a reliable ultrastructural

95   investigation. All taphonomically altered tubes have been discarded from further studies. Almost

96   all specimens encrust a variety of invertebrate fossils, oncoids, and hiatus concretions, and have

97   been derived from various localities with Middle and Upper Jurassic (upper Bajocian – lower

98   Kimmeridgian) deposits representing an array of paleoenvironments. The investigated material is

99   stored at the Institute of Earth Sciences in Sosnowiec, abbreviated GIUS 8-3589 (Callovian of

100 Zalas), GIUS 8-3730 (Gnaszyn Dolny), GIUS 8-3745 (Bolęcin), GIUS 8-3746 (Oxfordian of

101 Zalas), GIUS 8-3747 (Małogoszcz), GIUS 8-3750 (Ogrodzieniec-Świertowiec), GIUS 8-3751

102 (Krzyworzeka and Żarki). In ascending stratigraphical order, the localities are as follows:

103   Ogrodzieniec-Świertowiec: serpulids from this outcrop heavily encrust oncoids of

104 cyanobacterial genesis (Zatoń et al., 2012). The oncoids have been derived from condensed,

105 sandy, and carbonate layers, being overlain by clay sediments. This and the subsequent three

106 localities are situated within the area of the Polish Jura (Fig. 1). The deposits occur in the form of

107 dark siliciclastic sediments belonging to the Częstochowa Ore-bearing Clay Formation (e.g.,

108 Majewski, 2000; Matyja and Wierzbowski, 2000; Zatoń et al., 2011; Leonowicz, 2015). The late

109 Bajocian–early Bathonian age of the oncoid-bearing deposits was based on ammonites (Zatoń

110 and Taylor, 2009a; Zatoń et al., 2012), dinoflagellate cysts, and foraminifers (Słowiński, 2019).

111 Due to the origin of oncoids, the paleoenvironment is interpreted to be shallow marine, located

112 within the photic zone, and slightly below a fair-weather wave base (Zatoń et al., 2012).

113   Gnaszyn Dolny: serpulid tubes derived from this locality in majority encrust belemnite

114 rostra and oyster shells. The fossils come from middle Bathonian mudstones originating in

115 marine environment, below the storm wave base (Gedl and Kaim, 2012; Gedl et al., 2012).

116   Krzyworzeka: polychaetes from this site encrust carbonate hiatus concretions. The

117 concretion-bearing sediments from this locality are confined to the upper Bathonian (Poulsen,

118 1998). The deposits from Krzyworzeka belong to the northern sedimentary region of the Polish

119 Jura and originated in a calm outer shelf environment (Zatoń et al., 2011; Sadlok and Zatoń,

120 2020), located below the storm wave base (Różycki, 1953; Leonowicz, 2013).

121   Żarki: the deposits from which the serpulids encrusting hiatus concretions have been

122 derived are confined to the northern sedimentary region of the Polish Jura, and are represented by

123 the upper Bathonian mudstones (Zatoń and Taylor, 2009b). Sediments within this location

124 originated in a relatively calm but interrupted by episodic storm events (Leonowicz, 2015),

125 marine paleoenvironment (Marynowski et al., 2007; Leonowicz, 2012; 2013).

126   Bolęcin: the outcrop is situated approximately 6 km east of Chrzanów. The serpulid tubes

127 have been found within sandy limestones, presumably referring to the so-called "Balin Oolite."

128 Serpulid tubes have been found fixed to a variety of fossils including bivalves, gastropods, and

129 ammonites, as well as belemnite rostra. These condensed sediments (see Tarkowski et al., 1994;

130 Mangold et al., 1996) deposited presumably in an open marine paleoenvironment and are late

131 Bathonian-early Callovian in age (Mangold et al., 1996).

132   Zalas: the fossil material collected from this locality comes from two sites: 1) an active

133 quarry with sandy limestones forming a hardground of middle-earliest late Callovian age

134 (Giżejewska and Wieczorek, 1977; Dembicz and Praszkier, 2007); here, the serpulids encrust a

135 wide variety of invertebrate fossils, notably large *Ctenostreon proboscideum* (J. Sowerby and

136 G.B. Sowerby, 1820) bivalves. Hardground deposits originated in a deeper open marine setting

137 corresponding to a shelf environment (Dembicz and Praszkier, 2007; Zatoń, Wilson and Zavar,

138 2011); 2) overlying, lower Oxfordian light limestones hosting sponge bioherms (Matyja, 2006;

139 Matyszkiewicz, Kochman and Duś, 2012), to which serpulid tubes were attached.

140   Małogoszcz: serpulid fauna has been derived from an active quarry located in close

141 proximity to the town of Małogoszcz. This site is located in the southwestern part of the

142 Mesozoic margin of the Holy Cross Mountains. The tubes are attached to bivalve shells,

143 particularly the oyster *Actinostreon gregareum* (J. Sowerby, 1815). Lower Kimmeridgian

144 fossiliferous deposits are referred to as the Skorków Lumachelle (Kutek, 1994; Machalski, 1998;

145 Zatoń and Machalski, 2013). These shell beds were deposited during episodic storms in a

146 relatively shallow marine paleoenvironment (Machalski, 1998).

147
148 **Methods**

149   Before the preparation of specimens for the SEM examination, they were coated with

150   ammonium chloride and photographed using the Canon EOS camera. All previously selected

151   samples were cut longitudinally, polished, and etched with a 5% solution of acetic acid for one

152   minute prior to the SEM study. Part of these tube portions were oriented and mounted in epoxy

153   resin before polishing. Subsequently, the serpulid tube microstructure investigations were

154   performed on a SEM Zeiss EVO MA15 under a back-scattered electron detector (BSE) in a low

155   vacuum regime (Department of Geology, University of Tartu, Estonia). The sections were also

156   inspected under an environmental scanning electron microscope (ESEM) Philips XL30, and a

157   Quanta 250 scanning electron microscope using BSE imaging (both at the Institute of Earth

158   Sciences in Sosnowiec). The beam voltage was operated at 20 kV.

159   **Results**

160   During the examination of 12 taxa within eight genera representing two major clades,

161   three kinds of ultrastructure were distinguished: irregularly oriented prismatic structure (IOP),

162   spherulitic prismatic structure (SPHP), and simple prismatic structure (SP) (Table 1).

163   ***Filograninae (BI)***

164   Members of the clade Filograninae, formerly referred to as BI, are represented in the

165   herein material by two genera: *Metavermilia* and *Filogranula*, the latter one consisting of two

166   species: *F. runcinata* (J. de C. Sowerby, 1829) and *F. spongiophila* (J. Słowiński, O. Vinn, M.

167   Jäger et al., 2022).

168   The tube wall of *Metavermilia* cf. *striatissima* (F.T. Fürsich, T.J. Palmer, and K.L.

169   Goodyear, 1994) is single-layered, and composed of an irregularly oriented prismatic structure

170   (IOP) (Fig. 2). Minute (maximally a few μm), needle-like crystals are deployed more or less

171   evenly within the entire tube wall. Their crystallization axes are longitudinal and lack a uniform

172   orientation.

173   The tube of *Filogranula runcinata* is presumably single-layered and is composed of a

174   spherulitic, regularly oriented prismatic microstructure (SPHP) (Fig. 3). It is formed by crystals

175   of prismatic shape exhibiting a slightly spherulitic arrangement. Some internal parts of the tube

176   are built of irregularly oriented, tiny, elongated crystals indicating an irregularly oriented

177   prismatic structure (IOP). However, the boundary between the two putative layers is transitional

178   and the latter microstructure occurs rather like inclusions in certain areas of the tube wall.

179   Growth lines are apparent across almost the entire tube. Some minor, external parts of the section

180   may appear like fine homogeneous granular microstructure; however, more likely it corresponds

181   to the differences in preservation between the external and internal parts of the tube due to the

182   diagenetic alteration of irregularly oriented prismatic microstructure.

183   The tube of *Filogranula spongiophila* consists of a single layer that is composed of a

184   simple, regularly oriented prismatic structure (SP) (Fig. 4). Growth increments are visible across

185   almost the whole tube (Fig. 4C-E).

186

187

188   ***Serpulinae, tribe Serpulini (AI)***

189   This tribe is represented in the investigated material by one genus comprising two

190   species: *Cementula spirolinites* (Münster in Goldfuss, 1831) and *Cementula radwanskae* (J.

191   Słowiński, O. Vinn, M. Jäger et al., 2022).

192   The tube wall of *C. spirolinites* is single-layered and consists of a simple prismatic

193   structure (SP) (Fig. 5). This microstructure is formed by parallel prismatic crystals oriented

194   perpendicularly to each growth line showing incremental zonation. The crystals are arranged

195   perpendicularly or obliquely to the tube wall.

196   The tube microstructure of the investigated specimens of *C. radwanskae* is altered in

197   most places. However, some places exhibiting faint growth increments indicate possibly a simple

198   (SP) or spherulitic prismatic structure (SPHP) constituting a single layer (Fig. 6). Certain areas

199   with tiny, elongated irregularly oriented crystals presumably are an effect of a diagenetic

200   distortion of the tube wall.

201   ***Serpulinae, tribe Ficopomatini (AII)***

202   The tribe Ficopomatini, formerly referred to as AII, includes here 5 genera with 7 species.

203   *Propomatoceros lumbricalis* (E.F. Schlotheim, 1820) possesses a tube wall consisting of two or

204   three layers (Fig. 7). The majority of the examined specimens have two-layered tubes. The

205   external part is formed by a spherulitic prismatic structure (SPHP), which consists of parallel

206   crystals of a slightly spherulitic arrangement. The inner part has an irregularly oriented prismatic

207   microstructure (IOP) comprising elongated, but relatively short, tiny crystals with inconsistent

208   orientation axes. In some areas of the tubes' wall, the IOP structure is diagenetically altered

209   superficially resembling a fine homogeneous granular structure. The putative three-layered tube

210   wall (Fig. 7D) is built of the external and internal (uncertain) parts composed of a spherulitic

211 prismatic structure (SPHP). The middle part shows a fine homogeneous granular microstructure,

212 which may be either a primary microstructure or similarly to other specimens, an obliterated IOP

213 structure. In contrast to two-layered *P. lumbricalis* tubes, no areas exhibiting irregularly oriented

214 prismatic structures have been found. As such, it is not evident, whether these microstructures

215 are primary or have undergone diagenetic alteration. The external parts exhibit incremental

216 zonation with prominent chevron-shaped growth lines. The crystals are continuously and

217 regularly positioned through successive growth increments.

218   In the herein material *Nogrobs* is represented by three species: *N.* aff. *quadrilatera* (A.

219 Goldfuss, 1831), *N.* aff. *tetragona* (J. de C. Sowerby, 1829), and *N?* aff. *tricristata* (A. Goldfuss,

220 1831), which, however, share all the major microstructural characters. The tube walls of all the

221 species have two layers, which are separated from each other with a sharp boundary. The

222 external layer is composed of a simple prismatic structure (SP), whereas the internal layer is

223 composed of very thin, short, needle-like crystals, which make up an irregularly oriented

224 prismatic structure (IOP) (Fig. 8).

225   *Mucroserpula* sp. (H. Regenhardt, 1961) possesses a two-layered tube wall (Fig. 9). The

226 internal layer is composed of an irregularly oriented prismatic structure (IOP) consisting of

227 bunches of densely packed, short but elongated crystals lacking uniform orientation axes. The

228 external layer is composed of a regular spherulitic prismatic structure (SPHP), which constitutes

229 the major part of the tube wall. Within this layer, crystals are oriented perpendicularly with

230 respect to each incremental zone and have a somewhat prismatic arrangement. The chevron-

231 shaped growth lines are very well-visible alongside almost the whole tube length. The border

232 between the two layers is somewhat transitional.

233   The tube wall of *Placostegus planorbiformis* (Münster in Goldfuss, 1831) is single-

234 layered, and composed of a simple prismatic structure (SP) (Fig. 10). All crystals are more or

235 less parallel within each incremental zone. Within the outermost part of the tube, the crystals are

236 oriented perpendicularly to the tube wall.

237   The specimens of undetermined serpulid, Serpulidae sp. possess a two-layered tube wall

238 (Fig. 11). The external part features a regularly oriented simple prismatic structure (SP). The

239 internal, thinner part, separated from the external with a sharp boundary is formed by an

240 irregularly oriented prismatic structure (IOP) composed of densely packed, minute, elongated

241 crystals.

242

Discussion

Tube ultrastructure evolution and its phylogenetic constraints

Three distinct kinds of ultrastructure have been identified within 12 taxa corresponding to the two of three main clades of serpulids – Filograninae and Serpulinae (Kupriyanova, ten Hove and Rouse, 2023). These microstructures comprise irregularly oriented prismatic structure (IOP), spherulitic prismatic structure (SPHP), and simple prismatic structure (SP) (see Table 1), which are among the most prevalent microstructure kinds in fossil serpulids (Vinn et al., 2008; Vinn, 2020). Six of these taxa have single-layered tubes and six are two-layered, of which one taxon perhaps may possess either two or three ultrastructural layers (see discussion). The majority of both Cenozoic and contemporary serpulids are single-layered, only about one-third of serpulid species have at least two or up to four distinct ultrastructural layers (Vinn et al., 2008). During the Jurassic, the percentage of multi-layered serpulid species was lower, constituting approximately 25% (Vinn and Furrer, 2008). It may have resulted from the evolutionary pattern where more complex tube walls with at least two layers were more common from the beginning of the Cenozoic onward – the growing complexity of microstructures combined with relatively fast biomineralization likely enhanced the strengthening abilities of the tubes. It can also be explained by the vagaries of the fossil record resulting in incomplete preservation of the outermost layers, which might be similar to the case of calcareous sabellids (Vinn, ten Hove and Mutvei, 2008; Słowiński, Banasik and Vinn, 2023).

Sanfilippo (1998) presented a concept to utilize the ultrastructural diversity of serpulids to assess their generic determination. Further studies revealed that microstructure characters may be species-dependent (Vinn, 2007; Vinn et al., 2008; Kupriyanova and Ippolitov, 2015), which limits the application of tube microstructures in deciphering the generic affiliation of serpulids. Regardless, ultrastructural fabrics of tubes may still be used to approach the relationships between distinct kinds of structures throughout the evolution of the main serpulid clades (e.g., Vinn et al., 2008; Vinn and Kupriyanova, 2011; Vinn, 2013; Ippolitov and Rzhavsky, 2014; 2015a; b).

The most recent phylogenetic analyses indicate that serpulids are split into three major clades – Filograninae, Spirorbinae, and Serpulinae, the last of which is further subdivided into two tribes: Serpulini and Ficopomatini (Kupriyanova, ten Hove and Rouse, 2023). The family

273   Serpulidae until recently was maintained to comprise two major clades referred to as B and A,

274   separated into BI, BII, AI, and AII (Kupriyanova, Macdonald and Rouse, 2006, Kupriyanova et

275   al., 2009; Kupriyanova and Nishi, 2010). Formerly recognized clades BI and BII generally may

276   be related to Filograninae and Spirorbinae, whereas AI and AII, both settled within Serpulinae,

277   correspond to the tribes Serpulini and Ficopomatini, respectively. Apart from Spirorbinae

278   (former BII), members of all clades are present in the material studied.

279   Clade Filograninae is possibly rooted even in the Permian with primitive tubes such as

280   *Filograna* (Sanfilippo et al., 2017; Ramsdale, 2021), and abundantly represented in the fossil

281   record during the Mesozoic by many strongly ornamented tubes with several keels, e.g.,

282   *Vermiliopsis*, *Metavermilia*, and *Filogranula*, the latter two of which are present in the material

283   investigated. *Metavemilia* cf. *striatissima* is single-layered and possesses irregularly oriented

284   prismatic microstructure (IOP), which has been also found in the recent *Metavermilia*

285   *multicristata* (Vinn et al., 2008). It is characteristic of this clade and is also the most common

286   microstructure in the recent serpulids encompassing ca 60% of species (Vinn, 2007). IOP

287   microstructure most often builds the wall of single-layered tubes, or alternatively the inner part

288   of multi-layered tubes (see Vinn et al., 2008).

289   The representatives of Filograninae are generally characterized in the fossil record by

290   more or less uniform fabrics of tube microstructures forming irregularly oriented structures,

291   notably irregularly oriented prismatic structure (IOP). Secretion of such microstructures seems to

292   be governed by the lower biological control of an animal, compared to more advanced

293   microstructures. The first confirmed appearance of such ultrastructure dates back to the Early

294   Jurassic, possibly being present already in the Triassic (Vinn, Jäger and Kirsimäe, 2008). Such a

295   simpler way of tube formation may indicate its plesiomorphic character and earlier origin.

296   Another representative of this clade in the investigated material is the genus *Filogranula*

297   comprising the recently discovered new species *F. spongiophila* (Słowiński, Vinn, Jäger et al.,

298   2022), which has been studied with respect to ultrastructure for the first time, and by *F.*

299   *runcinata*. The tube wall of *F. spongiophila* is single-layered and has a simple prismatic structure

300   (SP), whereas *F. runcinata* possesses one well-preserved layer composed of spherulitic prismatic

301   structure (SPHP) and a dubious IOP layer consisting of somewhat distorted, occasionally

302   occurring areas of tiny, irregularly oriented crystals. As a result, the tube wall is interpreted as

303   single-layered, composed of SPHP structure. Such microstructure occurs commonly in the clade

304   Serpulinae comprising both formerly established "A" clades. The systematic position of the

305   fossil *Filogranula* seems to be complicated, as the Recent *Filogranula* is considered to be settled

306   within Filograninae, relatively closely related to *Vermiliopsis* and *Metavermilia* (Kupriyanova,

307   ten Hove and Rouse, 2023). While the Cretaceous *Filogranula cincta* (A. Goldfuss, 1831) is

308   classified as belonging to Filograninae too, the Jurassic *Filogranula runcinata* was considered to

309   be placed in Serpulinae, within the tribe Ficopomatini (see Ippolitov et al., 2014; Koči and Jäger,

310   2015), due to its prismatic microstructure, characteristic of the serpulid tubes appearing

311   transparent in the Recent species, such as e.g., *Placostegus*. On the other hand, prismatic

312   structures are not a fully satisfactory character in differentiating between former A and B clades.

313   Ippolitov and Rzhavsky (2014; 2015a; b) found out that some spirorbins may also have their

314   tubes composed of regularly oriented prismatic microstructures, in spite of the fact, that

315   Spirorbinae is phylogenetically closely related to Filograninae, which commonly form

316   irregularly oriented structures.

317   Serpulinae constitutes two well-supported tribes – Serpulini and Ficopomatini

318   (Kupriyanova, ten Hove and Rouse, 2023). The first unequivocal members of Serpulinae very

319   likely existed since the Triassic (Assmann, 1937) if not even since the Permian (Sanfilippo et al.,

320   2017; 2018). In contrast to Filograninae, which have mostly non-oriented structures, serpulids

321   within this lineage have a more advanced biomineralization system and are capable of forming

322   complex microstructures, such as e.g., oriented, lamello-fibrillar, or oriented-fibrillar (see Vinn

323   et al., 2008; Vinn and Kupriyanova, 2011). During the Jurassic, serpulid microstructure diversity

324   was relatively modest (ten kinds; see Vinn, 2020) compared to an array of contemporary and

325   Cenozoic ones (Vinn, 2007). The most sophisticated microstructures in serpulids evolved in the

326   Eocene (e.g., Vinn, 2008; Buckman, 2020). Although such complex microstructures as lamello-

327   fibrillar or regularly ridged prismatic appeared quite late in the evolution of serpulids, the

328   oriented prismatic structures evolved at the latest during the Middle Jurassic. Simple and

329   spherulitic prismatic microstructures are very common and characteristic of the Jurassic

330   Serpulinae and are considered to be apomorphic. Oriented prismatic structures are unknown

331   from any genus of Filograninae; however, they were found to persist in the Cretaceous clade

332   Spirorbinae (Ippolitov and Rzhavsky, 2015a; b), which may mean, that either it is plesiomorphic,

333   or the prismatic structures have evolved at least twice.

334   The tribe Serpulini is represented in the Jurassic by characteristically coiled *Spiraserpula*

335 and related *Cementula*, which is present in the herein material. *C. spirolinites* and *C. radwanskae*

336 are both single-layered and possess their tube walls built of simple prismatic microstructure (SP),

337 though in the latter it is somewhat obliterated. Simple and spherulitic prismatic microstructures

338 exhibit the predominantly uniform orientation of calcium carbonate crystals which determines

339 the optical transparency of the tubes (Zibrowius and ten Hove, 1987), supported also by the

340 dense arrangement of crystals and their large size (Vinn and Kupriyanova, 2011). In contrast, the

341 recent tubes with IOP microstructure most often are optically opaque (Vinn et al., 2008).

342   All the main members of the Jurassic representatives of Ficopomatini are present in the

343 investigated material. They contain genera with various morphotypes comprising a robust,

344 single-keeled *Propomatoceros*, a three-keeled *Mucroserpula*, quadrangular tubes attributed most

345 often to *Nogrobs*, and a well-defined, planispirally coiled *Placostegus*. Serpulids in this tribe

346 commonly possess two layers of tube walls having the outer dense layer built of ordered

347 prismatic structures (simple or spherulitic), and the internal layer composed of irregularly

348 oriented prismatic structure. Two-layered tubes appeared in the Jurassic (Vinn and Furrer, 2008)

349 and have their external layer denser than the internal, which is composed of thinner mineral

350 microstructure. Dense outer protective layers (DOL) have been found in tube walls of serpulids

351 inhabiting diverse environments (see Vinn and Kupriyanova, 2011). Consequently, rather than

352 being dependent on the environment, the advent of DOLs during the Jurassic appears to be a

353 significant evolutionary adaptation of serpulids. Except for one species in the clade Filograninae,

354 dense, outer layers exist exclusively in the clade Serpulinae (Vinn and Kupriyanova, 2011).

355   *Propomatoceros lumbricalis* and *Mucroserpula* possess here two well-distinguishable

356 layers: internal IOP and external SPHP. A single *Propomatoceros* specimen may have three

357 layers, which, however, is ambiguous, as its internal layer may be diagenetically obliterated, and

358 therefore all the specimens are considered two-layered. As discussed previously (Ippolitov et al.,

359 2014; Słowiński et al., 2022), it cannot be ruled out, that at least in some populations,

360 *Mucroserpula* and *Propomatoceros* may represent the same genus. The diagnostic characters of

361 both genera are highly transitional, subjective, and dependent to a large extent on different

362 variables, such as ontogenetic stage or diagenesis (see Słowiński et al., 2022). Nonetheless, the

363 microstructural fabrics of the two genera in our investigation are essentially the same and typical

364 of Ficopomatini.

365   *Nogrobs* consists here of three species: *N.* aff. *quadrilatera, N?* aff. *tricristata,* and *N.* aff.

366   *tetragona*. All of them are two-layered composed of internal IOP and external SP microstructure.

367   Apart from *Nogrobs*, Jurassic quadrangular fossils of serpulids that share morphological

368   similarities with this genus were attributed by various authors to different, partially uncertain

369   genera - *Tetraserpula, Tetraditrupa, Glandifera, Tubulostium, Tectorotularia,* and *Ditrupula*.

370   Kupriyanova and Ippolitov (2015) examined and reviewed a number of extant and fossil taxa

371   having tusk-shaped, tetragonal in cross-section tubes, concluding, that these morphologically

372   similar forms belong to several different genera, most likely being an effect of convergence. Not

373   surprisingly, these recent taxa cannot be synonymized with the fossil *Nogrobs*. Nevertheless, the

374   authors claim that at least the majority of fossil *Nogrobs* species may be members of a single

375   clade, as opposed to morphologically-related recent species. According to its external tube layer

376   composed of simple prismatic microstructure (responding to a transparent tube), the three

377   investigated species fit well Ficopomatini, confirming previous ultrastructural studies

378   (Kupriyanova and Ippolitov, 2012). It has to be noted, however, that the recent *Nogrobs*

379   *grimaldii* (P. Fauvel, 1909) has been found to possess an opaque tube (Kupriyanova and Nishi,

380   2011).

381   The only exception not having a two-layered tube wall within this tribe is *Placostegus*,

382   represented here by *P. planorbiformis*, which has a single layer made entirely of a simple

383   prismatic structure (SP). Similarly, contemporary *P. tridentatus* (J.C. Fabricius, 1779) possesses

384   a tube wall composed of a simple prismatic microstructure resulting in a completely transparent

385   tube (ten Hove and Kupriyanova, 2009: 8, fig. 1F; Vinn and Kupriyanova, 2011).

386   The undetermined serpulid taxon Serpulidae sp., described recently by Słowiński et al.

387   (2022) has been studied here with respect to its microstructure. Although the investigated

388   specimens externally resemble a few genera, such as *Propomatoceros*, *Placostegus*, and

389   *Metavermilia*, they do not exactly fit any of those taxa (see Słowiński et al., 2022). The

390   specimens possess a tube wall composed of two layers – external simple prismatic (SP), and

391   internal irregularly oriented prismatic microstructure (IOP), which is of a very close resemblance

392   to other members of Ficopomatini, notably *Nogrobs*.

393

394   ***Ecological implications and comparisons with sabellids***

395   Serpulids perform biologically controlled biomineralization where their cellular activity

396 regulates the nucleation and extracellular growth of the calcium carbonate crystals by the ion

397 uptake from the surrounding water (see Neff, 1971a; b) using a secretory epithelium, mediated

398 and controlled by the organic matrix (Vinn, Kirsimäe and ten Hove, 2009; Vinn, 2021a). As a

399 result, serpulids accomplish a specified crystal orientation within the tube wall, which is

400 reflected by their variety of ultrastructural fabrics - the growth direction of crystals may be

401 anisotropic, semi-oriented, or oriented (Weedon, 1994; Vinn et al., 2008). Apart from a matrix-

402 mediated crystallization (Vinn, 2021a), an alternative explanation has been proposed recently to

403 define the crystal orientation mechanism, which is based on a variable application of the

404 serpulid's collar rotational force between the formation of ordered and unordered microstructures

405 (Buckman and Harries, 2020). Considering the fact that the same growth increments may occur

406 across zones with diverse ultrastructures makes (Vinn, 2021a; b) this model strongly disputable.

407   The serpulid biomineralization system differs from that of other tube-dwelling

408 polychaetes. By the formation of the cylindrical and parable layers (see Jäger, 1983) serpulids

409 are capable of forming multi-layered tubes arranged in distinct microstructures (see Vinn et al.,

410 2008). Importantly, the parable layer is formed by adding secretory increments to the rim of the

411 worm's aperture allowing it to actively modify the external morphology according to the tube's

412 sculpture, but also depending on the temporary ecological requirements. Such a solution results

413 in a wide array of serpulid tube characters including attachment structures and base widenings of

414 the tube, which combined with the ability to form several layers greatly improves the durability

415 of the tube. Fossil cirratulids (Vinn, 2009; Taylor et al., 2010) and sabellids (Vinn, ten Hove and

416 Mutvei, 2008; Słowiński, Banasik and Vinn, 2023) possess single-layered tube wall composed of

417 a spherulitic prismatic structure. The presence of only cylindrical layer in sabellids strongly

418 impairs their biomineralization abilities. Unlike serpulids having mostly chevron-shaped growth

419 lines (see Weedon, 1994), they form their tubes by secreting calcareous material along distinct

420 growth lamellae oriented parallel to the tube wall (Vinn, ten Hove and Mutvei, 2008; Słowiński

421 et al., 2022). Subsequent increments are added to the internal surface of the tube, and therefore

422 *Glomerula* is unable to modify its simple tube architecture. A much longer secretion zone in

423 sabellids compared to serpulids enables them for a fast calcification incurring comparably lower

424 physiological costs, which allows them to considerably prolong their tubes. On the other hand,

425 such fast dispersal may be required by the diminishing inside of the tube, insufficient for the

426   growing worm. Interestingly, cirratulids perform a double-phased, combined controlled, and

427   influenced biomineralization. The products of an influenced biomineralization such as

428   agglutinated xenolithic granules within a calcareous matrix, as well as the anisotropic orientation

429   of different-sized crystals, indicate, that cirratulids govern even a weaker than sabellids control

430   over biomineralization (Guido et al., 2024).

431   A much more advanced biomineralization system of serpulids and the resulting variety of

432   microstructures are an important evolutionary adaptation for this taxon, which is an obligatory

433   tube-dweller. The emergence of multi-layered tubes with dense, outer protective layers during

434   the Jurassic could have been triggered by the intensified predation during the Mesozoic Marine

435   Revolution (Vermeij, 1977). With the skeleton development, serpulids could perform

436   competitive strategies against other organisms instead of avoiding competition or temporary

437   paleoenvironmental vagaries. Gradual increase in abundance of serpulids during the Mesozoic

438   and Cenozoic (see Ippolitov et al., 2014 for a review), and their advantage over other organisms

439   allowed for higher plasticity and divergence of different morphotypes (Vinn et al., 2023 (in

440   press)). Different morphogenetic programs in turn enhanced their functional utilization not only

441   by mechanical strengthening of the tubes but also by optimizing their space by planispiral

442   coiling, providing a higher feeding tier, avoiding being overgrown or coated by sediment thanks

443   to upward growth. Free-living serpulids with tusk-shaped tubes were presumably adapted to live

444   in or on the surface of soft sediment during episodes of increased sedimentation rates (see Vinn

445   et al., 2023 for a review (in press)). Sabellid biomineralization system allowed them to quickly

446   elongate their tubes but these polychaetes did not exhibit such diverse morphotypes. Instead,

447   they could grow irregularly away from the initial point of encrustation and perform an

448   opportunistic, fugitive strategy (see Taylor, 2016; Słowiński, Banasik and Vinn, 2023).

449   Additionally, it could be the outcome of biomineralization's lack of significance in this group as

450   calcareous sabellids were restricted to a single genus in the family.

451

452

453

454   **Conclusions**

455   The first thorough assessment of the ultrastructural diversity of Middle and Late Jurassic

456   serpulid tubes has been conducted. The obtained data reveal a characteristic of Jurassic serpulids,

457 a relatively low diversity of ultrastructural fabrics, which generally correspond to certain clades.

458 Amongst 12 taxa representing two (Filograninae and Serpulinae) of the three main serpulid

459 clades, six of them possess tube walls composed of a single layer, and six are two-layered. There

460 are certain evolutionary trends in tube ultrastructures. The representatives of the clade

461 Filograninae are single-layered and have their tube walls built of a primitive, irregularly oriented

462 prismatic microstructure (IOP). The majority of members of possibly apomorphic clade

463 Serpulinae possess two-layered tube walls, where the denser, external layer is composed of

464 oriented, prismatic microstructures (either spherulitic (SPHP) or simple(SP)), and the internal is

465 irregularly oriented prismatic (IOP). The exceptions are *Placostegus planorbiformis* and the

466 genus *Cementula*, which are single-layered, and built of simple prismatic structure (SP).

467   Serpulid tube ultrastructures reflect their biomineralization abilities providing important

468 paleoecological signatures. Formation of the regularly oriented microstructures of Serpulinae

469 requires a higher biological control over biomineralization compared to the more primitive,

470 anisotropic microstructures of Filograninae. The development of serpulid ultrastructure diversity

471 was likely triggered by the evolutionary importance of the tubes for this group. The formation of

472 dense outer protective layers in serpulids was presumably induced by increased predation rates

473 during the Mesozoic Marine Revolution. A variety of microstructure kinds and the ability to

474 form multi-layered tubes allowed serpulids to employ different morphogenetic programs, which

475 had an impact on their functional utilization.

476   The differences in the biomineralization system between serpulids and other tube-

477 dwelling polychaetes resulted from the importance of tubes for the former taxon. The complex

478 biomineralization system of serpulids resulted in a multiplicity of forms and an ability to form

479 robust, strongly ornamented tubes, which mechanically strengthened their durability. Although

480 higher energy expenditure of skeletal secretion decreased the rate of tube formation, the solid

481 attachment and skeleton robustness allowed for a competitive advantage over other encrusters.

482 Conversely, sabellid primitive biomineralization abilities presumably were elicited by the

483 unimportance of skeleton for this taxon resulting in a simplicity of forms. On the other hand, it

484 enabled a fast spreading over substrate shunning competition and disadvantageous conditions by

485 utilizing an opportunistic strategy of quick tube elongation.

486

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490

491 **References**

492   Assmann P. 1937. Revision der Fauna der Wirbellosen der oberschlesischen Trias.

493 *Abhandlungen der Preußischen Geologischen Landesanstalt* 170: 1–134.

494   Bałuk W, Radwański A. 1997. The micropolychaete *Josephella commensalis* sp.n.

495 commensal of the scleractinian coral *Tarbellastraea reussiana* (Milne-Edwards & Haime, 1850)

496 from the Korytnica Clays (Middle Miocene; Holy Cross Mountains, Central Poland). *Acta*

497 *Geologica Polonica* 47: 211–224.

498   Barnes RD. 1965. Tube-building and feeding in chaetopterid polychaetes. *Biological*

499 *Bulletin* 129: 217–233. DOI: 10.2307/1539840.

500   Bornhold BD, Milliman JD. 1973. Generic and environmental control of carbonate

501 mineralogy in serpulid (polychaete) tubes. *Journal of Geology* 81: 363–373. DOI:

502 10.1086/627876.

503   Buckman JO. 2020. The tube of *Ditrupa bartonensis* (Annelida, Serpulidae), from the

504 Eocene of southern England: Observations on microstructure and its significance.

505 *Palaeontologia Electronica* 23: a37. DOI: 10.26879/1098.

506   Buckman JO, Harries DB. 2020. Reef forming *Serpula vermicularis* from Scotland and

507 Ireland: Tube structure, composition and implications. *Zoologischer Anzeiger* 288: 53–65. DOI:

508 10.1016/j.jcz.2020.07.003.

509   Chamoy L, Nicola M, Ravaux J, Quennedey B, Gaill F, Delachambre J. 2001. A novel

510 chitin-binding protein from vestimentiferan *Riftia pachyptila* interacts specifically with β-chitin.

511 *Journal of Biological Chemistry* 276: 8051–8058. DOI: 10.1074/jbc.M009244200.

512   Dembicz K, Praszkier T. 2007. Kelowej południowo-wschodniej części Jury Krakowsko-

513 Częstochowskiej. *Tomy Jurajskie* 4: 71–76.

514   Fabricius O. 1779. *Reise nach Norwegen mit Bemerkungen aus der Naturhistorie und*

515 *Oekonomie*. Carl Ernst Bohn: Hamburg. 388 pp.

516   Fauvel P. 1909. Deuxiéme note préliminaire sur les Polychétes provenantdes campagnes

517 de l'Hirondelle et de la Princesse-Alice, ou déposéesdans la Musée Océanographique de

518 Monaco. *Bulletin de l'Institute Océeanographique* 142: 1–76.

519   Fischer R, Oliver CG, Reitner J. 1989. Skeletal structure, growth, and paleoecology of the

520   patch reef-building polychaete worm *Diplochaetetes mexicanus* Wilson, 1986 from the

521   Oligocene of Baja California (Mexico). *Geobios* 22: 761–775. DOI: 10.1016/S0016-

522   6995(89)80071-3.

523   Fischer R, Pernet B, Reitner J. 2000. Organomineralization of Cirratulid tubes – Fossil

524   and Recent examples. *Facies* 42: 35–50. DOI: 10.1007/BF02562565.

525   Fournier J, Etienne S, Le Cam JB. 2010. Inter- and intraspecific variability in the

526   chemical composition of the mineral phase of cements from several tube-building polychaetes.

527   *Geobios* 43: 191–200. DOI: 10.1016/j.geobios.2009.10.004.

528   Fürsich FT, Palmer TJ, Goodyear KL. 1994. Growth and disintegration of bivalve-

529   dominated patch-reefs in the Portlandian (Upper Jurassic) of southern England. *Palaeontology*

530   37: 131–171.

531   Gedl P, Kaim A. 2012. An introduction to the palaeoenvironmental reconstruction of the

532   Bathonian (Middle Jurassic) ore-bearing clays at Gnaszyn, Kraków-Silesia Homocline, Poland.

533   *Acta Geologica Polonica* 62: 267–280. DOI: 10.2478/v10263-012-0014-y.

534   Gedl P, Kaim A, Leonowicz P, Boczarowski A, Dudek T, Kędzierski M, Rees J, Smoleń

535   J, Szczepanik P, Sztajner P, Witkowska M, Ziaja J. 2012. Palaeoenvironmental reconstruction of

536   Bathonian (Middle Jurassic) ore-bearing clays at Gnaszyn, Kraków-Silesia Homocline, Poland.

537   *Acta Geologica Polonica* 62: 463–484. DOI: 10.2478/v10263-012-0026-7.

538   Giżejewska M, Wieczorek J. 1977. Remarks on the Callovian and lower Oxfordian of the

539   Zalas Area (Cracow Upland, Southern Poland). *Bulletin de l'Académie Polonaise des Sciences,*

540   *Série des Sciences de la Terre* 24: 167–175.

541   Goldfuss A. 1831. *Petrefacta Germaniae. I. Divisio secunda: Radiariorum Reliquiae -*

542   *Strahlenthiere der Vorwelt*. Arnz and Co.: Düsseldorf. 165–240.

543   Guido A, D'Amico F, DeVries TJ, Kočí T, Collareta A, Bosio G, Sanfilippo R. 2024.

544   Double-phased controlled and influenced biomineralization in marine invertebrates: The

545   example of Miocene to recent reef-building polychaete cirratulids from southern Peru.

546   *Palaeogeography, Palaeoclimatology, Palaeoecology* 639: 112060. DOI:

547   10.1016/j.palaeo.2024.112060.

548   Hausen H. 2005. Comparative structure of the epidermis in polychaetes (Annelida).

549   *Hydrobiologia* 535: 25–35. DOI: 10.1007/s10750-004-4442-x.

550   Hove HA ten, Kupriyanova EK. 2009. Taxonomy of Serpulidae (Annelida, Polychaeta):

551   the state of affairs. *Zootaxa* 2036: 1–126.

552   Ippolitov AP, Rzhavsky AV. 2014. Tube morphology, ultrastructures and mineralogy in

553   recent Spirorbinae (Annelida: Polychaeta: Serpulidae). I. General introduction. Tribe

554   Paralaeospirini. *Invertebrate Zoology* 11: 293–314. DOI: 10.15298/invertzool.11.2.01.

555   Ippolitov AP, Rzhavsky AV. 2015a. Tube morphology, ultrastructures and mineralogy in

556   recent Spirorbinae (Annelida: Polychaeta: Serpulidae). II. Tribe Spirorbini. *Invertebrate Zoology*

557   12: 61–92. DOI: 10.15298/invertzool.12.1.03.

558   Ippolitov AP, Rzhavsky AV. 2015b. Tube morphology, ultrastructures and mineralogy in

559   recent Spirorbinae (Annelida: Polychaeta: Serpulidae). III. Tribe Circeini. *Invertebrate Zoology*

560   12: 151–173. DOI: 10.15298/invertzool.12.2.03.

561   Ippolitov AP, Vinn O, Kupriyanova EK, Jäger M. 2014. Written in stone: history of

562   serpulid polychaetes through time. *Memoirs of Museum Victoria* 71: 123–159. DOI:

563   10.24199/j.mmv.2014.71.12.

564   Jäger, M. 1983. Serpulidae (Polychaeta sedentaria) aus der norddeutschen höheren

565   Oberkreide – Systematik, Stratigraphie, Ökologie. Geologisches Jahrbuch, Reihe A 68: 3–219.

566   Jäger M. 2005. Serpulidae und Spirorbidae (Polychaeta sedentaria) aus Campan und

567   Maastricht von Norddeutschland, den Niederlanden, Belgien und angrenzenden Gebieten.

568   *Geologisches Jahrbuch A* 157: 121–249.

569   Klompmaker AA. 2012. Drill hole predation on fossil serpulid polychaetes, with new

570   data from the Pliocene of the Netherlands. *Palaeogeography, Palaeoclimatology, Palaeoecology*

571   321–322: 113–120. DOI: 10.1016/j.palaeo.2012.01.024.

572   Kočí T, Bosio G, Collareta A, Sanfilippo R, Ekrt B, Urbina M, Malinverno E. 2021. First

573   report on the cirratulid (Annelida, Polychaeta) reefs from the Miocene Chilcatay and Pisco

574   Formations (East Pisco Basin, Peru). *Journal of South American Earth Sciences* 107: 103042.

575   DOI: 10.1016/j.jsames.2020.103042.

576   Kočí T, Jäger M. 2015. *Filogranula cincta* (Goldfuss, 1831), a serpulid worm

577   (Polychaeta, Sedentaria, Serpulidae) from the Bohemian Cretaceous Basin. *Sborník Národního*

578   *Muzea v Praze, řada B, Přírodní védy. Acta Musei Nationalis Pragae, Series B, Historia*

579   *Naturalis* 71: 293–300. DOI: 10.14446/AMNP.2015.293.

580   Kupriyanova EK, ten Hove HA, Rouse GW. 2023. Phylogeny of Serpulidae (Annelida,

581   Polychaeta) Inferred from Morphology and DNA Sequences, with a New Classification.

582   *Diversity* 15: 398. DOI: 10.3390/d15030398.

583   Kupriyanova EK, ten Hove HA, Sket B, Trontelj P, Zakšek V, Rouse GW. 2009.

584   Evolution of a unique freshwater cave-dwelling serpulid polychaete *Marifugia cavatica* Absolon

585   and Hrabě, 1930. *Systematics and Biodiversity* 7: 389–401.

586   Kupriyanova EK, Ippolitov AP. 2012. Are Mesozoic shallow-water serpulids (Annelida,

587   Polychaeta) ancestors of the Recent deep-sea fauna? Abstracts of the 13th Deep-Sea Biology

588   Symposium, Wellington, New Zealand.

589   Kupriyanova EK, Ippolitov AP. 2015. Deep-sea serpulids (Annelida: Polychaeta) in

590   tetragonal tubes: on a tube convergence path from the Mesozoic to Recent. *Zootaxa* 4044: 151–

591   200. DOI: 10.11646/zootaxa.4044.2.1.

592   Kupriyanova EK, Macdonald TA. Rouse GW. 2006. Phylogenetic relationships within

593   Serpulidae (Sabellida, Annelida) inferred from molecular and morphological data. *Zoologica*

594   *Scripta* 35: 421–439. DOI: 10.1111/j.1463-6409.2006.00244.x.

595   Kupriyanova EK, Nishi E. 2010. Serpulidae (Annelida, Polychaeta) from Patton-Murray

596   Seamounts, Gulf of Alaska, North Pacific Ocean. *Zootaxa* 2665: 51–68. DOI:

597   10.11646/zootaxa.2665.1.3.

598   Kupriyanova EK, Nishi E. 2011. New records of the deep-sea *Nogrobs grimaldii*

599   (Serpulidae: Annelida). *Marine Biodiversity Records* 4: 1–4. DOI:

600   10.1017/S1755267211000674.

601   Kutek J. 1994. Jurassic tectonic events in south-eastern cratonic Poland. *Acta Geologica*

602   *Polonica* 44: 167–222.

603   Leonowicz P. 2012. Sedimentology and ichnology of Bathonian (Middle Jurassic) ore-

604   bearing clays at Gnaszyn, Kraków-Silesia Homocline, Poland. *Acta Geologica Polonica* 62:

605   281–296.

606   Leonowicz P. 2013. The significance of mudstone fabric combined with palaeoecological

607   evidence in determining sedimentary processes–an example from Middle Jurassic of southern

608   Poland. *Geological Quarterly* 57: 243–260. DOI: 10.7306/gq.1092.

609   Leonowicz P. 2015. Ichnofabrics of shallow-marine mudstone, the result of changing

610   environmental conditions: an example from the Middle Jurassic ore-bearing clay from southern

611   Poland. *Facies* 61: 11. DOI: 10.1007/s10347-015-0438-4.

612   Machalski M. 1998. Oyster life positions and shell beds from the Upper Jurassic of

613   Poland. *Acta Palaeontologica Polonica* 43: 609–634.

614   Majewski W. 2000. Middle Jurassic concretions from Częstochowa (Poland) as indicators

615   of sedimentation rates. *Acta Geologica Polonica* 50: 431–439.

616   Mangold C, Marchand D, Thierry J, Tarkowski R. 1996. Les Ammonites de l'Oolite de

617   Balin (Pologne); nouvelles données et réinterprétation stratigraphique. *Reuve de Palèobiologie*

618   15: 55–77.

619   Marynowski L, Zatoń M, Simoneit BRT, Otto A, Jędrysek MO, Grelowski C,

620   Kurkiewicz S. 2007. Compositions, sources and depositional environments of organic matter

621   from the Middle Jurassic clays of Poland. *Applied Geochemistry* 22: 2456–2485. DOI:

622   10.1016/j.apgeochem.2007.06.015.

623   Matyja BA. 2006. Stop A17—Zalas Quarry. Callovian transgressive to condensed pelagic

624   deposits, Lower to lowermost Middle Oxfordian deposits of sponge megafacies. In:

625   Wierzbowski A, Aubrecht R, Golonka J, Gutowski J, Krobicki M, Matyja BA, Pieńkowski G,

626   Uchman A, eds. *Jurassic of Poland and Adjacent Slovakian Carpathians*. Field Trip Guidebook

627   of 7th International Congress on the Jurassic System Poland, Kraków, September 6–18, 2006,

628   70–72. Kraków, Poland.

629   Matyja BA, Wierzbowski A. 2000. Ammonites and stratigraphy of the uppermost

630   Bajocian and Lower Bathonian between Częstochowa and Wieluń, Central Poland. *Acta*

631   *Geologica Polonica* 50: 191–209.

632   Matyszkiewicz J, Kochman A, Duś A. 2012. Influence of local sedimentary conditions on

633   development of microbialites in the Oxfordian carbonate buildups from the southern part of the

634   Kraków-Częstochowa Upland (South Poland). *Sedimentary Geology* 263–264: 109–132.

635   Morton B, Harper EM. 2009. Drilling predation upon *Ditrupa arietina* (Polychaeta:

636   Serpulidae) from the Mid-Atlantic Açores, Portugal. *Açoreana, Suplemento, Açores* 6: 157–165.

637   Neff JM. 1971a. Ultrastructural studies of the secretion of calcium carbonate by the

638   serpulid polychaete worm, *Pomatoceros caeruleus*. *Zeitschrift für Zellforschung und*

639   *Mikroskopische Anatomie* 120: 160–186. DOI: 10.1007/BF00335534.

640   Neff JM. 1971b. Ultrastructure of calcium phosphate-containing cells in the serpulid

641 polychaete worm *Pomatoceros caeruleus*. *Calcified Tissue Research* 7: 191–200. DOI:

642 10.1007/BF02062606.

643   Nishi E, Rouse GW. 2013. First whale fall chaetopterid; a gigantic new species of

644 *Phyllochaetopterus* (Chaetopteridae: Annelida) from the deep sea off California. *Proceedings of*

645 *the Biological Society of Washington* 126: 287–298. DOI: 10.2988/0006-324X-126.4.287.

646   Perkins, T.H. 1991: *Calcisabella piloseta*, a new genus and species of Sabellinae

647 (Polychaeta: Sabellidae). *Bulletin of Marine Science* 48: 261–267.

648   Pillai TG. 1993. A review of some Cretaceous and Tertiary serpulid polychaetes of the

649 genera *Cementula* and *Spiraserpula* Regenhardt 1961, *Laqueoserpula* Lommerzheim 1979 and

650 *Protectoconorca* Jäger 1983. *Paläontologische Zeitschrift* 67: 69–88. DOI:

651 10.1007/BF02985871.

652   Pillai TG, ten Hove HA. 1994. On recent species of *Spiraserpula* Regenhardt, 1961, a

653 serpulid polychaete genus hitherto known only from Cretaceous and Tertiary fossils. *Bulletin of*

654 *the Natural History Museum, London (Zoology)* 60: 39–104.

655   Poulsen N. 1998. Upper Bajocian to Callovian (Jurassic) dinoflagellate cysts from central

656 Poland. *Acta Geologica Polonica* 48: 237–245.

657   Ramsdale R. 2021. A possible serpulid tube worm of the genus *Filograna* from the upper

658 Permian Cadeby Formation of South Yorkshire, UK. *Proceedings of the Yorkshire Geological*

659 *Society* 63: pygs2020-016. DOI: 10.1144/pygs2020-016.

660   Regenhardt H. 1961. Serpulidae (Polychaeta sedentaria) aus der Kreide Mitteleuropas,

661 ihre ökologische, taxionomische und stratigraphische Bewertung. *Mitteilungen aus dem*

662 *Geologischen Staatsinstitut in Hamburg* 30: 5–115.

663   Reish DJ. 1952. Discussion of the Colonial Tube-Building Polychaetous Annelid

664 *Dodecaceria fistulicola* Ehlers. *Bulletin of the Southern California Academy of Sciences* 51:

665 103–107.

666   Rouse GW, Pleijel F. 2001. *Polychaetes*. Oxford: Oxford University Press. 354 pp.

667   Różycki SZ. 1953. Górny dogger i dolny malm Jury Krakowsko-Częstochowskiej.

668 *Przegląd Instytutu Geologicznego* 17: 1–420.

669   Sadlok G, Zatoń M. 2020. Ichnology of the Middle Jurassic hiatus concretions from

670   Poland: implications for their formation, exhumation, and palaeoenvironment.

671   *Palaeobiodiversity and Palaeoenvironments* 100: 757–771. DOI: 10.1007/s12549-019-00410-6.

672   Sanfilippo R. 1998. Tube morphology and structure of the bathyal Maditerranean serpulid

673   *Hyalopomatus variorugosus* Ben-Eliahu et Fiege, 1996 (Annelida, Polychaeta). *Rivista Italiana*

674   *di Paleontologia e Stratigrafia* 104: 131–138. DOI: 10.13130/2039-4942/6124.

675   Sanfilippo R, Rosso A, Reitano A, Insacco G. 2017. First record of sabellid and serpulid

676   polychaetes from the Permian of Sicily. *Acta Palaeontologica Polonica* 62: 25–38. DOI:

677   10.4202/app.00288.2016.

678   Sanfilippo R, Rosso A, Reitano A, Viola A, Insacco G. 2018. New serpulid polychaetes

679   from the Permian of western Sicily. *Acta Palaeontologica Polonica* 63: 579–584. DOI:

680   10.4202/app.00448.2017.

681   Schlotheim EF von 1820. *Die Petrefactenkunde auf ihrem jetzigen Standpunkte*. Gotha:

682   Becker. 437 pp.

683   Słowiński J. 2019. Środkowojurajskie onkoidy z okolic Ogrodzieńca. Unpublished M.Sc.

684   Thesis, University of Silesia, Sosnowiec. 57 pp.

685   Słowiński J, Banasik K, Vinn O. 2023. Insights into mineral composition and

686   ultrastructure of Jurassic sabellid tubes (Annelida, Polychaeta): the evolution of sabellid

687   calcification and its palaeoecological implications. *Lethaia* 56: 1–12. DOI: 10.18261/let.56.3.8.

688   Słowiński J, Surmik D, Duda P, Zatoń M. 2020. Assessment of serpulid-hydroid

689   association through the Jurassic: A case study from the Polish Basin. *PLOS ONE* 15: e0242924.

690   DOI: 10.1371/journal.pone.0242924.

691   Słowiński J, Vinn O, Jäger M, Zatoń M. 2022: Middle and Late Jurassic tube-dwelling

692   polychaetes from the Polish Basin: diversity, palaeoecology and comparisons with other

693   assemblages. *Acta Palaeontologica Polonica* 67: 827–864. DOI: 10.4202/app.01006.2022.

694   Sowerby J. 1815. *The Mineral Conchology of Great Britain*. London: The Author. 234

695   pp.

696   Sowerby J, Sowerby GB. 1820. *The Genera of Recent and Fossil Shells, For the Use of*

697   *Students in Conchology and Geology*. London: G.B. Sowerby. 275 pp.

698   Sowerby J de C. 1829. *The Mineral Conchology of Great Britain*. London: The Author.

699   230 pp.

700 Stewart RJ, Weaver JC, Morse DE, Waite JH. 2004. The tube cement of *Phragmatopoma*

701 *californica*: a solid foam. *Journal of Experimental Biology* 207: 4727–4734. DOI:

702 10.1242/jeb.01330.

703 Tanur AE, Gunari N, Sullan RMA, Kavanagh CJ, Walker GC. 2010. Insights into the

704 composition, morphology, and formation of the calcareous shell of the serpulid *Hydroides*

705 *dianthus*. *Journal of Structural Biology* 169: 145–160. DOI: 10.1016/j.jsb.2009.09.008.

706 Tarkowski R, Thierry J, Marchand D, Mangold C, Delance JH, Garcia JP, Laurin B.

707 1994. L'"oolithe de Balin" (Pologne méridionale). Nouvelles observations et interprétations

708 stratigraphiques. The "Balin Oolithe" (Southern Poland). New observations and stratigraphical

709 interpretations. *Geobios* 27: 461–467.

710 Taylor PD. 2016. Competition between encrusters on marine hard substrates and its fossil

711 record. *Palaeontology* 59: 481–497. DOI: 10.1111/pala.12239.

712 Taylor PD, Vinn O, Kudryavtsev A, Schopf JW. 2010. Raman spectroscopic study of the

713 mineral composition of cirratulid tubes (Annelida, Polychaeta). *Journal of Structural Biology*

714 171: 402–405. DOI: 10.1016/j.jsb.2010.05.010.

715 Vermeij GJ. 1977. The Mesozoic marine revolution: evidence from snails, predators and

716 grazers. *Paleobiology* 3: 245–258.

717 Vinn O. 2007. Taxonomic implications and fossilization of tube ultrastructure of some

718 Cenozoic serpulids (Annelida, Polychaeta) from Europe. *Neues Jahrbuch für Geologie und*

719 *Paläontologie Abhandlungen* 244: 115–128. DOI: 10.1127/0077-7749/2007/0244-0115.

720 Vinn O. 2008. Tube ultrastructure of the fossil genus *Rotularia* Defrance, 1827

721 (Polychaeta, Serpulidae). *Journal of Paleontology* 82: 206–212. DOI: 10.1666/06-125.1.

722 Vinn O. 2009. The ultrastructure of calcareous cirratulid (Polychaeta, Annelida) tubes.

723 *Estonian Journal of Earth Sciences* 58: 153–156. DOI: 10.3176/earth.2009.2.06.

724 Vinn O. 2013. SEM Study of semi-oriented tube microstructures of Serpulidae

725 (Polychaeta, Annelida): implications for the evolution of complex oriented microstructures.

726 *Microscopy Research and Technique* 76: 453–456. DOI: 10.1002/jemt.22186.

727 Vinn O. 2020. Biomineralization of Polychaete Annelids in the Fossil Record. *Minerals*

728 10: 858. DOI: 10.3390/min 10100858.

729 Vinn O. 2021a. Biomineralization in Polychaete Annelids: A Review. *Minerals* 11: 1151.

730 DOI: 10.3390/min11101151.

731   Vinn O. 2021b. The Role of Aragonite in Producing the Microstructural Diversity of
732   Serpulid Skeletons. *Minerals* 11: 1435. DOI: 10.3390/min11121435.

733   Vinn O, Furrer H. 2008. Tube structure and ultrastructure of serpulids from the Jurassic
734   of France and Switzerland, its evolutionary implications. *Neues Jahrbuch für Geologie und*
735   *Paläontologie, Abhandlungen* 250: 129–135. DOI: 10.1127/0077-7749/2008/0250-0129.

736   Vinn O, ten Hove HA, Mutvei H. 2008. On the tube ultrastructure and origin of
737   calcification in sabellids (Annelida, Polychaeta). *Palaeontology* 51: 295–301. DOI:
738   10.1111/j.1475-4983.2008.00763.x.

739   Vinn O, ten Hove HA, Mutvei H, Kirsimäe K. 2008. Ultrastructure and mineral
740   composition of serpulid tubes (Polychaeta, Annelida). *Zoological Journal of the Linnean Society*
741   154: 633–650. DOI: 10.1111/j.1096-3642.2008.00421.x.

742   Vinn O, Jäger M, Kirsimäe K. 2008. Microscopic evidence of serpulid affinities of the
743   problematic fossil tube "*Serpula*" *etalensis* from the Lower Jurassic of Germany. *Lethaia* 41:
744   417–421. DOI: 10.1111/j.1502-3931.2008.00093.x.

745   Vinn O, Jäger M, Słowiński J, Zatoń M. 2023. Convergent evolution of encrusting
746   calcareous tubeworms. *Palaeoworld* (in press). DOI: 10.1016/j.palwor.2023.04.001.

747   Vinn O, Kirsimäe K, ten Hove HA. 2009. Tube ultrastructure of *Pomatoceros*
748   *americanus* (Polychaeta, Serpulidae): Implications for the tube formation of serpulids. *Estonian*
749   *Journal of Earth Sciences* 58: 148–152. DOI: 10.3176/earth.2009.2.05.

750   Vinn O, Kupriyanova EK. 2011. Evolution of a dense outer protective tube layer in
751   serpulids (Polychaeta, Annelida). *Carnets de Géologie-Notebooks on Geology* Letter CG2011/05
752   (CG2011_ L05) 137–147. DOI: 10.4267/2042/43896.

753   Vinn O, Luque J. 2013. First record of a pectinariid-like (Polychaeta, Annelida)
754   agglutinated worm tube from the Late Cretaceous of Colombia. *Cretaceous Research* 41: 107–
755   110. DOI: 10.1016/j.cretres.2012.11.004.

756   Weedon MJ. 1994. Tube microstructure of Recent and Jurassic serpulid polychaetes and
757   the question of the Palaeozoic 'spirorbids'. *Acta Palaeontologica Polonica* 39: 1–15.

758   Zatoń M, Kremer B, Marynowski L, Wilson MA, Krawczyński W. 2012. Middle Jurassic
759   (Bathonian) encrusted oncoids from the Polish Jura, southern Poland. *Facies* 58: 57–77. DOI:
760   10.1007/s10347-011-0273-1.

761   Zatoń M, Machalski M. 2013. Oyster-microbial rolling stones from the Upper Jurassic

762 (Kimmeridgian) of Poland. *Palaios* 28: 839–850. DOI: 10.2110/palo.2013.025.

763   Zatoń M, Machocka S, Wilson MA, Marynowski L, Taylor PD. 2011. Origin and

764 paleoecology of Middle Jurassic hiatus concretions from Poland. *Facies* 57: 275–300. DOI:

765 10.1007/s10347-010-0244-y.

766   Zatoń M, Marynowski L, Bzowska G. 2006. Konkrecje hiatusowe z iłów rudonośnych

767 Wyżyny Krakowsko-Częstochowskiej. Przegląd Geologiczny 54: 131–138.

768   Zatoń M, Taylor PD. 2009a. Microconchids (Tentaculita) from the Middle Jurassic of

769 Poland. *Bulletin of Geosciences* 84: 653–660. DOI: 10.3140/bull.geosci.1167.

770   Zatoń M, Taylor PD. 2009b. Middle Jurassic cyclostome bryozoans from the Polish Jura.

771 *Acta Palaeontologica Polonica* 54: 267–288. DOI: 10.4202/app.2008.0088.

772   Zatoń M, Wilson MA, Zavar E. 2011. Diverse sclerozoan assemblages encrusting large

773 bivalve shells from the Callovian (Middle Jurassic) of southern Poland. *Palaeogeography,*

774 *Palaeoclimatology, Palaeoecology* 307: 232–244. DOI: 10.1016/j.palaeo.2011.05.022.

775   Zhao H, Sun C, Stewart RJ, Waite JH. 2005. Cement proteins of the tube-building

776 polychaete *Phragmatopoma californica*. *Journal of Biological Chemistry* 280: 42938–42944.

777 DOI: 10.1074/jbc.

778   Zibrowius H, ten Hove HA. 1987. *Neovermilia falcigera* (Roule, 1898) a deep- and cold-

779 water serpulid polychaete common in the Mediterranean Plio-Pleistocene. *Bulletin of Biological*

780 *Society of Washington* 7: 259–271.

Figure 1

Figure 1: Geology of the investigated area.

(A) geological sketch-map of Poland without the Cenozoic cover showing three sampled sites; HCM–Holy Cross Mountains; PJ–Polish Jura; 1–Bolęcin; 2–Zalas; 3–Małogoszcz. (**B**) geological map of the Polish Jura area without Quaternary cover, with sampled localities indicated (modified after Zatoń, Marynowski and Bzowska, 2006).
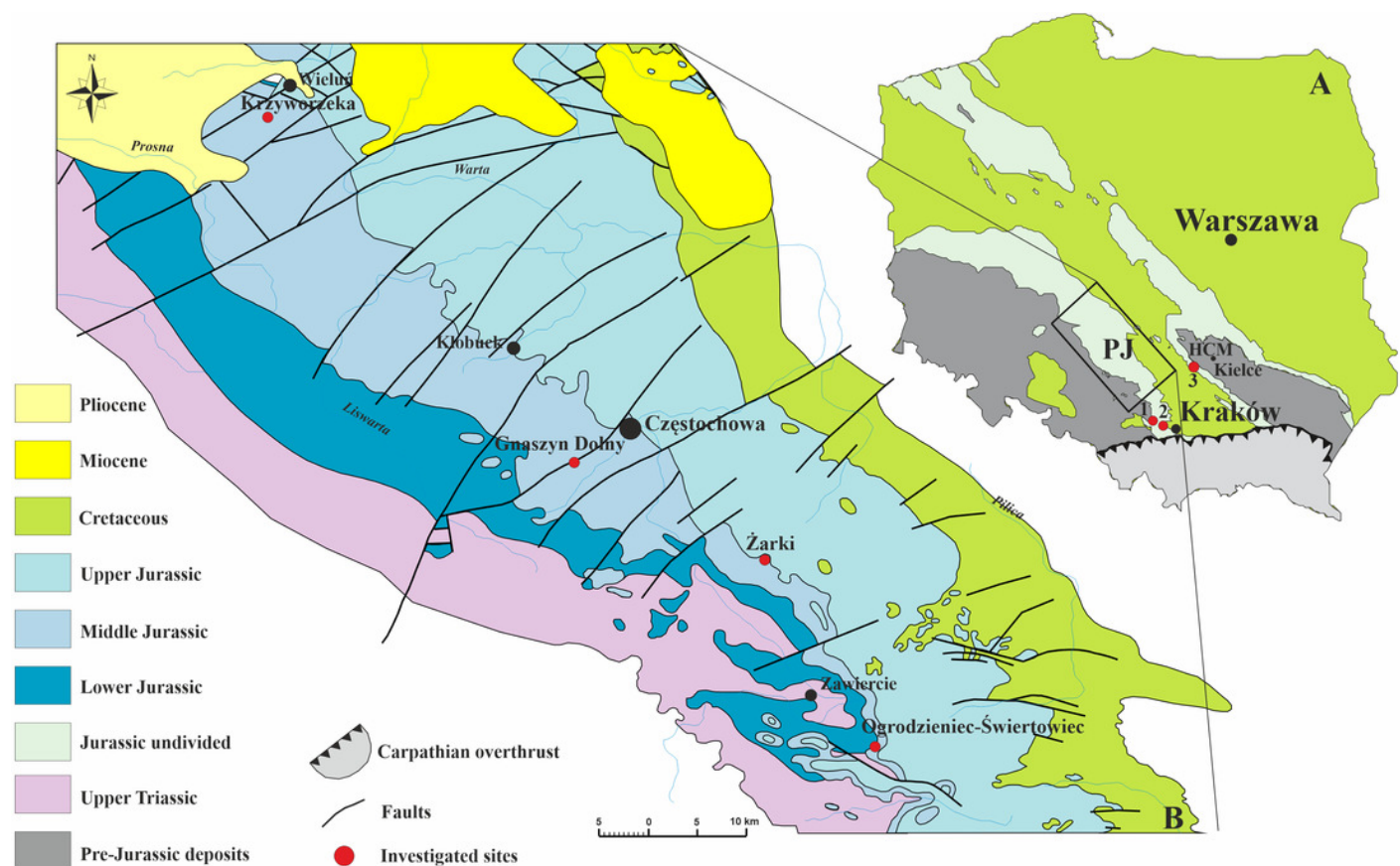
Figure 2

Figure 2: Selected specimens of *Metavermilia* cf. *striatissima* (F.T. Fürsich, T.J. Palmer, and K.L. Goodyear, 1994) from the Jurassic of Poland.

(A, B) *Metavermilia* cf. *striatissima* encrusting the interior of the boring *Gastrochaenolites* from the upper Bathonian of Krzyworzeka, Polish Jura (**A.** GIUS 8-3751/3; **B.** GIUS 8-3751/8). (**C, D**) Longitudinal sections of the tubes from the upper Bathonian of Krzyworzeka with visible irregularly oriented prismatic structure (IOP). (**C**) General look of the ground, polished and etched tube with visible thin, single-layered walls (GIUS 8-3751/3). (**D**) Close-up of the tube wall section showing densely packed, tiny, elongated prismatic crystals of irregular arrangement (GIUS 8-3751/3).
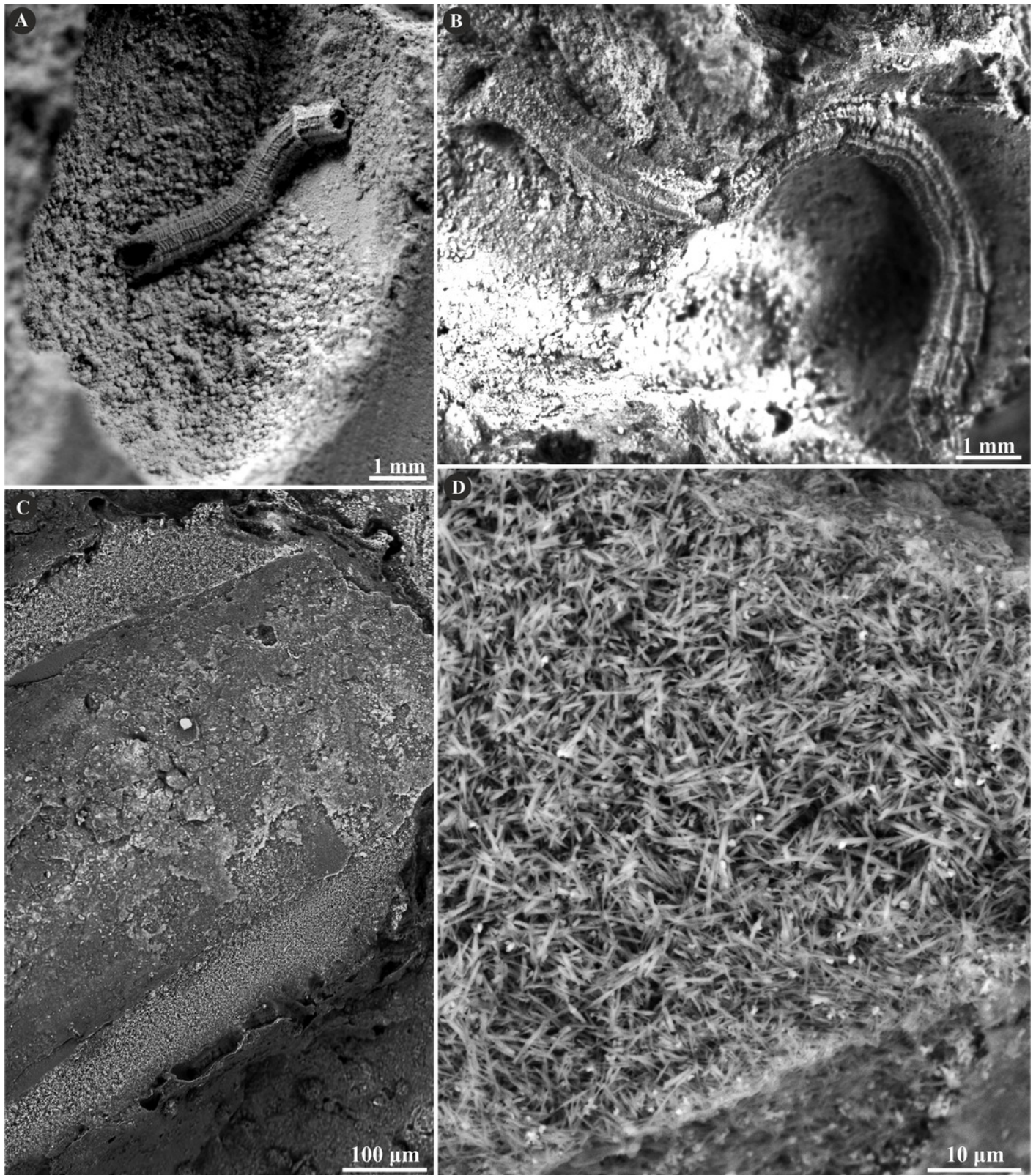
Figure 3

Figure 3: Selected specimens of *Filogranula runcinata* (J. de C. Sowerby, 1829) from the Jurassic of Poland.

(A, B) *Filogranula runcinata* from the middle Bathonian of Gnaszyn Dolny (**A.** GIUS 8-3730/10) and the Callovian of Zalas (**B.** GIUS 8-3589/6) encrusting shell fragments. (**C-F)** Longitudinal sections of the tubes showing a single-layered tube wall built of spherulitic prismatic structure (SPHP) with well-visible growth increments (GIUS 8-3730/10).
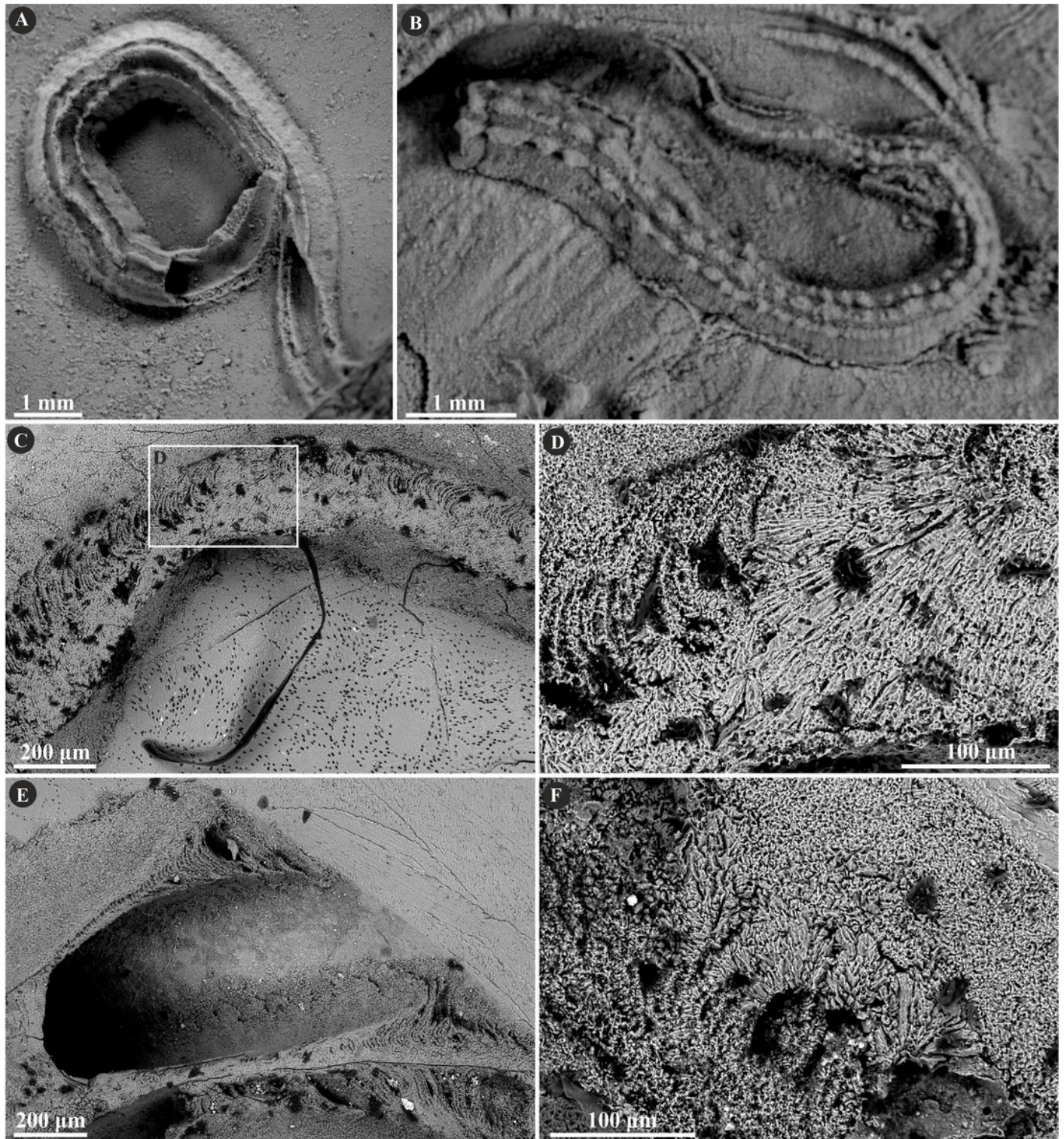
Figure 4

Figure 4: Selected specimens of *Filogranula spongiophila* (J. Słowiński, O. Vinn, M. Jäger, et al., 2022) from the Jurassic of Poland.

(A, B) *Filogranula spongiophila* from the Oxfordian of Zalas (**A.** GIUS 8-3746/2; **B.** GIUS 8-3746/3) encrusting sponge fragments. **(C-E)** Longitudinal sections of the tubes showing the simple prismatic structure (SP) with well-visible growth increments (GIUS 8-3746/9).
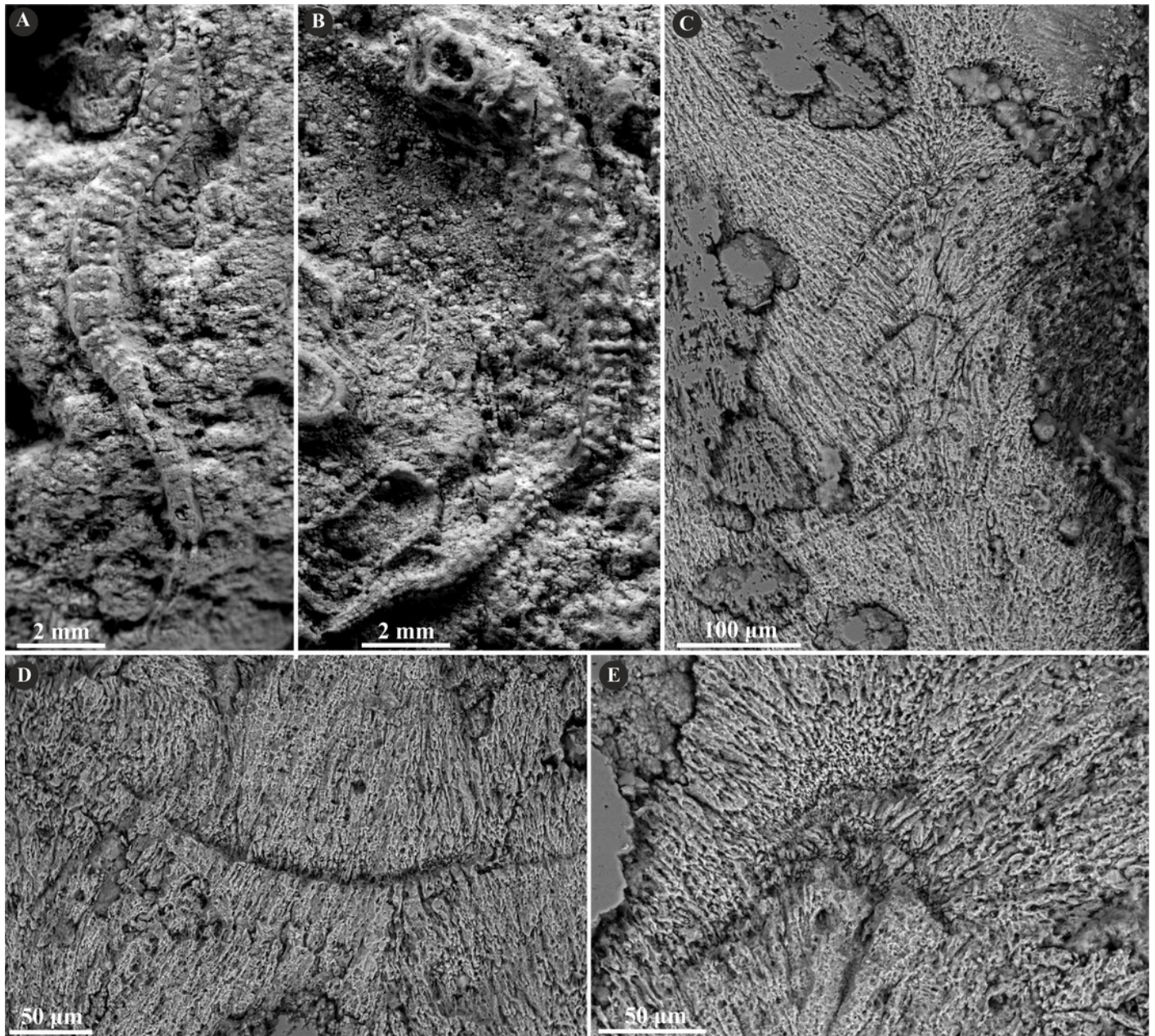
Figure 5

Figure 5: Selected specimens of *Cementula spirolinites* (Münster in Goldfuss, 1831) from the Jurassic of Poland.

(A) *Cementula spirolinites* from the Oxfordian of Zalas encrusting a sponge fragment (GIUS 8-3746/4). **(B-D)** Longitudinal sections of the tubes showing the simple prismatic structure (SP). **(B)** GIUS 8-3746/10; **(C, D)** GIUS 8-3746/11.
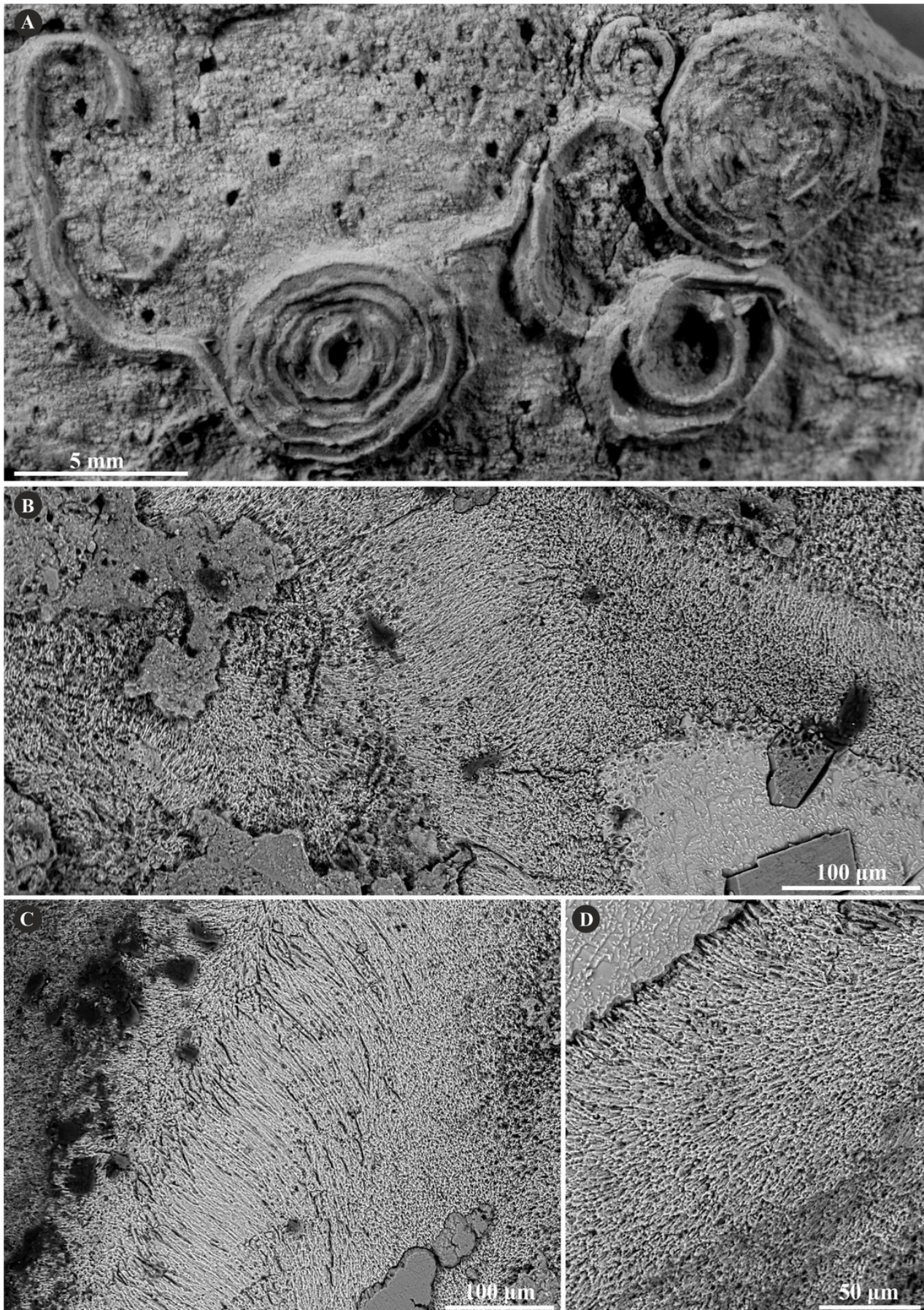
Figure 6

Figure 6: Selected specimens of *Cementula radwanskae* (J. Słowiński, O. Vinn, M. Jäger, et al., 2022) from the Jurassic of Poland.

(A, B) *Cementula radwanskae* from the Callovian of Zalas encrusting shell fragments (**A.** 8-3589/7; **B.** GIUS 8-3589/10). **(C-E)** Longitudinal sections of the tubes showing mostly altered, presumably simple prismatic microstructure (SP); GIUS 8-3589/18. Note the weak growth increments in **C**.
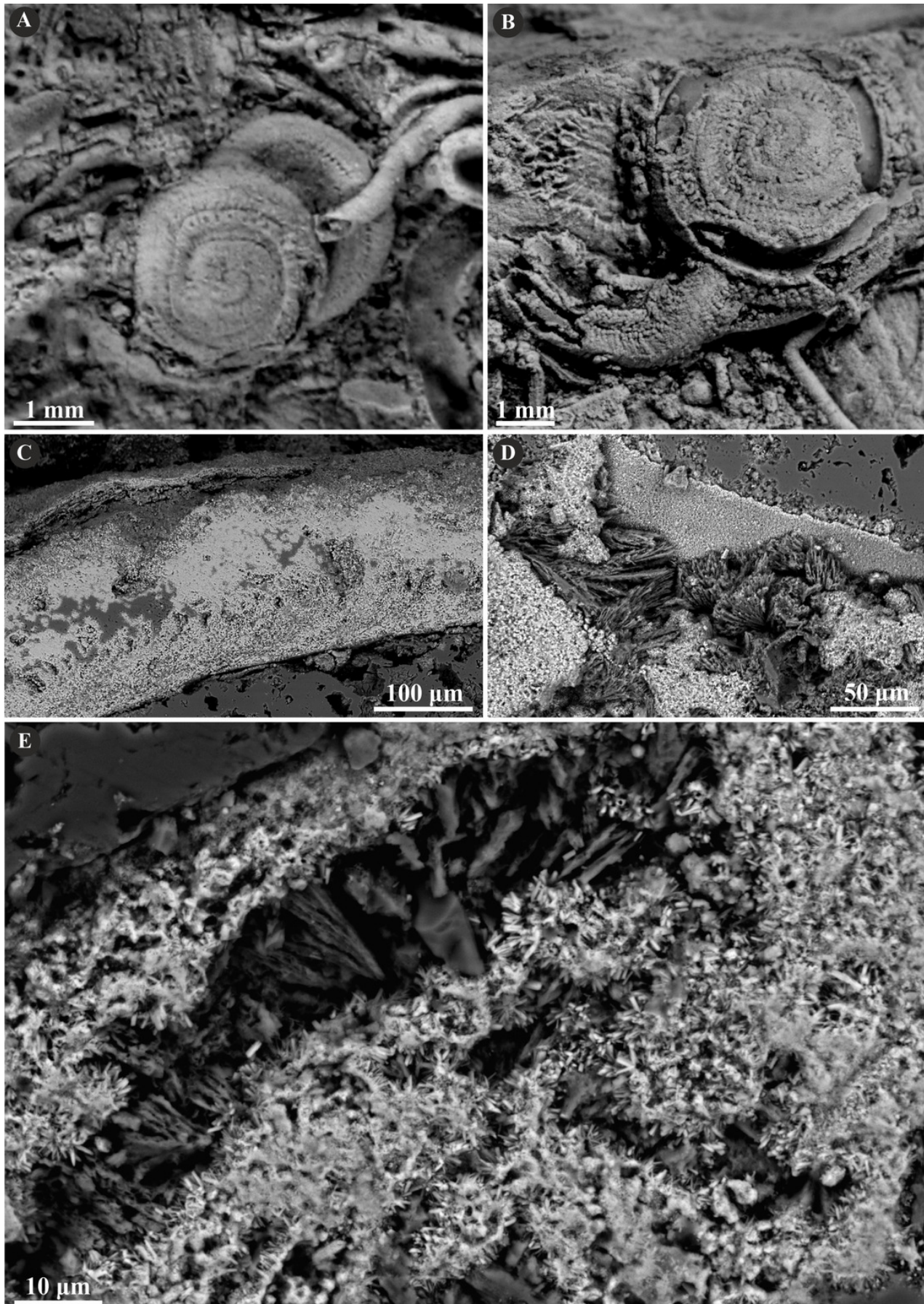
Figure 7

Figure 7: Selected specimens of *Propomatoceros lumbricalis* (E.F. Schlotheim, 1820) from the Jurassic of Poland.

(A, B) *Propomatoceros lumbricalis* encrusting a shell fragment from the Callovian of Zalas (**A.** GIUS 8-3589/11; **B.** GIUS 8-3589/12). **(C)** *Propomatoceros lumbricalis* encrusting an oyster shell from the middle Bathonian of Gnaszyn Dolny (GIUS 8-3730/12). **(D-J)** Sections of the tubes showing the ultrastructural details. **(D)** The longitudinal section of the *P. lumbricalis* tube from the upper Bathonian–lower Callovian of Bolęcin showing the putative three-layered tube (GIUS 8-3745/5). The external layer shows spherulitic prismatic structure (SPHP) with growth increments; the middle part exhibits presumably altered irregularly oriented prismatic structure (IOP) superficially resembling homogeneous structure; the internal layer shows uncertain spherulitic prismatic structure. **(E)** The longitudinal section of the two-layered *P. lumbricalis* tube from the middle Bathonian of Gnaszyn Dolny showing the external spherulitic prismatic structure (SPHP) with growth increments and the internal irregularly oriented prismatic structure (IOP) (GIUS 8-3730/30). **(F)** A close-up showing the internal layer built of irregularly oriented prismatic structure (IOP) with short, needle-like crystals of different length and orientation (GIUS 8-3730/30). **(G)** The longitudinal section of the *P. lumbricalis* tube from the lower Kimmeridgian of Małogoszcz (GIUS 8-3747/5) showing the spherulitic arrangement of crystals within the external tube layer. **(H, I)** Longitudinal sections of the two *P. lumbricalis* tubes from the middle Bathonian of Gnaszyn Dolny showing the external spherulitic prismatic structure (SPHP) with well-visible growth increments and the internal, partially recrystallized irregularly oriented prismatic structure (IOP) (**H.** GIUS 8-3730/31; **I.** GIUS 8-3730/32). **(J)** The lateral section of the *P. lumbricalis* tube from the middle Bathonian of Gnaszyn Dolny showing tubulae subdivided densely by septae (GIUS 8-3730/33).
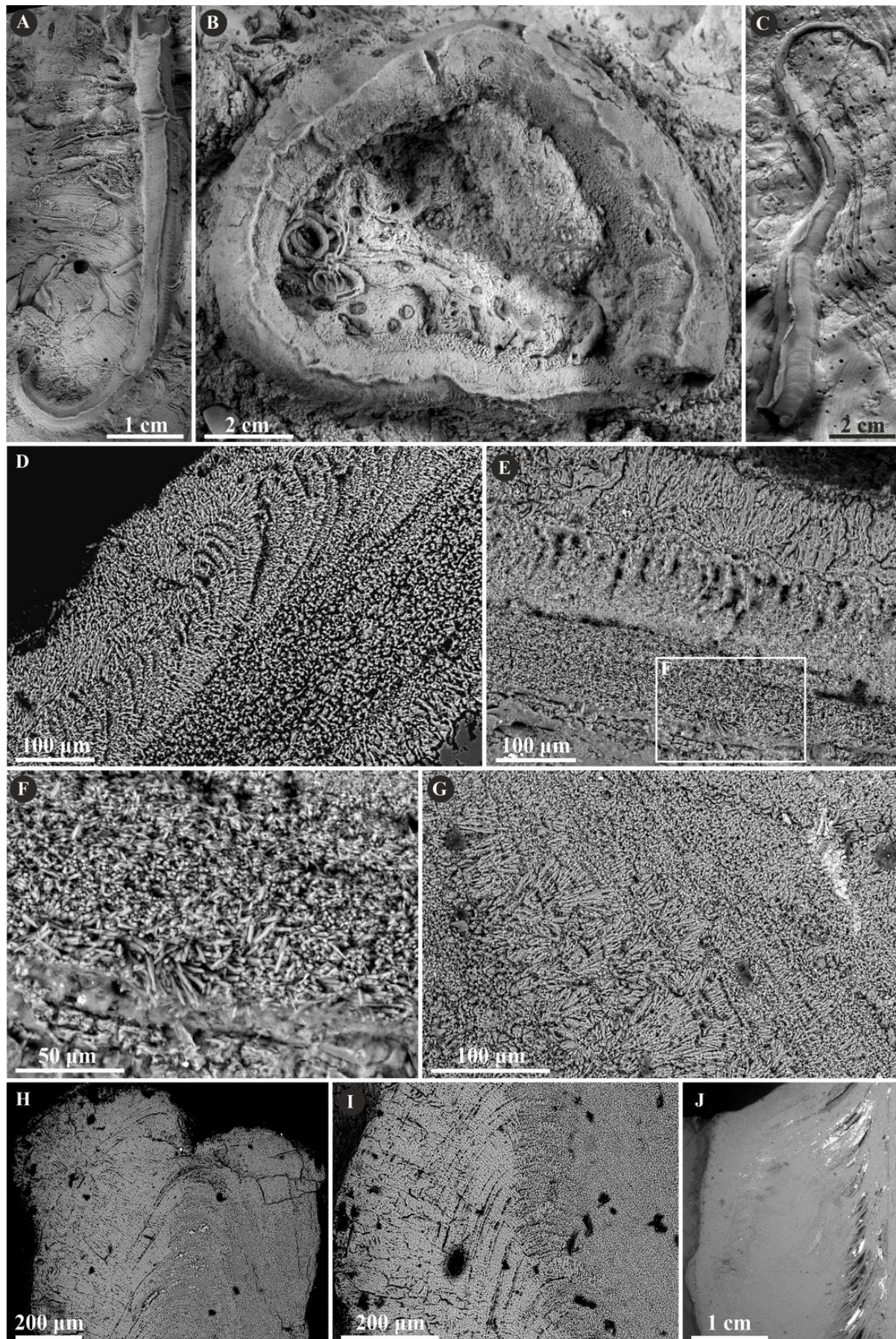
Figure 8

Figure 8: Selected specimens of *Nogrobs* from the Jurassic of Poland.

(A) Two specimens of *Nogrobs* aff. *quadrilatera* (A. Goldfuss, 1831) encrusting a belemnite rostrum from the middle Bathonian of Gnaszyn Dolny (GIUS 8-3730/17). **(B)** *Nogrobs*? aff. *tricristata* (A. Goldfuss, 1831) encrusting a belemnite rostrum from the middle Bathonian of Gnaszyn Dolny (GIUS 8-3730/19). **(C, D)** Free-lying tubes of *Nogrobs* aff. *tetragona* (J. de C. Sowerby, 1829) (**C.** GIUS 8-3730/24; **D.** GIUS 8-3730/25); lateral **(C$_1$)** and cross-section **(C$_2$, D)** view. **(E, F, G, I, J)** The longitudinal sections of the *Nogrobs* aff. *tetragona* (**E, F.** GIUS 8-3730/34), *Nogrobs*? aff. *tricristata* (**G.** GIUS 8-3730/20), and *Nogrobs* aff. *quadrilatera* (**I.** GIUS 8-3730/35; **J.** GIUS 8-3730/36) tubes from the middle Bathonian of Gnaszyn Dolny showing two distinct layers: the external simple prismatic structure (SP) with distinct growth lines and internal irregularly oriented prismatic structure (IOP). **(H, K)** A close-up of the longitudinal sections of the internal tube layer of *Nogrobs*? aff. *tricristata* (**H.** GIUS 8-3730/20) and *Nogrobs* aff. *quadrilatera* (**K.** GIUS 8-3730/36) showing irregularly oriented prismatic structure (IOP) with short, needle-like crystals of different length and orientation.
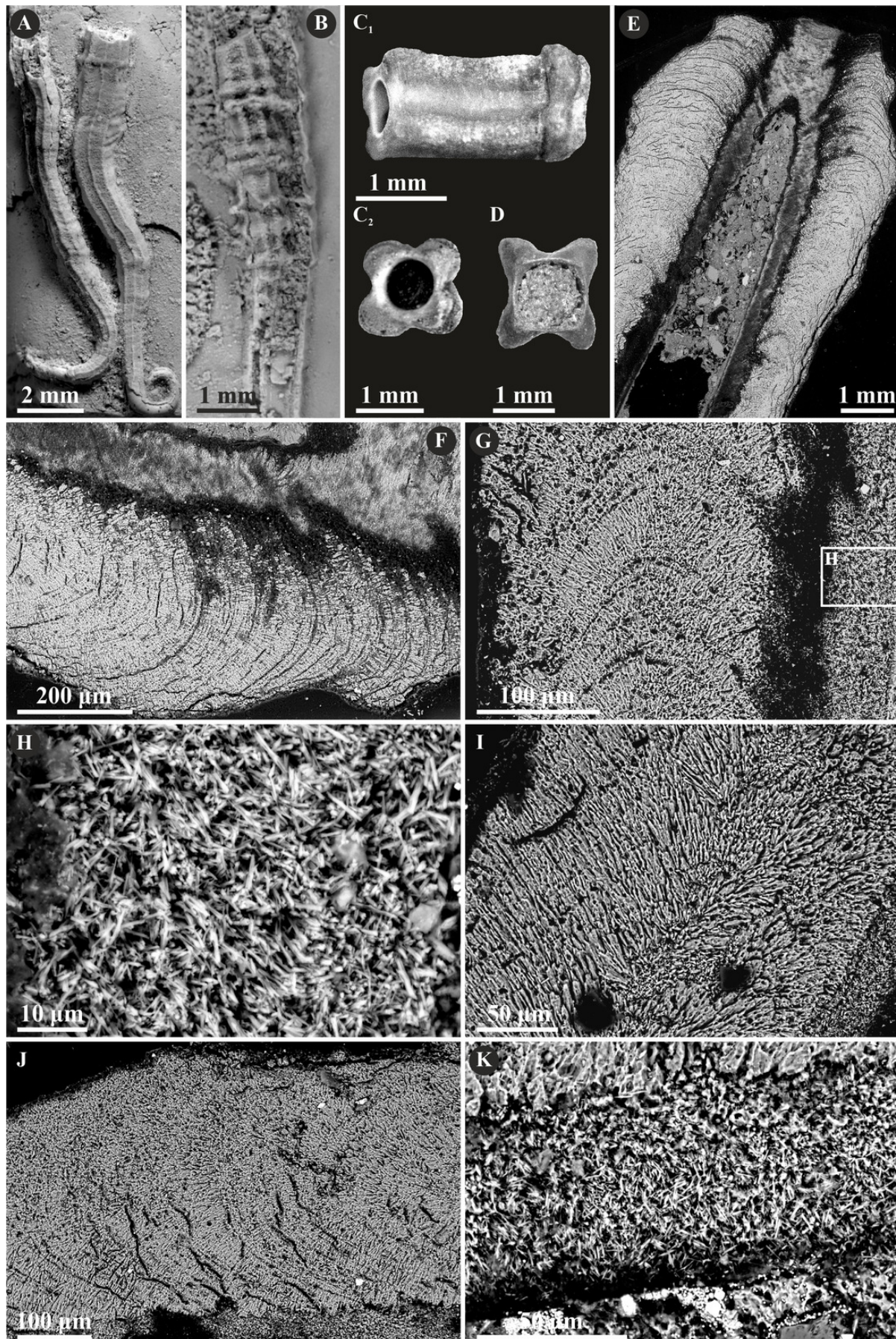
Figure 9

Figure 9: Selected specimens of *Mucroserpula* (H. Regenhardt, 1961) from the Jurassic of Poland.

(A, B) *Mucroserpula* sp. encrusting a fragment of a shell from the middle Bathonian of Gnaszyn Dolny (GIUS 8-3730/26); top (**A**) and cross-section view (**B**). **(C-E)** longitudinal sections of the *Mucroserpula* sp. tube from the middle Bathonian of Gnaszyn Dolny showing two distinct layers: the external spherulitic prismatic structure (SPHP) with distinct, chevron-shaped growth lines (**C**) and internal irregularly oriented prismatic structure (IOP) (GIUS 8-3730/26). **(F)** A close-up of the longitudinal section of the internal tube layer showing irregularly oriented prismatic structure (IOP) with short, needle-like crystals of different length and orientation (GIUS 8-3730/26).
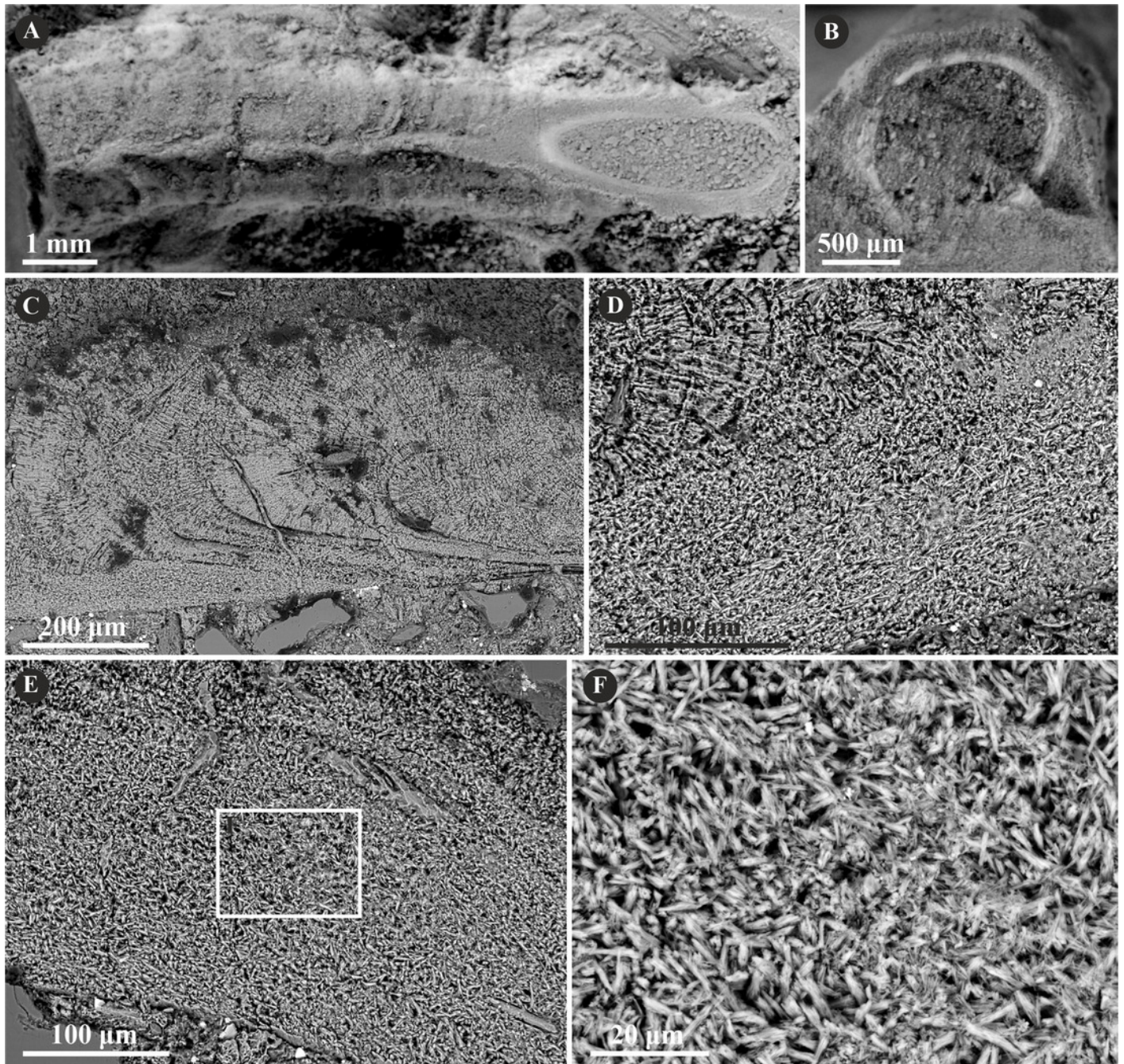
Figure 10

Figure 10: Selected specimens of *Placostegus planorbiformis* (Münster in Goldfuss, 1831) from the Jurassic of Poland.

(A) *P. planorbiformis* encrusting a sponge fragment from the Oxfordian of Zalas (GIUS 8-3746/8). **(B-D)** Longitudinal sections of the tubes showing the simple prismatic structure (SP) with well-visible growth increments (GIUS 8-3746/8).
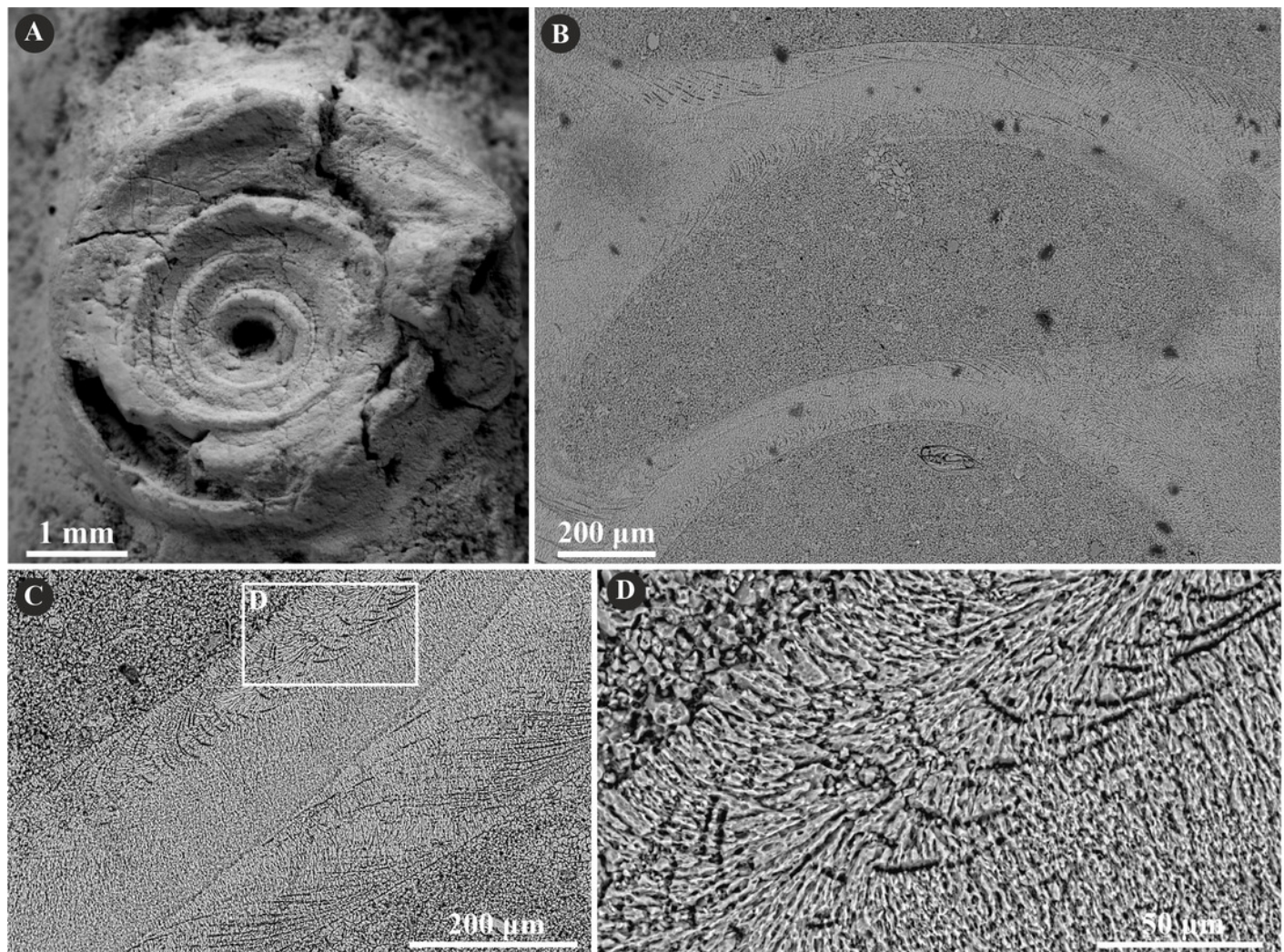
Figure 11

Figure 11: Selected specimens of Serpulidae sp. from the Jurassic of Poland.

(A) Dense aggregation of closely spaced Serpulidae sp. 3 (see Słowiński et al., 2022) encrusting a fragment of a belemnite rostrum from the middle Bathonian of Gnaszyn Dolny (GIUS 8-3730/28). **(B-E)** Longitudinal sections of the Serpulidae sp. tube from the middle Bathonian of Gnaszyn Dolny showing two distinct layers: the external simple prismatic structure (SP) and internal irregularly oriented prismatic structure (IOP) (GIUS 8-3730/28).
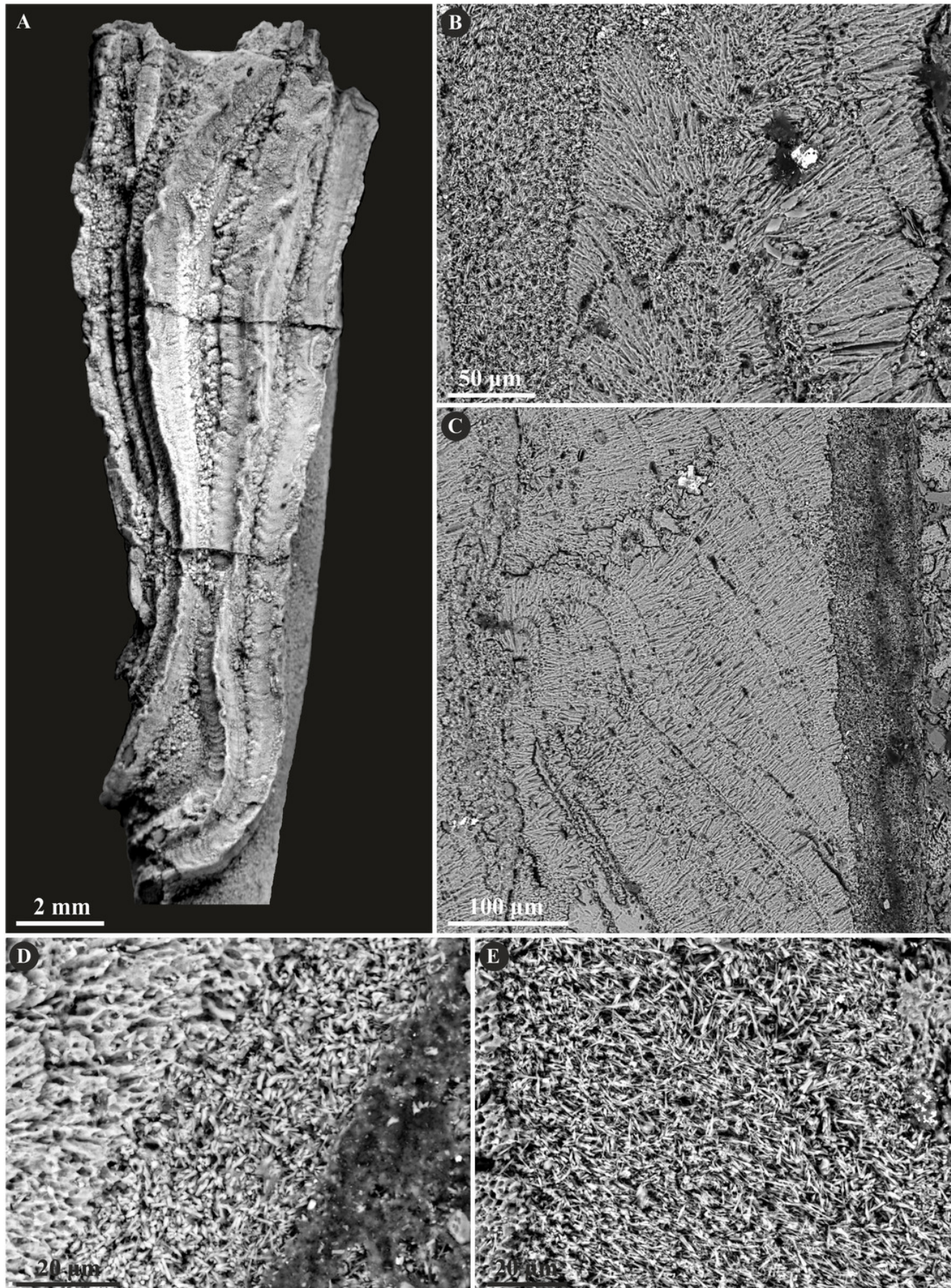
Table 1: Ultrastructural diversity of the Jurassic serpulid tubes from Poland.

IOP – irregularly oriented prismatic structure, SPHP – spherulitic prismatic structure, SP – simple prismatic structure. Numbers (1, 2, 3) indicate the position of the layer within the tube counted from the exterior. Square brackets denote partially preserved or equivocal microstructure precluding a fully reliable recognition. Green, yellow, and blue correspond to Filograninae, Serpulini, and Ficopomatini respectively.

Taxon	Ultrastructure			Number of individuals investigated
	IOP	SPHP	SP	
Metavermilia cf. *striatissima*	1			3
Filogranula runcinata	[2]	1		5
Filogranula spongiophila			1	3
Cementula spirolinites			1	9
Cementula radwanskae			[1]	4
Propomatoceros lumbricalis	2	1, [3]		8
Nogrobs aff. *quadrilatera*	2		1	3
Nogrobs? aff. *tricristata*	2		1	1
Nogrobs aff. *tetragona*	2		1	2
Mucroserpula sp.	2	1		3
Placostegus planorbiformis			1	3
Serpulidae sp.	2		1	3
Total				47