

Putative hydroid symbionts recorded by bioclaustrations in fossil molluscan shells: a revision and reinterpretation of the cecidogenus *Rodocanalís*

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Abstract: The fossil record yields a peculiar phenomenon in different kinds of molluscan shells: bioclaustrations formed around (epi)symbionts during growth of the hosts' shell margin. Four morphologies, two of them formerly considered bioerosion traces, are here united in the parataxonomy of bioclaustration structures under the revised cecidogenus *Rodocanalís*. These are: (1) simple linear grooves (*Rodocanalís linearis* csp. nov.) formed below the periostracum in Pleistocene to Recent endobenthic bivalves; (2) series of distally ramifying grooves (*Rodocanalís runicus*) in Silurian orthoconic nautiloids; (3) irregular networks of grooves (*Rodocanalís reticulatus*) in Jurassic to Cretaceous bivalves and gastropods; and (4) regular reticulate networks (*Rodocanalís geometricus* csp. nov.) in Jurassic to Cretaceous gastropods. The linear grooves might be associated with commensal worms, while multiple lines of reasoning point towards hydrozoan symbionts in the case of the

branched and anastomosing grooves. After the hydrozoan larva settles and the first polyp becomes fixed on the calcareous ostracum at the shell margin, the process of bioclaustration commences when the periostracum surrounds the base of the polyp, which moves towards the external shell surface, while the hydrorhizae develop in the only possible direction: towards the shell growth margin. This enables new polyps to originate at the shell edge by budding, while the bioclaustration of the stolonial hydrorhizae advances. We consider the nature of this symbiotic relationship as mutualism, with the hydrozoan symbiont taking advantage of the host's feeding current or food debris, and the molluscan host profiting from the defensive capability of the hydrozoan's cnidocysts.

Key words: bioclaustration, bioerosion, symbiosis, cecidotaxonomy, ichnotaxonomy, *Rodocanalís*.

DISTINGUISHING bioerosion traces, formed when animals, plants and microbes sculpt or penetrate surfaces of hard substrates (Bromley 1994), from bioclaustrations, which are formed when a living skeleton-secreting organism overgrows a living symbiont (Palmer & Wilson 1988), is often difficult. This is because the morphologies of these structures can be very similar and because there are combinations of bioerosion and bioclaustration, resulting in compound boring–bioclaustrations (Tapanila & Ekdale 2007). However, one clear criterion and several auxiliary properties help distinguish true bioerosion trace fossils from bioclaustrations (occasionally termed pseudo-borings), namely cut versus deflected growth increments and margins in the skeleton of the host organism

(Tapanila & Ekdale 2007). This character reflects the contrast of destructive bioerosion traces forming from the outside and constructive bioclaustrations growing together with the host substrate (Tapanila & Ekdale 2007, fig. 19.1).

The difficulty in identifying and addressing bioerosion trace fossils versus bioclaustration structures is mirrored in their categorization and taxonomy. According to Bertling *et al.* (2006), bioerosion traces are trace fossils but bioclaustrations are not. This is because with bioclaustrations it is not the symbiont that directly modifies the substrate, but the 'substrate' host organism that modifies itself, a clear conceptual distinction recently underlined by Bertling *et al.* (2022). However, the exclusion of

bioclastration structures from the realm of trace fossils is controversial (see discussions in Tapanila & Ekdale 2007 and Klompmaker *et al.* 2014). Following the concept of Bertling *et al.* (2006, 2022), only trace fossils are eligible for ichnotaxonomical treatment as ichnotaxa, whereas bioclastrations are to be treated as cecidotaxa (Bertling *et al.* 2022), a separate collective group of parataxa governed and protected by the International Code for Zoological Nomenclature (ICZN 1999). This concerns approximately two dozen ichnogenera established for bioclastrations (for a list, see Wisshak *et al.* 2019, p. 4) that should now be considered cecidogenera.

Following the concept of cecidology, we here elaborate on a suite of closely related bioclastrations recorded in different kinds of molluscan skeletal substrates throughout the Phanerozoic. Two of these have previously been considered bioerosion traces and consequently established as ichnotaxa, namely reticulate grooves in Lower Jurassic bivalves from southeast Germany, established by Schloz (1972) as the ichnotaxon *Rodocanalisis reticulatus*, and conspicuous rune-shaped structures in upper Silurian orthoconic nautiloid shells from Bohemia, described by Marek (1982) as the ichnotaxon *Runia runica*. A detailed assessment of a linear third type, recorded in Quaternary infaunal bivalves from Argentina, was provided by Richiano *et al.* (2018), who refrained from a taxonomic treatment. A fourth and geometrically complex set of surface grooves was first recognized by Keyserling (1846), who considered it an ornamental feature of a new gastropod species he named *Turbo rhombodes*. Similar structures have repeatedly been reported since, without taxonomic treatment, from various Jurassic gastropod host species (e.g. Szabó 1992; Schubert *et al.* 2008; Ferrari & Kaim 2019), and we here provide additional material from the Lower Cretaceous of Arctic Canada. All four types of bioclastrations were formed during the growth of the host shell margin of different molluscs. They represent a series of morphologies with an increasing complexity from single linear elements to strictly geometrical, anastomosing patterns. In this contribution, we unite these closely related bioclastrations under the cecidogenera *Rodocanalisis* Schloz, 1972 and reinterpret both their process of formation and the nature of the symbiotic relationship.

MATERIAL AND METHOD

All type specimens were documented by means of digital macrophotography and/or a digital camera attached to a microscope. In addition, scanning electron microscopy (SEM) images in Figures 2, 5 were acquired with a TESCAN VEGA3 at 20 KeV under low-vacuum conditions (no sputter coating needed) with an offset backscatter

electron (BSE) detector. The SEM microphotograph in Figure 4D was taken with a Zeiss EVO10 scanning electron microscope with a low-vacuum secondary electron (SE) detector, the image in Figure 4G with a Zeiss EVO 40 SEM with a BSE detector after gold sputter coating using a Cambridge PELCO 91000, and Figure 4H, I with an FEI Quanta 200 SEM applying the SE detector at 20 KeV.

Morphometric measurements were performed on SEM and microscopy images of the type material (exclusively) using the VEGA TC software and ImageJ, respectively. Measurements of the network cell lengths refer to the spaces between the network grooves in the direction of growth; the width was measured perpendicular to the length. Measurements of the width of the grooves in reticulate forms were taken midway between junctions. All descriptive statistics, as well as the boxplots and x - y plots with linear regression trendlines and correlation coefficients, were computed in MS-EXCEL.

All of the graphs and photos are oriented so that the growth of the shell and its bioclastration was from left to right.

The term ‘symbiosis’ is here used in its original, broad definition as a close and long-term interaction between two different animals, be it parasitic, commensalistic or mutualistic (de Bary 1878; Martin & Schwab 2013).

Institutional abbreviations. DCG-MLP, Geology Department of the La Plata Museum, Argentina; IGB, Institute of Geology and Palaeontology at the University of Stuttgart, Germany; MGUH, Natural History Museum of Denmark, Copenhagen, Denmark; NHMUK, Natural History Museum, London, UK; NM, National Museum of Natural History in Prague, Czech Republic; SMF, Senckenberg Museum Frankfurt, Germany; SMNS, Stuttgart State Museum of Natural History, Germany.

SYSTEMATIC CECIDOLOGY

Rodocanalisis Schloz, 1972

1972 *Rodocanalisis* Schloz, p. 162.

1982 *Runia*; Marek, p. 402.

LSID. <https://zoobank.org/nomenclaturalActs/92CA2BC8-45F5-4B0C-9477-6C40018FB0AD>

Type cecidospecies. *Rodocanalisis reticulatus* Schloz, 1972, by original designation.

Additional cecidospecies. *Rodocanalisis runicus* (Marek, 1982) comb. nov., *Rodocanalisis linearis* csp. nov., *Rodocanalisis geometricus* csp. nov.

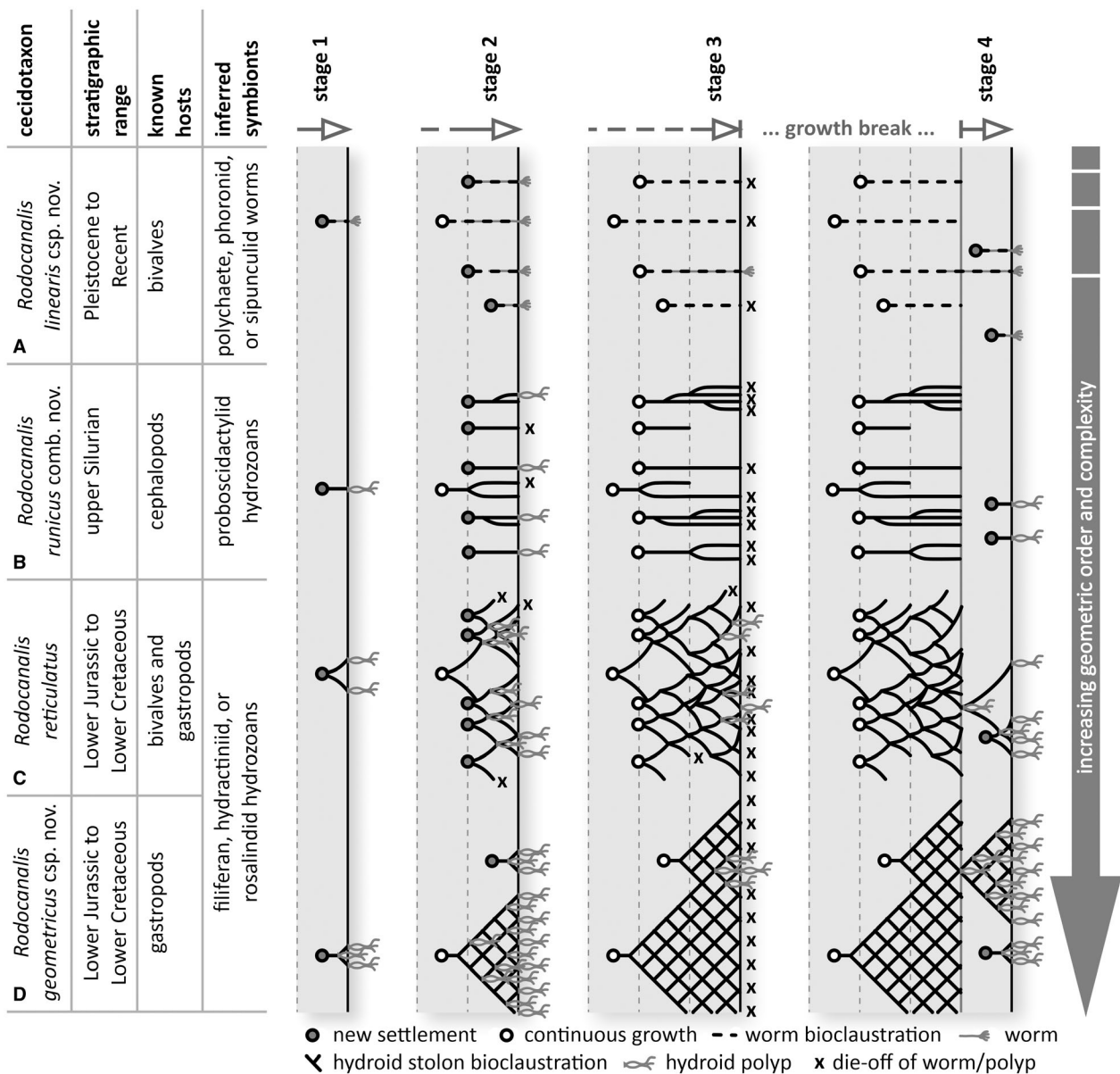


FIG. 1. Synthesis of the developmental stages of the four closely related bioclaustrations, here subsumed within the cecidogenus *Rodocanalis* Schloz. The geometric patterns of the bioclaustrations (in order of increasing geometric order and complexity) are shown in relation to the growth increments/breaks at the molluscan hosts' shell margins, and the development and episodic die-off of the putative symbionts.

Original diagnosis. [Originally referred to as description; translated from German.] Grooves on the shell surface of lamellibranchiates (Limidae). These are about as wide as deep (c. 0.1–0.3 mm). There is no connection to closed tunnels.

Revised diagnosis. Bioclaustration structure composed of grooves, approximately as wide as deep, on the surface of molluscan shells, oriented or ramifying towards the shell's growth margin.

Description. *Rodocanalis* addresses a suite of cecidospecies with a morphology ranging from unbranched linear grooves to strictly geometrical and anastomosing networks. All of these have in common an orientation and direction of growth towards the growth margin of various molluscan shells, and they all show a characteristic dependency on major growth breaks at which the grooves may or may not terminate. The general morphology of the included cecidospecies and their temporal development in relation to the growth of the molluscan host shells is illustrated in Figure 1.

Remarks. Schloz's (1972) diagnosis, originally referred to as a description, was emended to better accommodate the revised suite of included cecidospecies. Schloz (1972) originally established *Rodocanalis* as an ichnogenus, based on his interpretation of these structures as etchings, and thus as a bioerosion trace fossil. Following our interpretation that *Rodocanalis* represents bioclaustrations, we consider it a cecidotaxon, also governed by the ICZN; hence, its nomenclatural validity is not affected.

Rodocanalis reticulatus Schloz, 1972

Figures 1C, 2A–F

- 1972 *Rodocanalis reticulatus* Schloz, p. 162; pl. 30, figs 1–2.
 1975 *Rodocanalis reticulatus*; Häntzschel, p. W133; pl. 81, fig. 2a–c [2a and 2c reproduced from Schloz 1972, pl. 30, figs 1–2].
 1983 unnamed grooves on *Helicacanthus insuetus*; Beizel, p. 15; fig. 6b.
 1992 unnamed grooves on *Proconulus baldensis*; Szabó, p. 105; pl. 1–4.

Type specimens. The single valve of the bivalve *Plagiostoma giganteum* Sowerby, 1814 carrying the holotype (Fig. 2A) was originally stored at the former Institute of Geology and Palaeontology at the University of Stuttgart (inventory number IGB S.1100) and was subsequently lost before or while the collection was moved to the Stuttgart State Museum of Natural History (G. Schweigert, pers. comm. 2021). The complete shell of *Plagiostoma giganteum* that was originally designated as paratype (Fig. 2B–F) is stored at the Stuttgart State Museum of Natural History (SMNS 22194). Although *Rodocanalis reticulatus* appears on both valves of that bivalve, only the one on the left valve was highlighted by Schloz (1972) by means of white paint (Fig. 2B–D), and corresponds to figure 2 on his plate 30, implying that this specimen is what he considered the paratype trace. For practical reasons and for the sake of nomenclature, we here consider the interconnected whitened structure as a single ‘colony’, in other words, a single specimen of *R. reticulatus*. Given the loss of the holotype, for clarifying the type locality, and for clarifying the taxonomic status as cecidotaxon, we hereby designate the paratype as the neotype. While type locality and stratum were only very generally indicated by Schloz (1972, p. 164) as Hettangian to lower Sinemurian strata exposed in south Germany, the label is more specific and indicates that the specimen originates from the Arietenkalk-Formation (Sinemurian, Lower Jurassic) of Stuttgart-Vaihingen in southwest Germany.

Original diagnosis. [Originally referred to as description; translated from German.] *Rodocanalis* with reticulate or garland-like arranged etching grooves, between which scale-shaped shell parts have remained.

Revised diagnosis. Reticulate or garland-like network of grooves, between which scale-shaped shell parts of variable dimension have remained; grooves curve and diverge from dichotomous branching points.

Original description. [Translated from German.] The etch marks consist of 0.15–0.25-mm-wide and 0.1–0.2-mm-deep grooves. These are always open, in no case closed tunnels, but may undercut the shell obliquely if formed asymmetrically, especially along growth lines. The edge of the grooves is sharp or rounded, their surface usually rough, scarred and occasionally showing a division into pits arranged in rows. The ostracum of the *Plagiostoma* shells shows fine growth lines, which behave like contour lines in the area of the grooves but are often overprinted by fine ridge-like etching patterns in the marginal area. This simulates a primary disturbance of the growth lines. The etching grooves never penetrate the ostracum and are neither associated with cleavage cracks nor with crystal axes or crystal boundaries.

Occasionally the grooves are filled with granular calcite, which may rise ridge-like above the shell surface but shows no biogenic structure. The grooves run in two preferred directions: oblique to the growth lines and in various arcuate shapes, forming a garland or a characteristic network. The shell surface preserved between the grooves is reminiscent of fish scales. The grooves pass ridge ornaments without any noticeable change. The overall arrangement of the networks or individual grooves shows a clear relationship to growth lines of the etched shell. The grooves are mostly restricted to growth-parallel zones or limited by growth lines and they are absent in the lunula. On the double-valved *Plagiostoma*, the reticulations are developed on both valves approximately in the same shell area, but are different in the course of the individual grooves.

Supplementary description. Schloz's (1972) original description (see above) is detailed and in accordance with our observations, except for where he interpreted *R. reticulatus* as an etching trace. It should be added that the network cells are quite variable in outline and dimensions (mean, $313.1 \pm 132.6 \times 264.3 \pm 153.4 \mu\text{m}$; $n = 100$; Table 1; Figs 1C, 2A–D). From the dichotomous branching points, the grooves typically curve in a diverging fashion (Fig. 2D, E). Grooves were found to vary in width between $41.2 \mu\text{m}$ and $183.5 \mu\text{m}$ (mean, 101.1 ± 32.3 ; $n = 100$; Table 1). In the perimeter of the grooves, the shell's growth lines are deflected away from the direction of growth (Fig. 2E, F).

As for the respective structures in gastropod host shells, Szabó (1992) noted that all ‘colonies’ are bounded by a definite, straight ‘primary’ canal that runs from the parietal lip of the gastropod to the periphery and on to the suture, without crossing the latter and without any posterior branch.

Hosts. Mainly associated with the bivalve *Plagiostoma giganteum* (e.g. Schloz 1972). Additional records from the gastropod species *Proconulus baldensis* (Szabó 1992) and *Helicacanthus insuetus* (Beizel 1983), as well as from the genera *Eucyclus* and *Amberleya* (Beizel 1983).

Palaeobiogeographical distribution. Central-European epicontinental sea (France, Germany; Schloz 1972), Northern Tethys (Hungary; Szabó 1992), boreal Khatanga Sea (Siberia; Beizel 1983).

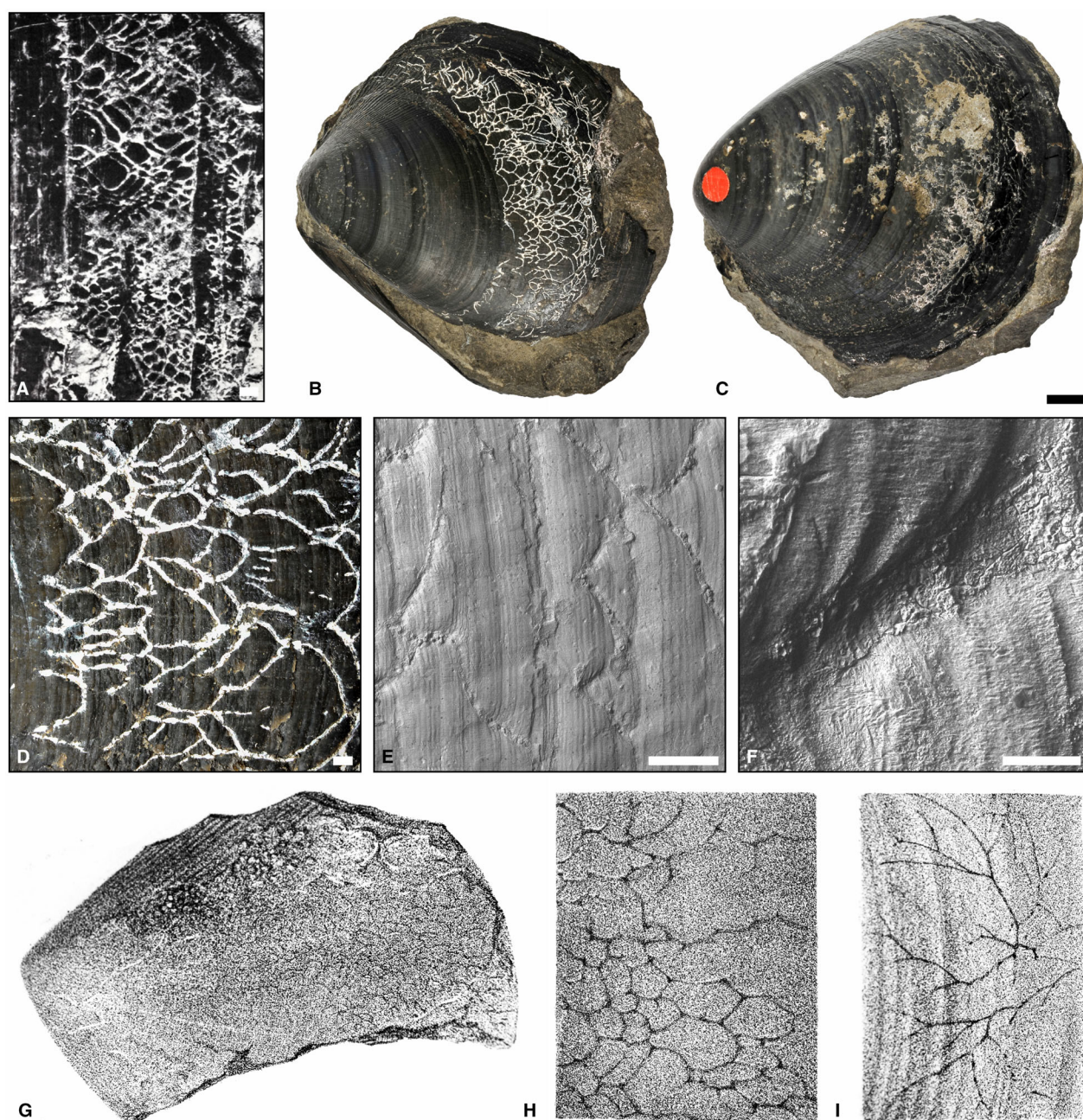


FIG. 2. Type material of *Rodocanalís reticulatus* and its potential senior synonym *Talpina squamosa*. A, photograph illustrating the lost holotype of *Rodocanalís reticulatus* (IGB S.1100; reproduced from Schloz 1972, pl. 30, fig. 1). B, a complete shell of the bivalve *Plagiostoma giganteum* (SMNS 22194) from the Lower Jurassic of Stuttgart-Vaihingen, Germany, with its left valve showing the former paratype of *Rodocanalís reticulatus*, herein designated as neotype; the structure was highlighted in white paint by Schloz (1972). C, right valve of the same individual with corresponding embedment structures but left in their original state. D, close-up of B, showing the typical branching and network pattern with a marked heterogeneity in shape and size of the network cells. E–F, SEM overview and detail of the grooves, partly with a calcitic infill, illustrating the deflected growth increments of the bivalve. G, reproduction of an illustration of a *Plagiostoma* from the Lower Jurassic of France, showing a structure similar to *R. reticulatus*, described as *Talpina squamosa* by Terquem & Piette (1865, pl. 18, fig. 16), which is considered a *nomen dubium* herein. H, close-up of *T. squamosa*, reproduced from Terquem & Piette (1865, pl. 18, fig. 17). I, another *nomen dubium*, *Talpina porrecta*, described by and reproduced from Terquem & Piette (1865, pl. 18, fig. 18). Scale bars represent: 1 mm (A–E); 100 μ m (F); no scale provided for G–I in original publication.

TABLE 1. Descriptive statistics of morphometric measurements in the four *Rodocanalis* cecidospecies.

	<i>R. linearis</i>	<i>R. runicus</i>	<i>R. reticulatus</i>	<i>R. geometricus</i>
Groove width (µm)				
Mean ± SD	175.6 ± 59.1	206.2 ± 58.6	101.1 ± 32.3	71.2 ± 10.7
Min–max	89.2–388.7	103.0–351.3	41.2–183.5	46.0–106.7
n	100	100	100	100
Network cell length (µm)				
Mean ± SD	n/a	n/a	313.1 ± 132.6	200.6 ± 72.2
Min–max			98.4–788.4	81.7–537.6
n			100	100
Network cell width (µm)				
Mean ± SD	n/a	n/a	264.3 ± 153.4	146.5 ± 35.9
Min–max			80.0–746.4	59.9–294.4
n			100	100

Stratigraphic range. Lower Jurassic (Hettangian; Schloz 1972) to Lower Cretaceous (Beizel 1983).

2004 *Runia runica*; Marek, p. 37; fig. 1 [reproduced from Marek 1982, pl. 2, fig. 1].

Remarks. A potential subjective senior synonym of *Rodocanalis reticulatus* is *Talpina squamosa* Terquem & Piette, 1865, which also occurs in shells of Early Jurassic *Plagiostoma* and shows a similar branching pattern described as resembling fish scales, but according to the original description in Terquem & Piette (1865, pp. 133–135) the traces are borings that are visible due to the transparency of the host shell and show openings to the substrate surface at intersections or gallery terminations. Unfortunately, we failed to track down the type material in Paris (collections at the Muséum National d'Histoire Naturelle, at the Musée de Minéralogie MINES at ParisTech, and at Sorbonne Université) and Lyon (collections at the Université Claude Bernard), as had Schloz (1972) and Plewes (1996) before us. Furthermore, the relevant figures (pl. 18, figs 16–17; here reproduced in Fig. 2G, H) are mislabelled as *Talpina porrecta* (which is actually shown on fig. 18; here reproduced in Fig. 2I), and the species name given on this plate is *T. squamata* instead of *T. squamosa*. It remains impossible to determine whether *T. squamosa* is a specimen of *R. reticulatus* with a secondary spar infill of the grooves and thus seemingly representing tunnels below the surface, or whether it is a boring with affinity to the strongly anastomosing *Dictyoporus nodosus*. Given these circumstances, we propose to consider both *T. squamosa* and *T. porrecta* *nomina dubia* and to retain *Rodocanalis reticulatus* as the valid taxon.

Rodocanalis runicus (Marek, 1982) comb. nov.

Figures 1B, 3

- 1877 'ornements noirs, linéaires ou bifurques'; Barrande, p. 192; pl. 509, figs 8–12.
- ? 1979 *Rodocanalis* sp.; Mayoral & Sequeiros, p. 129; pl. 4, fig. 1 (label 5).
- 1982 *Runia runica* Marek, p. 402; pl. 1, figs 1–4; pl. 2, figs 1–2.
- 2004 *Runia*; Finks *et al.*, p. 40; fig. 29/4a–b [reproduced from Marek 1982, pl. 1, fig. 1; pl. 2, fig. 1].

Type specimens. The holotype includes five series of bioclastration structures in an orthoconic nautiloid cephalopod, deposited in the collections of the Palaeontological Department of the National Museum of Natural History in Prague (inventory number NM L 20273). Three paratypes in cephalopod shells were originally figured by Barrande (1877, pl. 509, figs 8–12) and are stored in the same collection under the inventory numbers NM L 14151, NM L 14152 and NM L 14153. In accordance with the original diagnosis of *R. runicus* involving several 'horizontal series' of individual grooves, we here consider the multiple sets of grooves as a single 'specimen' of *R. runicus*. This is also to conform with the original designation of a holotype and three paratypes instead of a single groove as holotype or individual grooves as syntypes. The type material comes from the Kopanina Formation (Ludlow Series, upper Silurian) in the Barrandian area, Central Bohemia, Czech Republic. However, the holotype and the three paratypes all come from different localities in the Barrandian area; the holotype was found at the type locality Lejškov Hill near Zdice, and the origin of the three paratypes was specified by Barrande (1877) as Karlstein (NM L 14151), Wohrada (NM L 14152), and Gross-Kuchel (NM L 14153). According to Chlupáč (2002), 'Karlstein' is a cumulative designation for localities situated on the left bank of the river Berounka near the small town of Karlštejn, 'Wohrada' equates to Praha-Velká Ohrada (later mostly referred to as the Dalejské údolí, Daleje Valley), where the Kopanina Formation is exposed in the Mušlovka Quarry, and 'Gross-Kuchel' today is Praha-Velká Chuchle, where the Kopanina Formation was exposed in small quarries and pits in the forested area of Chuchelský háj (GPS: around 50.01533° N, 14.38301° E).

Original diagnosis. Borings in the calcareous matter of the orthoconic nautiloid shells consist of horizontal series. They are arranged one above another, and each of them consists of vertical almost straight, short, nodular to cylindrical narrow tunnels, the cross-sections of which are circular. Individual tunnels have the shape of short, dotted lines in early ontogenetic stages; later they acquire the shape of nodular to cylindrical lines; still later they branch fork-like on their upper ends



FIG. 3. Type material of *Rodocanalís runicus* in orthoconic nautiloid cephalopods from the Kopanina Formation (Ludlowian, upper Silurian) of the Barrandian area, Czech Republic. A–B, overview and close-up photographs of the holotype of *Rodocanalís runicus* (NM L 20273). C–D, lithograph and photograph of one of the paratypes, originally described as cephalopod species *Orthoceras runicum* by Barrande (NM L 14153; lithograph reproduced from Barrande 1877, pl. 509, fig. 12). E, close up of D, showing some of the remaining original shell surface with *Rodocanalís runicus* (brown) and two layers of exfoliation of the recrystallized shell (grey) with black matter partly tracing the deeper portions of the bioclaustrations. F, photograph of the original shell portion coated with ammonium chloride, showing the cephalopod's growth increments interrupted by the (partly healed?) grooves of *Rodocanalís runicus*. G, cross-section of the completely recrystallized shell in one of the other paratypes, with *Rodocanalís runicus* grooves (arrows), deeper than wide, preserved as black infill (NM L 14151). Scale bars represent: 1 mm (B, E–G); 1 cm (A, D).

into two or three branches. In late ontogenetic stages secondary branching of the branches may occur. The tunnels of one series are of the same ontogenetic stage, but the series may

differ from each other in the grade of development (periodical attack of infection). Series follow the growth lines of the shell. (Marek (1982) provided this explicit diagnosis for his new

(ichno)genus *Runia* only, which by monotypy refers also to its type (ichno)species.)

Revised diagnosis. Initially straight grooves that repeatedly ramify uni- or bilaterally, with the angular branches curving fork-like to follow a course parallel to the main groove; typically occurring in series.

Original description. Narrow, short almost straight, at first dotted, later nodular or cylindrical tunnels with circular cross-section. Tunnel diameter is *c.* 0.1–0.2 mm. In later ontogenetic stages the tunnels divide fork-like at acute angles into two or three branches; the branches further divide in the same way. Tunnels are more narrow on their lower ends and gradually grow in the diameter toward the forking, and end in a deeper pit. The length of the rod-like borings is usually 2–3 mm (maximum 8 mm). The whole length of the forks is 4–6 (11) mm. The individual borings are arranged into horizontal series that follow the growth lines (shell aperture). The gaps between the tunnels of one series are 1–2 (3.5) mm. There are usually several series above each other, with irregular gaps of 4–6 (11) mm. Individual borings may be also connected by a simple horizontal tunnel. Individual series may or may not differ in the stage of ontogenetic development, probably as the result of periodical attack of infection. Where the original shell wall is preserved, the tunnels are (secondary?) filled up with the dark matter.

Supplementary description. The original description is in accordance with our own reinvestigation of the holotype (Fig. 3A, B) and the paratypes (Fig. 3C–G), with the one crucial exception that the structures are not closed tunnels but open grooves. These grooves are only visible where the original shell surface is preserved, such as on paratype NM L 14153. (Fig. 3D–F). On this paratype the grooves are very shallow and are indicated only by a conspicuous black mineralization (Fig. 3D, E). In lower tiers of the recrystallized and partly exfoliated shell structure, the course of the bioclastrations is only partly traced by means of the black mineralization (Fig. 3D, E). Cross-sections of the latter show that the grooves are deeper than wide (Fig. 3G). In the type material, the width of the grooves varies between 103.0 µm and 351.3 µm (mean, 206.2 ± 58.6; *n* = 100; Table 1).

Hosts. Orthoconic nautiloid cephalopod shells are the only known host substrate (Marek 1982).

Palaeobiogeographical distribution. Barrandian area, Prague Basin (Bohemia, Czech Republic; Marek 1982).

Stratigraphic range. Silurian (Ludlow Series; Marek 1982).

Remarks. The former ichnogenus *Runia* Marek, 1982, is here regarded as a subjective junior synonym of *Rodocanalisis* Schloz, 1972, and its type ichnospecies *Runia runica* Marek, 1982 is transferred to *Rodocanalisis* accordingly. The specific epithet takes the gender of the genus name *Rodocanalisis* (male) and is thus changed to *runicus*.

Based on Marek's (1982) interpretation of *Runia runica* as an early sponge boring, Finks *et al.* (2004), in the revised version of the Porifera volume of the *Treatise on Invertebrate Palaeontology*, erroneously considered *Runia* a clionaid sponge biotaxon and assigned it to the Family Clionaidae, together with several other ichnotaxa for invertebrate bioerosion traces of various kinds, including *Clionoides* Fenton & Fenton, 1932, *Clionolithes* Clarke, 1908, *Entobia* Bronn, 1837, *Filuroda* Solle, 1938 and *Palaeosabella* Clarke, 1921.

Records from the infaunal bivalve *Protocardia*, reported by Mayoral & Sequeiros (1979), are uncertain, because they are illustrated only in schematic drawings and need confirmation.

It should be noted that only advanced cecidogenetic stages of *R. runicus* show the full morphology with multiple branching points, a character that is best developed in the holotype (Fig. 3A, B). Earlier developmental stages, or the incompletely preserved black mineralizations on lower tiers of exfoliated shell layers, often appear as unbranched parallel lines that could then be misinterpreted as *R. linearis* (see Marek 1982, pl. 1, figs 2–3). In some specimens, the black mineralization has traced the horizontal growth increment too, giving the false impression that the grooves are linked to each other (Marek 1982, pl. 1, fig. 3).

Rodocanalisis linearis csp. nov.

Figures 1A, 4

- 1944 unmentioned; shown on *Tagelus plebeius*; Carceles, pl. 13, fig. 100.
- ? 1979 *Rodocanalisis* sp.; Mayoral & Sequeiros, p. 124; pl. 1, fig. 1 (label 5).
- 2010 unmentioned; on *Tagelus affinis*, *T. dombeii* and *T. plebeius*; Huber, p. 349.
- 2017 unnamed grooves on *Tagelus plebeius*; Lejarraga, p. 164, bottom figure.
- 2018 unnamed grooves on *Tagelus plebeius*; Richiano *et al.*, p. 165; figs 4–7.

LSID. <https://zoobank.org/NomenclaturalActs/D7575A4B-ADC1-4274-81A7-A988C80A4661>

Derivation of name. Based on *linearis* (Latin for 'linear'), referring to the straight and unbranched morphology of the structure.

Type specimens. The material comes from the Puente de Pasqua Formation (Pleistocene) at its type locality at Puente de Pasqua, central Bahía Samborombón, Buenos Aires Province, Argentina (35°55'S, 57°44'W; Aguirre & Whatley 1995). The type material is stored at the Geology Department of La Plata Museum (inventory number DCG-MLP-0007-907) and constitutes the left and right valves of a single shell of the bivalve *Tagelus plebeius* with numerous *Rodocanalisis linearis* csp. nov., one of which is here designated as the holotype (arrow in Fig. 4B, C and close-up in Fig. 4D) and all the others as paratypes.

Diagnosis. Regular, unbranched, elongate grooves with depressions, oriented perpendicular to the substrate growth lines.

Description. Grooves are never connected or branching, and they occur only in the outer, aragonitic shell layer of the central part of the bivalve shell, where they run perpendicular to the shell margin and start and terminate at prominent growth lines/breaks (Fig. 4A–D). The host's growth lines are deflected away from the shell margin and where grooves cross the more prominent growth breaks, they may form slight depressions (Fig. 4C, G–I). The walls of the grooves are sloped to slightly overhanging (Fig. 4C, D). The grooves are 1–10 mm long and *c.* 100 µm wide at *c.* 100–150 µm depth. In the type material, the width of the grooves was determined to range between 89.2 µm and 388.7 µm (mean, 175.6 ± 59.1 ; *n* = 100; Table 1). In modern material, the grooves are developed below the periostracum and are visible from the outside as dark lines due to the translucence of this organic shell layer (Fig. 4E, F).

Hosts. Reported exclusively from various species of the endobenthic bivalve *Tagelus*, including *T. affinis*, *T. dombeii* and *T. plebeius* (Huber 2010).

(Palaeo)biogeographical distribution. Pacific and Atlantic coasts of South America.

Stratigraphic range. Pleistocene to Recent.

Remarks. *Rodocanalís linearis* is very common in modern and Holocene *Tagelus plebeius* (on 47% of the 991 shells investigated by Richiano *et al.* 2018). Consequently, it is often shown, but left unmentioned, in illustrations of bivalves in this genus (for examples, see the synonymy list above).

Records from the bivalve *Plagiostoma giganteum*, reported by Mayoral & Sequeiros (1979), are uncertain given that they are illustrated only in schematic drawings and need confirmation.

Rodocanalís geometricus csp. nov.

Figures 1D, 5

- 1846 Ornament of *Turbo rhombodes*; Keyserling, p. 318; pl. 18, figs 19–20.
- 1886 Ornament of *Turbo* cf. *rhombodes*; Lahusen, p. 8; pl. 2, fig. 12a.
- 2008 Artefact or trace fossil on *Tylotrochus subimbricatus*; Schubert *et al.*, p. 22; fig. 3A–G.
- 2013 unmentioned; on *Eucycloscala duocostata* and *Coelostylina* sp.; Gründel & Mitta, pl. 3, fig. 7; pl. 5, fig. 16; pl. 6, figs 2–3.
- 2019 Ornament of *Calliotropis biarmata*; Ferrari & Kaim, p. 273; fig. 3A–J.

LSID. <https://zoobank.org/NomenclaturalActs/C7F1902B-9ABE-4025-9C98-8FF1CDDF8F41>

Derivation of name. Based on *geometricus* (Latin for ‘geometric’), referring to the conspicuous geometric branching pattern of the structure.

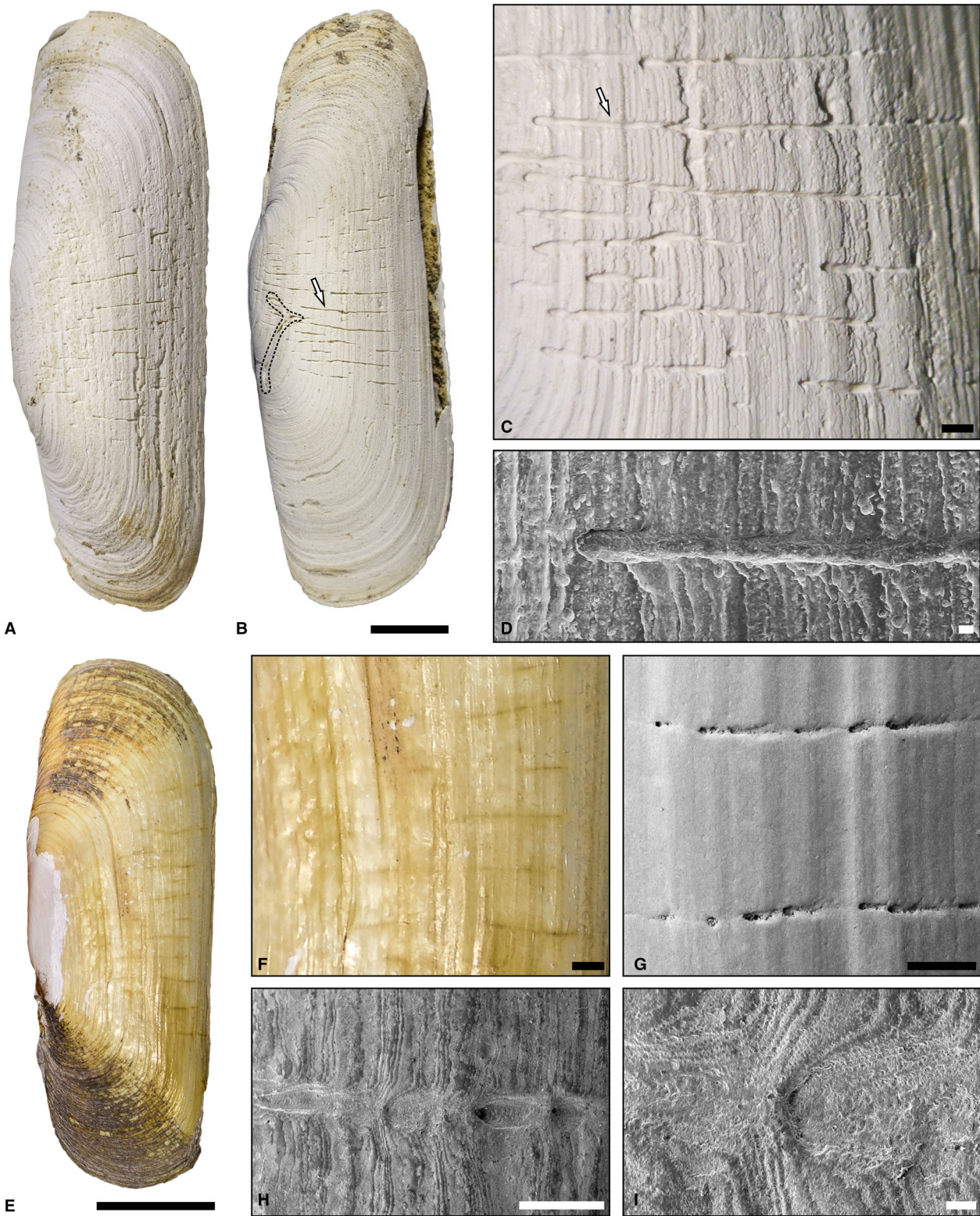
Type specimens. As with *R. reticulatus*, we consider the entire interconnected network structure as a single colony, or a single specimen of *R. geometricus*. The holotype (Fig. 5A–D) and the paratype (Fig. 5E–H) are both preserved on gastropod shell fragments collected in Reptile Creek, *c.* 3 km northeast of Eureka weather station, Fosheim Peninsula, Ellesmere Island, Nunavut, Arctic Canada (WGS84: 80.0025, –85.8009). The type stratum is the Deer Bay Formation, lower Valanginian (following Kemper 1975), Lower Cretaceous. The specimens are curated in the Geology and Palaeontology collections of the Natural History Museum of Denmark, Copenhagen, under accession numbers MGUH 34115 (holotype) and MGUH 34116 (paratype).

Diagnosis. Regular network of grooves, between which scale-shaped shell parts of relatively uniform dimension have remained; grooves run straight or curve slightly in a converging fashion towards the dichotomous junctions.

Description. Ordered network of anastomosing grooves (Figs 1D, 5) with lenticular to rhombic shell peninsulas of relatively uniform shape and dimension (mean 200.6 ± 72.2 by 146.5 ± 35.9 µm; *n* = 100; Table 1). The holotype (Fig. 5A–D) shows several points of initial bioclaustration that rapidly and readily integrate to form a coherent meshwork of grooves; the earliest network cells are larger and more elongate, while those near the prominent growth breaks appear to be smaller than average. This variation in mesh-size is also apparent in the paratype specimen (Fig. 5E) that shows larger network cells after the first major growth break. A specimen in Gründel & Mitta (2013, pl. 3, fig. 7) shows that the regular mesh size can markedly change at major growth breaks. Grooves have an annular ornamentation (Fig. 5C) and are approximately as deep as they are wide (width, 71.2 ± 10.7 µm; *n* = 100; Table 1). The surface of the peninsulas has a deflected shell ornamentation and their edges are sharp and sub-vertical (Fig. 5C, D). The paratype (Fig. 5E–H) shows the typical cascading re-establishment of individual strains of the network where the symbiont has survived major growth breaks (Fig. 5F, G). As a result, the networks widen in a cladogram-like manner. The grooves are partly filled with a black, pyritized mineral. This infill has a smooth surface and is somewhat domed relative to the surrounding shell surface, resulting in a subcircular cross-section (Fig. 5H).

Hosts. Various gastropod species, including *Tylotrochus subimbricatus* (Schubert *et al.* 2008), *Eucycloscala duocostata* (Gründel & Mitta 2013), *Coelostylina* sp. (Gründel & Mitta 2013) and *Calliotropis biarmata* (Ferrari & Kaim 2019); the host species of the type material remains undetermined due to the fragmentary nature of the shells.

Palaeobiogeographical distribution. Sverdrup Basin (Arctic Canada; herein), Central-European epicontinental sea (Germany,



Poland; Schubert *et al.* 2008; Ferrari & Kaim 2019), boreal Khatanga Sea (Siberia; Keyserling 1846; Lahusen 1886), Unzha Basin, Central Russia (Gründel & Mitta 2013).

Stratigraphic range. Lower Jurassic (Pliensbachian; Schubert *et al.* 2008) to Lower Cretaceous (Valanginian; type material described herein).

FIG. 4. Pleistocene type material and modern representatives of *Rodocanalís linearis* csp. nov. in *Tagelus plebeius* bivalve shells from the coastal southwestern Atlantic of the Buenos Aires Province, Argentina. A–D, left (A) and right (B) valves of the *T. plebeius* shell from the Pleistocene at Puente de Pascua, Buenos Aires Province, Argentina, that carries the holotype (arrow) and the numerous paratypes of *R. linearis* (DCG-MLP-0007-907; the dashed line indicates overprint by a macrobioerosion trace); C, close-up of B showing the parallel arrangement and unbranched nature of the holotype (arrow) and several paratypes of *R. linearis*, running from the umbo-nal region towards the ventral margin of the host; D, SEM close-up of C showing the proximal part of the holotype of *R. linearis* with constant width. E–F, a modern *T. plebeius* from Punta Alta, Buenos Aires Province, Argentina, with periostracum still preserved, below which *R. linearis* has formed and is visible as dark lineaments (DCG-MLP-0007-908); F, close-up of E, showing the dark lineaments below the periostracum. G, SEM image of a modern *T. plebeius* from Miramar (Arroyo Durazno), Buenos Aires Province, Argentina, with the periostracum removed, showing the straight course and partly pitted nature of *R. linearis*. H–I, two SEM images of a Holo-cene *T. plebeius* from Cerro de La Gloria, Buenos Aires Province, Argentina, showing the deflection of the bivalve's growth increments and details of the intermitted deepening of *R. linearis*. Scale bars represent: 1 cm (A, B, E); 1 mm (C, F–H); 100 μ m (D, I).

Remarks. The pyrite infill shown in the paratype could potentially be considered as a body fossil of the original symbiont. If it was, as a biotaxon, it would not compete with *R. geometricus* for nomenclatural priority.

This type of bioclastration was first recognized by Keyserling (1846), who considered it an ornamental feature of a new Jurassic (?) gastropod species he named *Turbo rhombodes*. This biotaxon does not compete for priority with the new cecido-taxon established herein.

MORPHOMETRY OF *RODOCANALIS*

Several morphometric properties of the various *Rodocana-lis* type specimens were measured for the cecidospecies descriptions (see above) and comparative analyses. The width of the grooves (as well as their standard deviation) was found to decrease from the morphologically simple *R. linearis* and *R. runcus* towards the reticulate structures of *R. reticulatus* and further to the geometrically most complex and regular *R. geometricus* (Table 1; Fig. 6A). For the latter two cecidospecies, this goes along with a reduction in the size (length vs width) of the peninsulas of shell remaining in between the anastomosing grooves (Table 1; Fig. 6B). Thereby, the ratio between the length and the width, reflecting the regularity in shape of the network cells, is more constant in *R. geometricus*, resulting in a better coefficient of correlation ($r^2 = 0.75$) compared with *R. reticulatus* ($r^2 = 0.34$; Fig. 6B). On average, the network cells are more elongate in *R. geometricus*, resulting in a shallower regression trendline (0.43x) compared with *R. reticulatus* (0.67x; Fig. 6B).

PREVIOUS INTERPRETATIONS OF *RODOCANALIS* STRUCTURES

Keyserling (1846), who was the first to report and illustrate structures here assigned to *Rodocanalís*, considered them part of the original ornamentation of the Jurassic gastropods, which he named *Turbo rhombodes*,

accordingly. Several other workers have also considered *Rodocanalís* as part of the shell ornament in different gastropod species (e.g. Lahusen 1886; Ferrari & Kaim 2019). It should be noted, however, that in some gastropod species a very similar ornamentation does indeed occur (discussed in Schubert *et al.* 2008), as is the case for the Permian species '*Trochus*' *adrianensis* illustrated by Greco (1937).

Schloz (1972), when establishing *Rodocanalís* and its type species *R. reticulatus*, interpreted these features as etchings and thus as a bioerosion trace fossil in the surface of the infested bivalves. He even included this interpretation in what he considered an ichnogenus name (*rodere*, Latin for 'gnaw, erode'). Accordingly, *Rodocana-lis* was listed as a trace fossil (boring) in the 'Trace Fos-sils' part of the *Treatise on Invertebrate Paleontology* (Häntzschel 1975). Mayoral & Sequeiros (1979) followed that interpretation. Beizel (1983) regarded *R. reticulatus* as drilling networks created by encrusting bryozoans and noted that various phases of *R. reticulatus*, up to nine bands of which he had observed on gastropods, might be related to seasonal variations in the growth rate of these shells. Marek (1982), when establishing *R. runcus*, considered the structures as the work of bioeroding clionaid sponges and later (Marek 2004) revised his interpretation to include other excavating sponges as well as microboring algae and fungi as potential trace makers.

Plewes (1996, p. 119) was the first to suspect that *Rodocanalís* is a 'pseudo-etching' (without further specification) but was unable to confirm her hypothesis because she was unable to trace the holotype of *R. reticulatus* and did not consider the paratype or topotypic material for a reinvestigation. A genus-level relationship between *Rodo-canalís* and *Runia* was noted by two of us (MW and MAW) in Buatois *et al.* (2017, p. 158), stating that 'As with *Runia*, *Rodocanalís* may actually be a bioclastration on the growing margin of the bivalves similar to the structures made by hydroids in the skeletons of serpu-lids', a view built on here.

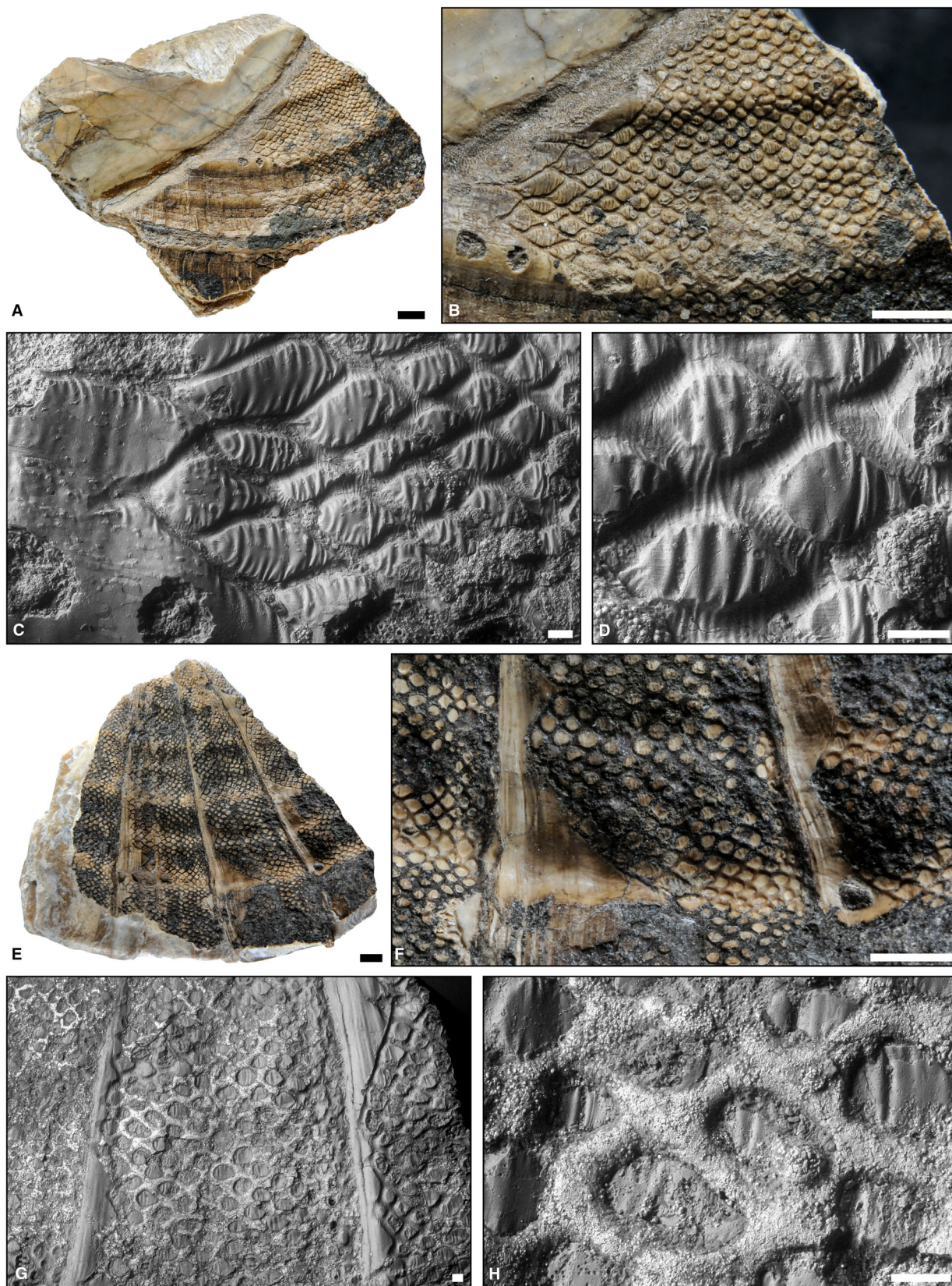


FIG. 5. Type material of *Rodocanalís geometricus* csp. nov. in gastropod shell fragments from the Lower Cretaceous of Ellesmere Island, Arctic Canada. A–B, overview and close-up of the shell fragment carrying the holotype (MGUH 34115); note the larger initial network cells. C–D, SEM overview and close-up of A, showing the intricate detail of the regularly anastomosing canal system and the sharp edges of the remaining shell peninsulas and their deflected surface sculpture. E–F, overview and close-up of the shell fragment carrying the paratype (MGUH 34116); note the cascading re-establishment of individual strains of the symbiont surviving major growth breaks; the grooves are partly filled with a pyritized (black) replacement of the original symbiont. G–H, SEM overview and close-up of the canal network in E with potential pyrite ‘body fossil’ of the symbiont. Note that the shell fragments are illustrated upside down, in order to display *R. geometricus* in growth direction to the right. Scale bars represent: 1 mm (A, B, E, F); 100 μm (C, D, G, H).

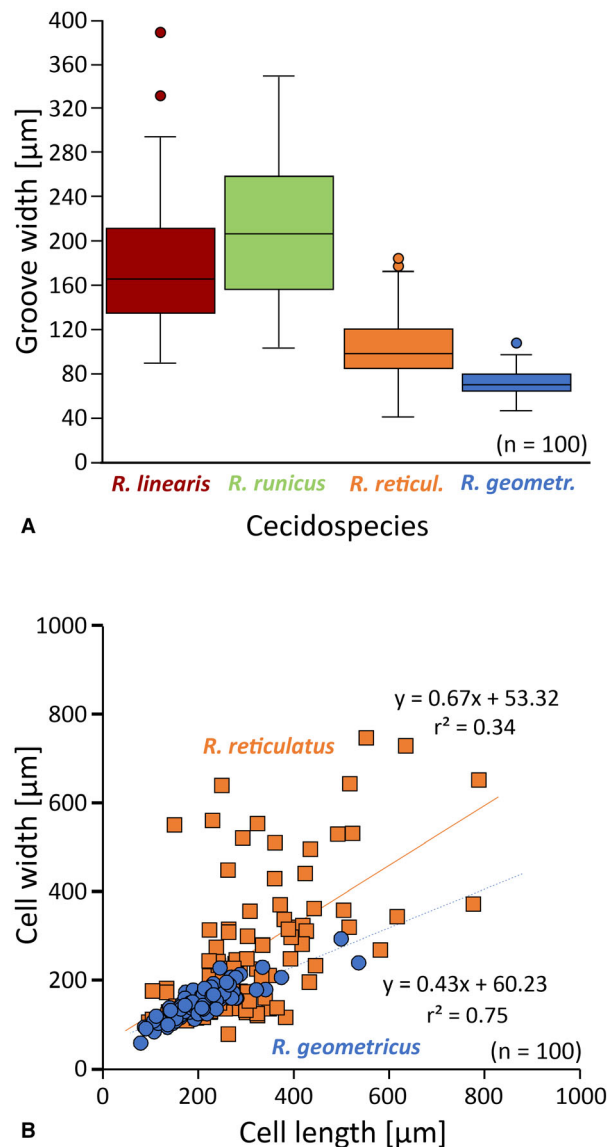


FIG. 6. Basic morphometric assessment of the various *Rodocanalís* cecidospecies. A, boxplot, including outliers, of the width of the grooves in the four cecidospecies in order of geometric complexity and regularity. B, length (oriented parallel to shell growth) versus width of the network cells in *R. reticulatus* and *R. geometricus* with linear regression trendlines and correlation coefficients r^2 .

Richiano *et al.* (2018), in their detailed investigation of linear grooves in the endobenthic bivalve *Tagelus*, herein established as *R. linearis*, discussed different processes of their formation, thereby dismissing bioerosion and concluding that constructive bioclastration below the periostracum is the most plausible explanation. However, the identity of the soft-bodied symbiont remained elusive.

HYDROID SYMBIONTS IN INVERTEBRATES, MODERN AND ANCIENT

Our hypothesis is that at least three out of the four *Rodocanalís* cecidospecies are likely to have been produced by colonial hydroids bioclastrated in molluscan skeletons. This is based on several modern and fossil examples of broadly similar associations. We thus briefly summarize here the known symbiotic relationships between hydroids and other invertebrates.

Hydroids have a remarkable ability to form symbioses with a variety of aquatic invertebrates, including gastropods, bivalves, corals, sponges, bryozoans, tunicates, serpulids, echinoids, crustaceans and other hydroids (Piraino *et al.* 1994; Puce *et al.* 2008). Of note for this study is the symbiotic relationship between the anthoathecate hydroid *Rosalinda lundalvi* and the limid bivalve *Acesta excavata* (Fig. 7C) recently described from cold-water coral mounds off the west coast of Mauritania, West Africa, by Gil *et al.* (2021). This hydroid grows at the ventral margin of the bivalve shell with a branching coenosarc complex remarkably similar to the structure of *Rodocanalís reticulatus*. However, *Rosalinda lundalvi* does not incorporate itself into the bivalve skeleton. In fact, most of these contemporary symbiotic relationships involve soft tissues only and thus have little chance of making it into the fossil record. However, representatives of three major clades are symbiotic with modern hydroids, involving modification of or incorporation within the host skeleton: corals, bryozoans and serpulids.

Symbioses of certain coral species involve direct interactions between the soft hydroid and the host's aragonitic skeleton. Pantos & Hoegh-Guldberg (2011) describe a

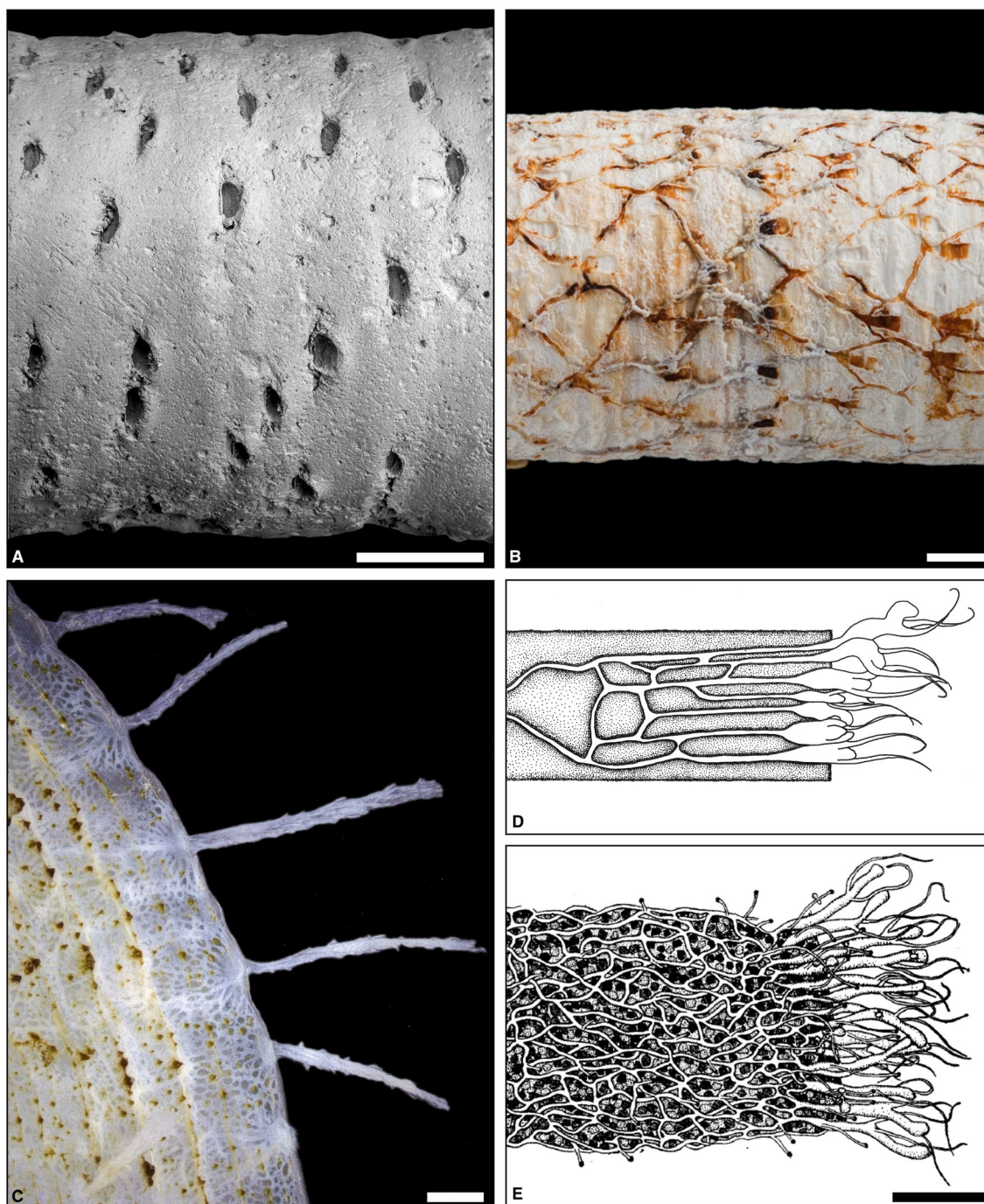


FIG. 7. Fossil and Recent hydrozoans with affinity to *Rodocanalisis* cspp. A, fossil tube worm *Parsimonia antiquata* from the Red Chalk (Hunstanton Formation, Albian, Lower Cretaceous) at Hunstanton, Norfolk, UK, showing the characteristic apertures formed by bioclastration around polyps of the fossil filiferan hydroid *Protulophila gestroi* (NHMUK A7625; photo courtesy of Paul Taylor, Natural History Museum, London; same specimen figured by Scrutton 1975, pl. 39, figs 6–8). B, reticulate stolons preserved together with the polyps of *Protulophila gestroi*, exposed by erosion from within the calcareous skeleton of the serpulid *Protula protensa* from the Miocene (?) of Latakia, Syria (NHMUK A229; photo courtesy of Paul Taylor, Natural History Museum, London). C, the anthoathecate hydroid *Rosalinda lundalvi* showing the coenosarc meshwork and hydranths aligned on the ventral margin of the clam *Acesta excavata* from Mauritania (SMF 12908; reproduced from Gil *et al.* 2021, fig. 15). D, schematic drawing of the colony pattern in the hydroid *Proboscoidactyla flavicirrata*, showing the stolon arrangement and the gastrozooids (modified after Campbell 1968a, fig. 1b). E, drawing of the hydroid *Proboscoidactyla flavicirrata* on the sabellid polychaete *Pseudopotamilla myriops*, based on extant material from Hokkaido, Japan (reproduced from Uchida & Okuda 1941, fig. 2). Scale bars represent: 1 mm (A–C, E).

symbiotic relationship between the colonial soft-bodied hydroid *Zanclaea margaritae* and the scleractinian coral *Acropora muricata*. Most colonial hydroids have a chitinous exoskeleton called the perisarc, which provides protection and support for the soft tissues. *Zanclaea margaritae*, however, lacks a perisarc and attaches its tissues directly to the skeleton of the host coral with specialized cells called desmocytes. The coral skeleton of *A. muricata* is modified at the ultrastructure scale where it was in contact with the hydroid (Pantos & Hoegh-Guldberg 2011). These features are only a few microns in dimension and thus are unlikely to be preserved in fossils. Manca *et al.* (2019) described skeletal tubular microstructures in scleractinian corals that host zancleid hydroids, although their relationship to the hydroids is unclear.

Osman & Haugness (1981) described a modern symbiotic relationship between stoloniferous zancleid hydroid colonies and the bryozoans *Celleporaria* and *Schizoporella*. These bryozoans secrete calcareous material around the hydroids, which maintain openings for their polyps. In the case of *Celleporaria*, the presence of the hydroids gives the bryozoan a competitive advantage over other bryozoans for substrate space, presumably by relying on the hydroid's stinging cells. Boero *et al.* (2000) described the symbiosis between the hydroid *Zanclaea divergens* and the bryozoan *Celleporaria sibogae*. Like *Z. margaritae*, *Z. divergens* lacks a perisarc given that it grows underneath the bryozoan skeleton (Boero *et al.* 2000). Most recently, López-Gappa & Liuzzi (2021) detailed a symbiotic relationship between the cyclostome bryozoan *Dispor-ella densiporoides* and the stoloniferous hydroid *Filellum bouvetensis* of the family Lafoeidae. In this case, the bryozoan formed numerous chimney-like calcareous tubes covering most of the hydroid symbiont, which constitute a type of bioclastration.

The earliest fossil record of a possible hydroid symbiosis is an Upper Ordovician (Katian) bioclastration in a trepostome bryozoan described by Palmer & Wilson (1988). In fact, it is this article that first defined 'bioclastration', using this structure they named *Catellocaula vallata* as an example. The bioclastrated organism was colonial, consisting of a series of stellate modules connected by stolons. The stolons and modules were often roofed over by the host bryozoan, leaving tunnels and cavities in the bryozoan skeleton.

Vinn *et al.* (2021) described several bioclastrations in upper Silurian cystoporate and trepostome bryozoans, including several attributed to hydroid–bryozoan symbioses. The hydroid apertures are surrounded by reactive bryozoan skeletal tissue and are not overgrown, indicating a *syn vivo* relationship. Stolons are not evident on the surface or within the bryozoan skeletons.

McKinney (2009) described a bioclastrated modular symbiont in Devonian fenestrate bryozoans, naming it

Caupokeras and referring it to hydroids. Suárez Andrés (2014) considerably expanded the known range of bryozoan hosts for *Caupokeras*, and further supported its assignment to hydroids. Suárez Andrés *et al.* (2020, 2021) described similar bioclastrations in Devonian trepostome bryozoans, again considering them most likely to represent symbiotic hydroids.

Serpulids are by far the most common skeletal invertebrates that have symbiotic relationships with hydroids. *Protulophila* is a bioclastration of a colonial hydroid found in serpulid skeletons from the Early Jurassic to the Recent (Scrutton 1975; Radwańska 1996; Taylor *et al.* 2015; Słowiński *et al.* 2020). *Protulophila* appears as a series of semi-circular to circular apertures in the outer skeleton of the serpulid hosts (Fig. 7A), often with adapical 'hoods' and in one case with proximal sinuses (Zágoršek *et al.* 2009; Słowiński *et al.* 2020). Exfoliating the serpulid skeleton, either by weathering or artificially, reveals a reticulate network of stolons and zooid chambers parallel to the growth direction of the serpulid tube (Fig. 7B). Non-destructive micro-computed tomography analyses by Słowiński *et al.* (2020) have revealed intricate details of this internal arrangement. The serpulid skeletal growth lines are deflected around the stolons and chambers, demonstrating the *syn vivo* nature of this symbiosis (Scrutton 1975). Recently, modern examples of *Protulophila* have been discovered in the Red Sea, Madagascar, Philippines, Indonesia, New Caledonia and New Zealand, with the inhabitants of these structures confirmed as hydroids (Taylor *et al.* 2015).

Finally, sabellid polychaetes are also known to develop symbioses with hydrozoans, as exemplified by the extant proboscicidactylid species *Proboscicidactyla flavicirrata* (Fig. 7D, E), which maintains a chain of polyps around the worm's tube aperture (e.g. Uchida & Okuda 1941; Campbell 1968a; Scrutton 1975).

HYDROID SYMBIONTS ASSOCIATED WITH *RODOCANALIS*?

The morphology and branching pattern of the *Rodocanalis* structures orientated towards the hosts' growth margin, together with the hosts' deflected growth increments (Fig. 1), support our interpretation of *Rodocanalis* as bioclastrations to be addressed by cecidotaxonomy, as opposed to a bioerosion phenomenon that would fall into the domain of trace fossil ichnotaxonomy.

In analogy to the known symbiotic associations of hydroids to various invertebrate clades outlined above, we propose that *Rodocanalis* is a bioclastration formed by molluscan hosts as a reaction to symbiotic hydroids settling and growing together with the shell at its active growth margin. There, the hydroids become partly

enclosed and profited from the resulting protection from predation or other disturbances. In the case of modern *R. linearis* forming in endobenthic bivalve shells, the symbiont is located below the shell's outer, organic layer, the periostracum, thus enhancing protection. With no periostracum preserved in the fossil host species, we can only speculate upon a similar formation below the periostracum, whereby such a scenario imposes problems in explaining the formation of an intact periostracum covering the distal parts of the bioclastration, given that this shell layer is secreted by the outer mantle lobe that must have reached around the symbiont to form the periostracum. In any case, we envision the hydroids' feeding organs as located at the hosts' active growth margin, reaching out into the ambient seawater from between the periostracum and the calcareous ostracum; a formidable place to profit from the bivalves' filter-feeding current, or from food debris in the case of carnivorous cephalopods or grazing gastropods. While this interpretation would reflect a commensalistic mode of symbiosis, one needs to evaluate potential profits for the molluscan host, too. One such advantage would be protection by the hydroid's defensive cnidocytes, such as reported by Kinne (1983) and Manning & Lindquist (2003), in which case the association is more likely to have been mutualistic in nature.

Once the hydroids have managed to settle at the active growth margin and stimulated the embedment process, the animals grew together with the growing margin and initiated budding to form colonies, resulting in the observed branching patterns. Two fundamentally different types of branching can be observed: the first one, represented by *R. runicus*, is characterized by grooves that repeatedly ramify uni- or bilaterally, but grooves never reunite to form a network with anastomoses (Fig. 1B). This branching pattern has a remarkable resemblance to the organization of the proboscoidactylid hydroid species *Proboscoidactyla flavicirrata* (Fig. 7D, E), a known symbiont in sabellid polychaetes (e.g. Uchida & Okuda 1941; Campbell 1968a; Scrutton 1975). In this particular species, a growth strategy atypical for most hydroids is developed: the polyp moves forward to the worm's tube edge and the stolon develops behind the polyp (Campbell 1968a). In this way the hydroid's polyps can keep up with the growth of the host, leading to bioclastration in the case of *R. runicus*. In *P. flavicirrata*, the development of anastomoses takes place in the proximal part of the stolons via secondary growth, which in the case of *R. runicus* was impossible because the stolons were covered by the bioclastration and growth was only possible forwards, with some lateral ramifications starting just behind the polyp (the proliferative zone). Hence, this mode of growth would explain the lack of anastomoses in *R. runicus*. Campbell (1968b) studied the settlement and metamorphosis of the *P. flavicirrata* planula, finding that

the symbiosis is mediated by the sabellid host. The worm catches the planula in the ciliary currents of its branchial tentacles and then transfers it to the tube rim by retracting and scraping the planula off onto the rim, where the larva starts the metamorphosis. For *R. runicus*, nautiloid cephalopods are the only known hosts, in which case a similar settlement process, involving the cephalopod's tentacles, can be envisaged. Interestingly, in Campbell's (1968b) opinion, the symbiont association between the hydroid and the worm seems to be non-specific, because the attraction is mediated by water currents set up by the branchial apparatus, and the planula plays a passive role in initiating the symbiosis, therefore other host clades seem conceivable, too.

The second principal branching pattern is developed in *R. reticulatus* and *R. geometricus*. Here, branches anastomose to form a network of a varying degree of complexity and regularity (Fig. 1C, D). These patterns can be explained by a hydroid symbiont, which, after larval settlement at the shell's growth margin, develops a first polyp that becomes fixed on the calcareous ostracum (i.e. usually the prismatic shell layer) and is surrounded at its base by the periostracum formed by the outer (secretory) mantle lobe. The polyp then moves together with the shell growth towards and along the external shell surface, while the stolonial hydrorhizae develop (in the only possible way) right at the shell's growth margin. This mode of growth enables the stolons to fuse and form anastomoses as well as new polyps originating by budding, while the bioclastration of the hydrorhizae advances. According to this model, there would be living polyps both on the outer surface of the shell and along the growth line. Bioclastration would affect only the hydrorhizae but would present circular openings at intersections for the polyps. Whereas the molluscan hosts profit from the larger number of polyps on the external shell by a more effective defence of the hydroid's cnidocytes against predators, the most proximal polyps become less efficient in feeding the hydroid, perhaps leading to a partial die-off of these polyps. An argument that could validate this development model in *Rodocanalis* is found in the fossil filiferan hydroid *Protulophila gestroi* and its recent relatives (see also above), the bioclastrations of which follow this pattern, and polyp openings are located on the outer surface of serpulid tubes (Scrutton 1975; Radwańska 1996; Taylor *et al.* 2015). *Protulophila* most closely resembles *R. geometricus* in its network of stolons, which are overgrown not by an organic periostracum but by a calcified layer of the worm tube containing polyp chambers (Fig. 7A, B). The reticulate hydrorhizae, in Recent species, are characteristic of stolonial colonies such as are found among the hydractiniids and rosaliids.

While all the above is readily plausible for the branching forms of *Rodocanalis*, the hydroid hypothesis is

questionable for the strictly linear and unbranched *R. linearis* for one reason in particular: the endobenthic environment of its host bivalve *Tagelus*. In such an environment, contact with the sediment and poor oxygenation are limiting factors for filter-feeding. Furthermore, the symbiont would not be located near the host's main feeding current at the siphons' openings reaching above the sediment surface. Instead, the symbiont possibly either reached out to or into the bivalve's mantle or mantle cavity for feeding, an orientation that would be better in line with the periostracum secreted by the outer mantle lobe covering and protecting the symbiont, or these symbionts had a detritivore trophic mode, as developed in various groups of polychaetes (e.g. terebellids, ampharetids, cirratulids and spionids). However, *in vivo* observations and dissection of modern *Tagelus* with the symbiont still in place are needed to better understand the symbiont identity and mode of symbiosis. Most recently, a worm symbiont, possibly a polychaete new to science, has been isolated from *R. linearis* bioclustrations in *Tagelus* specimens in northern Argentina and is presently under investigation and taxonomic description (C. Pereyra, pers. comm. 2021). A polychaete identity would be surprising, however, because in polychaetes the feeding organ and the anus are at opposing ends of their body and, as a result, polychaete bioerosion traces are U-shaped, with two openings, one for each purpose. Linear and unbranched bioerosion traces, in contrast, are usually associated with either phoronids or sipunculans, both kinds of worms having feeding and disposal organs at their posterior end (see detailed discussion in Wisshak *et al.* 2017). Nevertheless, those serpulid or sabellarid polychaetes that inhabit closed tubes manage defecation via transport of faecal pellets by ciliary currents along a ciliated groove or by bending the posterior (abdominal) part towards the tube aperture, respectively (Westheide & Rieger 1996; Ruppert *et al.* 2004). Hence, for now, we do not exclude any of these potential worm symbiont identities for *R. linearis*. Furthermore, given the capability for bioerosion evolved in these groups of worms, we cannot rule out the possibility that some bioerosion is in action in addition to the primary process of bioclustration, although the latter clearly is the main mechanism involved.

All four observed types of *Rodocanalis* developmental pattern, irrespective of the symbiont identity, demonstrate a close dependency on the hosts' shell growth in that the bioclustrations often terminate at prominent growth breaks (between stages 3 and 4 in Fig. 1), reflecting some period of relative inactivity of the molluscan hosts in phases of unfavourable environmental conditions or seasons. This inactivity compromises the ability of the symbionts to profit from the host's feeding activity, hence synchronizing good versus bad times in these host–

symbiont relationships and leading to a complete or partial episodic die-off of the symbionts. In the case of the putative hydroid symbionts, those polyps that managed to survive the period of inactivity were the starting points for renewed colony development upon the return of favourable conditions and the onset of shell growth. The existence of 'forms of resistance' or 'resting stages' in hydroids during unfavourable periods has been described by several authors (i.e. Calder 1990; Boero *et al.* 1992, 2003; Boero 1994) and in several species, demonstrating the group's capacity to cope with spells of unfavourable conditions to some degree. At least in *R. geometricus*, the pace of the host's growth apparently also had an influence on the mesh-size of the resulting network, with larger network cells reflecting higher growth rates and a condensed network reflecting a slowdown in growth, as is clearly recorded near the prominent growth breaks.

In conclusion, we consider a hydroid affinity of the three branching forms of *Rodocanalis* (*R. reticulatus*, *R. runicus* and *R. geometricus*) highly plausible and likely, whereas for the unbranched *R. linearis* other candidate invertebrates also need to be considered, the foremost being polychaete, sipunculan or phoronid worms. We expect *Rodocanalis* to be much more common in the fossil record than presently thought. Given the very scarce hydrozoan body fossil record (Muscente *et al.* 2016), we emphasize the potential of these bioclustrations for gaining a better understanding of the palaeoecology and evolution of hydroid symbionts in various molluscan hosts, presently including cephalopods, gastropods and bivalves. The suite of *Rodocanalis* cecidospecies provides a framework for addressing such bioclustration structures and enables integration of additional geometries if applicable.

SUBMARINES AND ISLANDS: ECOLOGIES OF THE MOLLUSCAN HOSTS

Although all of the recorded *Rodocanalis* structures were found associated with molluscs as hosts, the four cecidospecies are adapted to host taxa with rather different lifestyles, associated with three major mollusc clades. *Rodocanalis runicus* occurs exclusively in the shells of Silurian orthoconic nautiloids, which are generally regarded as actively swimming predators, some of them living as vertical migrants in pelagic settings, while others had a demersal lifestyle inhabiting coastal environments (e.g. Kröger *et al.* 2009; Peterman & Ritterbush 2021). For *R. runicus*, these hosts provided a threefold advantage. First, leftover food particles may have made for a nutritious diet; second, water currents that flowed into the mantle cavity towards the branchial apparatus were a potential vector for food particles; and third, settling on a

'submarine vessel' enabled the hydroids to venture into a habitat commonly barred to sessile creatures; a strategy taken by various types of pseudoplankton (Baird *et al.* 1989; Wignall & Simms 1990). Both *Rodocanalis geometricus* and *R. reticulatus* occur on gastropods, and the latter also on large limid bivalves. Taxonomically, these are very different hosts. Ecologically, however, they may offer a similar advantage: life on a benthic island. Soft, soupy sea floors are a rather hostile environment for most sessile invertebrates, and the shells of larger species that cope with these conditions can serve as a welcome settling space (Kauffman 1978, 1982; Tapanila & Ebbestad 2008). In the case of the gastropods, these benthic islands were mobile, and may have additionally provided food particles, particularly if the hosts were scavengers or omnivores. However, most of the gastropod taxa settled by *Rodocanalis* were probably herbivore benthic grazers. In contrast, the limid bivalve *Plagiostoma gigantea* was stationary, living as an epibenthic, orthothetic edgewise recliner *sensu* Seilacher (1984), whereby both valves served as a substrate for *Rodocanalis*. A range of epibionts is documented from a Triassic congener, *Plagiostoma striata* (Seilacher 1954). Similar to the hydroids involved in *Rodocanalis*, these taxa are not specifically adapted to *Plagiostoma*. However, while epibionts such as bivalves or brachiopods require only a substrate, it is evident that the symbiotic, bioclastrated hydroids needed a living mollusc host for help.

In this context, it is interesting to note that, unlike symbionts settling on the interior side of the shells (e.g. Huntley *et al.* 2021), *Rodocanalis* does not cause any thickening, callosities or blister pearls in the host shells. Instead, the hosts seem to make space for the hydroids in their shell, but otherwise follow their inherited programme with regard to shell growth and ornament.

CONCLUSIONS

1. The former ichnogenus *Rodocanalis* Schloz, 1972 is reinterpreted to represent bioclastrations (treated as cecidotaxa) formed around symbionts in the outer calcareous shell layer at the active growth margin in different kinds of mollusc shells.
2. The revised cecidogenus *Rodocanalis* includes simple linear grooves (*R. linearis* csp. nov.), sets of distally ramifying grooves (*R. runicus* comb. nov.; formerly *Runia runica*), irregular networks of grooves (*R. reticulatus*), and regular reticulate networks (*R. geometricus* csp. nov.).
3. While the linear grooves in *R. linearis* csp. nov. might be associated with commensalistic worms, we interpret the branched and anastomosing grooves of the other three cecidospecies to have formed around

the stolons of hydroid symbionts after settlement of the hydrozoan larva and fixation of the first polyp on the calcareous ostracum at the shell margin. This enabled new polyps to originate at the shell edge by budding, while the bioclastration of the stolonial hydrorhizae advanced with shell growth.

4. We consider the nature of this symbiotic relationship as mutualistic, with the hydrozoan symbiont profiting from protection and taking advantage of the host's feeding current or food debris, and the molluscan host profiting from the defensive capability of the hydrozoan's cnidocysts.
5. Due to their different lifestyles, the various known molluscan hosts either served as mobile or fixed benthic islands (gastropods and bivalves, respectively) or as submarine vessels (cephalopods).
6. The bifurcating form of *Rodocanalis* most closely resembles the growth pattern seen in the proboscideactylid *Proboscideactyla flavicirrata*, while the reticulate patterns show affinities with the fossil filiferan hydrozoan *Protulophila gestroi* and with Recent hydractiniids and rosalingids such as *Rosalinda*.
7. Given the very scarce hydrozoan body fossil record, we emphasize the potential of studying *Rodocanalis* cecidospecies to gain a better understanding of the palaeoecology and evolution of hydroid symbionts in various molluscan hosts.

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Author contributions. MW conceptualized the study, investigated the type specimens of *R. reticulatus* and *R. geometricus*, undertook the morphometrical analyses, prepared the figures, and wrote the

original draft. SS sent the type material of *R. geometricus* to MW for his opinion, and reviewed the ecology of the molluscan hosts. RM studied the type specimens of *R. runicus* stored in Prague. SR studied the type and additional material of *R. linearis* stored in Argentina. FR shared his expertise on extant hydrozoans and fostered the interpretation of the bioclastrations under study. MAW reviewed the fossil record and modern examples of hydrozoan symbioses. All authors were involved in the interpretation of the enigmatic bioclastrations under study, they critically reviewed and improved the manuscript, and they approved the final version thereof.

DATA ARCHIVING STATEMENT

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