HYDROID-SERPULID SYMBIOSIS IN THE MESOZOIC AND TERTIARY

by COLIN T. SCRUTTON

ABSTRACT. Several species of Mesozoic and Tertiary serpulids from Europe and the Middle East were infested by a colonial organism which is preserved as the mould of a stolonal network with polyp chambers buried in the peripheral zone of the calcareous tube. The polyp chambers open to the outer surface of the tube through small, usually semicircular apertures. The mould is the result of incorporation of the organism into the worm tube during calcification by the serpulid: it is not a boring. The organism is interpreted as a hydroid or group of related hydroids which lived commensally or possibly mutualistically with the serpulids. This hydroid-serpulid symbiosis is compared with the living symbiosis between the hydroids of *Proboscidactyla* and certain species of sabellid polychaetes.

The name of the fossil symbiont is *Protulophila gestroi* Rovereto.

THE strikingly patterned outer surface of a specimen of the serpulid *Parsimonia* sp. from the Gault Clay (Lower Cretaceous) of Kent (Pl. 42, figs. 1–2; text-fig. 2) originally prompted this investigation. The pyritic system of stolons and 'thecae' was at first thought to represent a colonial organism growing on the surface of the tube, but further intensive collecting at the same locality yielded abundant material indicating that this appearance was the result of the exfoliation of the tube. Unworn tubes showed only a series of small apertures scattered over the outer surface (see text-fig. 1). Specimens were recovered showing all stages from this perfectly preserved condition to tubes in which exfoliation revealed the internal network, usually infilled by pyrite.

A subsequent search of the extensive collection of fossil serpulid tubes in the Department of Palaeontology, British Museum (Natural History) yielded much additional material. Signs of the association were found on specimens ranging in age from Middle Jurassic to Pliocene and collected from various localities in Europe and the Middle East.

Few references to this association have been made in the literature. The earliest appears to be that of Sowerby (1829, p. 226, pl. 608, fig. 3) who recorded 'minute pores or short tubes' on the exterior of the Jurassic *Serpula tricarinata*. He was in doubt as to whether they were formed by the worm or some other organism. Wrigley (1951, p. 187), however, erected a new species of *Sclerostyla*, *S. perforata* from the Eocene, for specimens showing perforations in the walls of the tube (Pl. 41, fig. 9). He thus implied the perforations to be formed by the worm although he did not state this explicitly. He did stress, however, that because of their raised and rounded rim, they could not be the work of a parasitic borer.

The system of stolons and 'thecae' exposed by the exfoliation of an infested serpulid tube was first described and named by Rovereto (1901, p. 223, pl. 28, fig. 7*a–c*). He interpreted this pattern as the remains of a new genus and species of ctenostomatous bryozoan, *Protulophila gestroi*, which he considered to be adherent to the outer surface of tubes of *Protula firma* from the Pliocene of Italy (Pl. 42, figs. 3–4). In his discussion of the affinities of *Protulophila*, he noted that it had been considered by

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some specialists to be a hydroid and that its identification as a bryozoan was not entirely certain. His conclusions, however, were based on comparisons with other stoloniferous bryozoans such as *Hypophorella* which is also found associated with polychaete tubes. Finally, Walter (1965, p. 286), working with material from the Upper Jurassic of France in which the relationship between the internal system of stolons and chambers and the external apertures could be recognized, described the organism responsible as a new species of perforant ctenostome bryozoan *Immergentia*? *lissajousi*.

None of these records fully explores the nature of the relationship between the two organisms and none, in my opinion (except in the doubt expressed by Rovereto), correctly identifies the organism infesting the serpulid tubes. This organism is considered here to be a species (or possibly members of a group of closely related species) of colonial hydroid and reasons for this opinion are discussed more fully below. The earliest available name for the moulds left by the hydroids is *Protulophila gestroi* Rovereto.

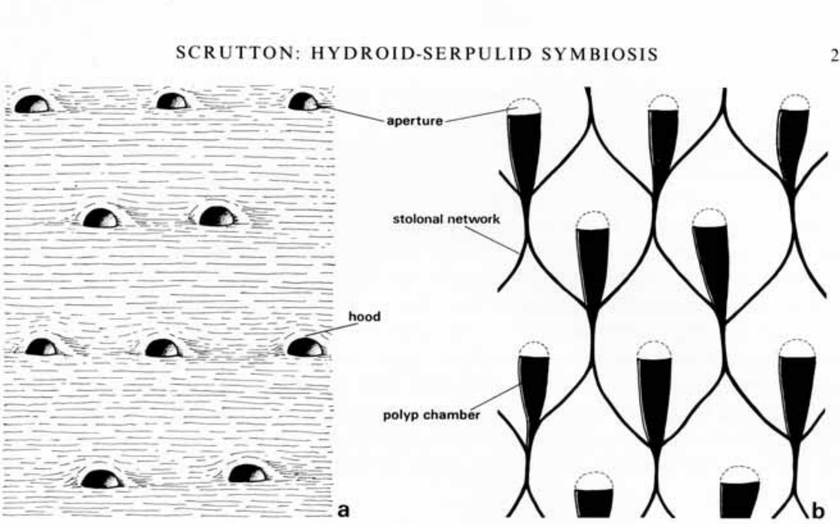
This report is based on the study of approximately 300 specimens, including those described by Walter (1965), Wrigley (1951), and some of those described by Rovereto (1901). Cross- and longitudinal sections have been made of some unabraded serpulid tubes to establish the shape and location of the internal chambers. In addition, two specimens have been serially sectioned for more precise information on the form of the apertures and internal chambers and the structure of the serpulid tube adjacent to them. Because of the small section interval required, between 10 and 30 μm, first attempts were made using acetate peels but since the peripheral layers of the tubes are much less compact than the inner layers plucking tended to destroy the area of maximum interest. Good results were eventually obtained by photographing successive polished surfaces through a polarizing reflected light microscope. The serpulid tubes were mounted with their long axes horizontal in bakelite blocks and prepared using standard techniques. This orientation gives tangential sections when the tube is first exposed and longitudinal sections when approximately half the tube has been removed. The microstructure in the serpulid tubes showed most clearly when viewed through partially crossed polars.

The material figured and listed in this paper is in the collections of the Department of Palaeontology, British Museum (Natural History) unless otherwise indicated.

DESCRIPTION OF THE SYMBIOSIS

External appearance

The external indication of this association is the presence of small pores or apertures scattered over the outer surface of a serpulid tube (text-fig. 1*a*). The apertures are subcircular to semicircular in outline with considerable variation in detailed shape. In semicircular apertures, the long axis is at right angles to the direction of growth of the serpulid tube, usually with the distal lip of the aperture curved and the proximal lip more or less flattened. Aperture size is also variable both within and between specimens. Over the collection as a whole, size varies from 0·10 × 0·22 mm and 0·12 × 0·18 mm to 0·16 × 0·40 mm and 0·20 × 0·36 mm depending on the height–width ratio. Subcircular apertures are *c.* 0·20 mm in diameter. The mean aperture



TEXT-FIG. 1. Morphological terms used in the description of *Protulophila gestroi*. *a*, external appearance. *b*, internal appearance with the serpulid tube exfoliated.

size is 0·15 × 0·28 mm. Within specimens, variation is much lower and the height–width ratio tends to be fairly constant.

The shape and appearance of the apertures vary from species to species of host serpulid. The most important factors influencing aperture morphology appear to be the rugosity of the serpulid tube and the depth to which the internal system of stolons and chambers is buried in the tube wall. Where the internal system is shallowly buried in smooth-walled tubes such as those of the Cretaceous serpulids *Parsimonia* sp. (Pl. 39, figs. 1–5) and *Rotularia* sp. A (Pl. 39, figs. 9–11), the apertural margin is more or less entire and a delicate cowl or hood is formed around the distal lip. The apertures on *Sclerostyla perforata* from the Eocene are similar (Pl. 41, fig. 9). With increasing tube rugosity and depth of burial of the stolons and chambers, the hoods become more massive and tend to overhang the aperture. In *Parsimonia antiquata* from the Lower Cretaceous (Pl. 39, figs. 6–8) the tube is quite smooth but deeper burial of the stolons and chambers is reflected in the development of strongly projecting hoods and associated shallow lateral pits, cut off by the growth of the flanks of the hood. *Rotularia phillipsi* from the Lower Cretaceous (Pl. 39, figs. 12–14) is slightly more rugate but has apertures similarly developed.

More strongly rugate tubes in which the stolons and chambers are deeply buried show correspondingly more elaborately developed apertures: for example, *Serpula sulcata* from the Upper Jurassic (Pl. 40, figs. 3–5). On some specimens of *S. sulcata* the apertures may be produced as short, thin-walled pipes, projecting beneath strongly arched and massive hoods (Pl. 40, figs. 6–10). This structure is also seen in serial section (Pl. 41, figs. 1–3). The most unusual appearance is presented by a specimen of *S. tricarinata* from the Jurassic (Pl. 40, figs. 11–12) on which some apertures project strongly as thick-walled pipes from the relatively smooth surface of the serpulid tube. Elsewhere on this tube, apertures similar to those on *S. sulcata* are present, although in this case the internal chambers and stolons are only very shallowly buried and in places the symbiont may have been exposed.

At their most regular, the apertures are arranged in a quincuncial pattern with a longer axis along the tube length. The most crowded and regularly spaced apertures have a repeat pattern with axes of 0·58 × 0·83 mm (A10924 *Parsimonia* sp., Lower Cretaceous). Spacing is quite variable, however, and on many specimens may be much wider than this. On some Jurassic serpulids apertures may only appear very spasmodically on the surface of the tube (Pl. 40, fig. 6).

Most of the available specimens lack the proximal and distal ends of the serpulid tube and usually apertures are present over their entire length. In some, however, where the tube is more or less complete, apertures may be lacking proximally whilst they are well developed distally. It is very rare for apertures to disappear towards the distal end of a tube. On occasional specimens with the distal extremity of the tube well preserved, small circumferentially elongated pits may be seen on or near the tube rim representing partially formed examples of the normally internal polyp chambers (Pl. 40, fig. 2).

Internal appearance

The apertures are the surface manifestation of small, compressed, subconical internal cavities which for most of their length lie parallel to the external wall of the serpulid tube but bend sharply outwards at their flared end to open at the surface (Pl. 41, figs. 4, 6; Pl. 42, figs. 8, 10). These cavities are here termed polyp chambers (text-fig. 1*b*). Their appearance is best seen in specimens in which exfoliation reveals the stolonal network from which the polyp chambers arise (Pl. 42, figs. 1–10). Stolons and chambers always lie more or less in a single plane at an approximately constant depth below the surface of the tube. In different serpulid species this depth varies and corresponds to a location either at, just outside, or just within the crest on the growing margin of the tube (compare Pl. 40, fig. 2 with Pl. 41, fig. 6; see also Pl. 41, fig. 4).

In tangential aspect the polyp chambers are sub-triangular and elongated along the long axis of the tube. They vary considerably in size and proportions from 0·24 × 0·84 mm and 0·30 × 0·76 mm to 0·28 × 1·10 mm and 0·40 × 1·20 mm even on the relatively few tubes that show them clearly. Variation within a single population is also high, however, and measurements of the chambers on the collection of *Parsimonia* sp. from the Gault Clay (Lower Cretaceous) of Ford Place in Kent range from 0·28 × 1·10 mm to 0·34 × 0·86 mm. In cross-section the polyp chambers tend to be

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EXPLANATION OF PLATE 39

Variation in the distribution and appearance of apertures of *Protulophila gestroi* Rovereto on species of serpulid tubes from the Cretaceous.

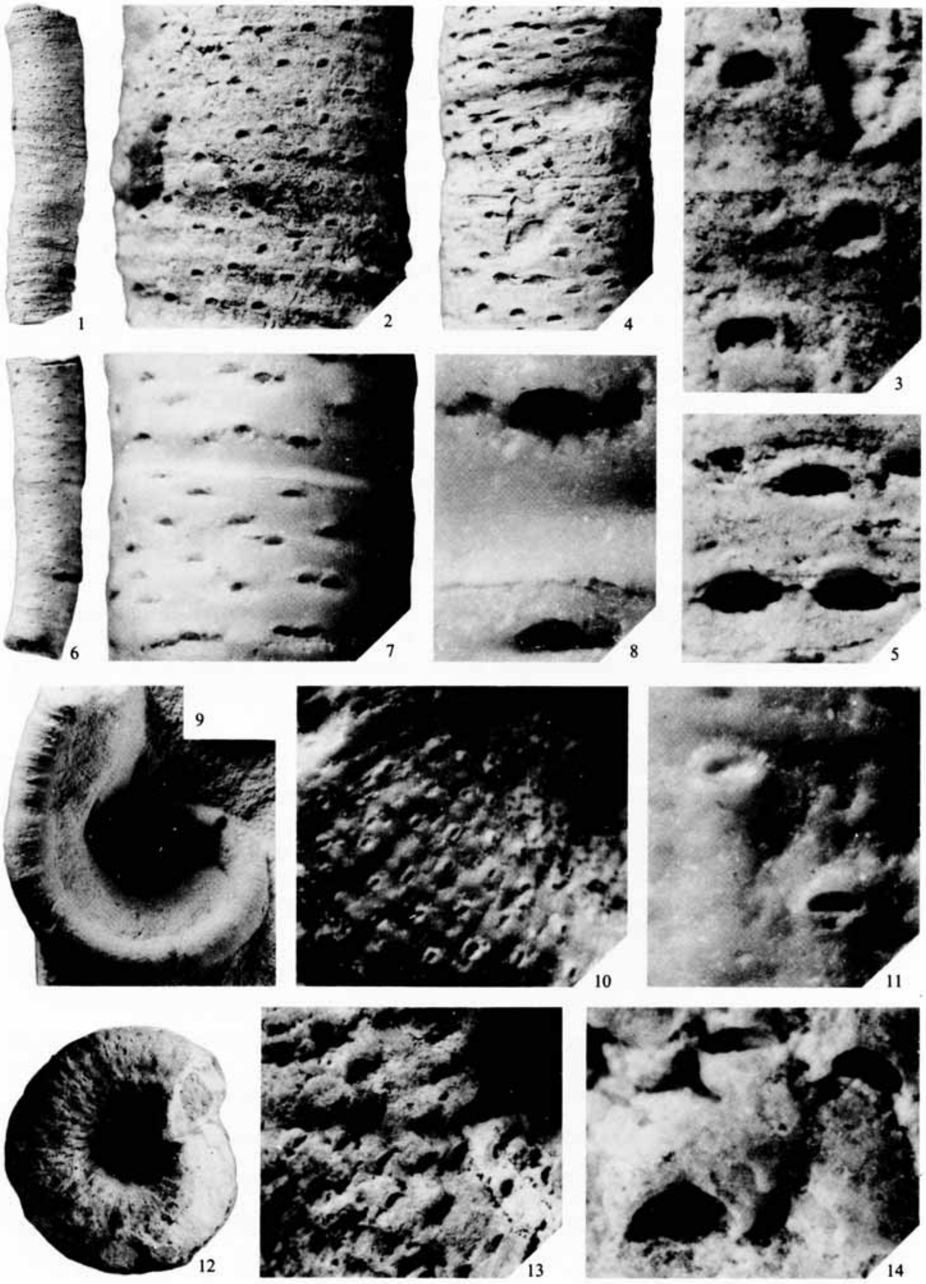
Figs. 1–5. *Parsimonia* sp. *H. orbignyi* Subzone, Gault Clay, Albian; Ford Place Clay pit, Wrotham, Kent. Figs. 1–3, A10889a; 1, × 2; 2, × 8; 3, × 35. Figs. 4–5, A10886; 4, × 8; 5, × 35.

Figs. 6–8. *Parsimonia antiquata* (Sowerby). A7625, Red Chalk, Albian; Hunstanton, Norfolk. 6, × 2; 7, × 8; 8, × 35.

Figs. 9–11. *Rotularia* sp. A. A10429, Grey Chalk, Cenomanian; Dover, Kent. 9, × 1·5; 10, × 8; 11, × 35.

Figs. 12–14. *Rotularia phillipsi* (Roemer). A5039, Speeton Clay, Neocomian; Speeton, Yorkshire. 12, × 2; 13, × 8; 14, × 35.

PLATE 39



SCRUTTON, *Protulophila gestroi*

compressed in the plane of the growth-lines of the serpulid tube (Pl. 41, fig. 7). Few measurements are available of chamber compression but it appears to be greater in *Parsimonia* sp., in which the chambers are shallowly buried (0·05 mm wide), than in *S. sulcata* (0·12 mm wide), in which the chambers are more deeply buried.

The stolonal network, consisting of filaments 0·04–0·05 mm diameter, has a diamond to hexagonal pattern when it is most regularly developed and the chambers arise at or close to the base point of each polygon in the network (text-fig. 1*b*). Network size measured transversely and longitudinally to the serpulid tube has minimum dimensions of 0·58 × 0·83 mm and several specimens have average dimensions of about 1·10 × 1·65 mm. The network pattern is strikingly clear and regularly developed in a specimen of *Parsimonia* sp. (Pl. 42, figs. 1, 2; text-fig. 2). In most cases, however, the network is much more irregular in pattern and density (Pl. 42, figs. 5–10) and some polygons may lack chambers (Pl. 42, figs. 3, 4). Examples can also be seen where the network re-establishes itself around the full circumference of a tube after partial disruption (Pl. 42, fig. 8; text-fig. 2).

Most specimens on which the polyp chambers and stolonal network can be seen are tubes of Cretaceous or Tertiary age. Jurassic serpulid tubes on which at least the general outline of stolons and chambers can be seen, appear to be rare (Pl. 41, fig. 8). The available evidence, however, suggests that there is no significant difference, except in depth of burial, between the development of stolons and chambers in Jurassic and post-Jurassic material.

The chambers and stolonal network are frequently infilled by pyrite and sometimes by limonite presumably after pyrite. No surface features are evident on the walls of the stolons and chambers which might reflect morphological details of the symbiont although slight crenulations can occur parallel to the growth-lines of the serpulid tube.

Tube structure of infested serpulids

Serpulid tubes normally possess clearly defined internal growth-lines reflecting the deposition of successive layers of calcium carbonate on the growing margin of the tube. In longitudinal section through the tube wall the growth-lines are asymmetrically arched with the crest of the curve usually strongly displaced towards the exterior surface; in tangential section the lines are parallel and straight, at right angles to the direction of tube growth.

EXPLANATION OF PLATE 40

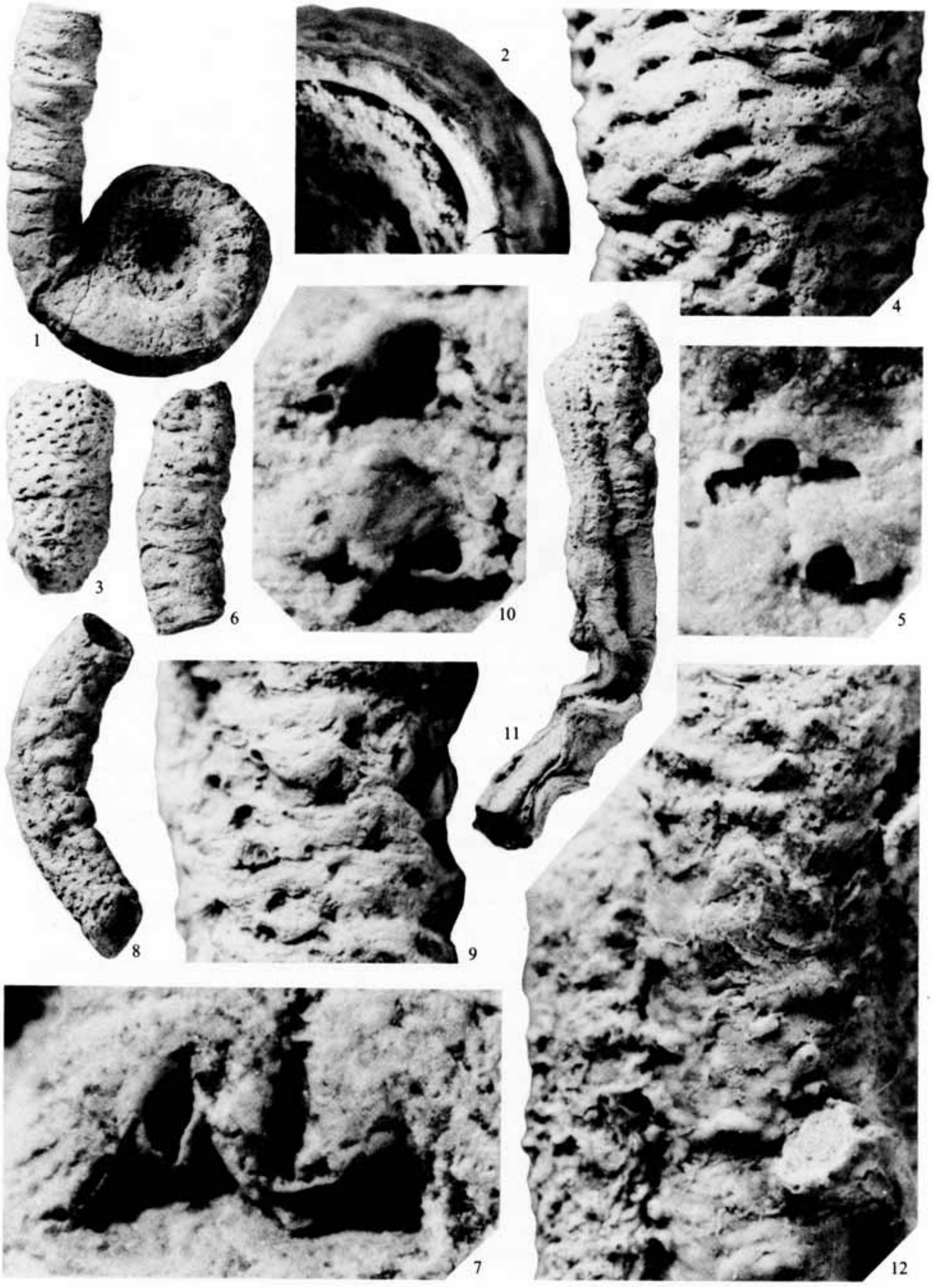
Variation in the distribution and appearance of apertures of *Protulophila gestroi* Rovereto on species of serpulid tubes from the Jurassic.

Figs. 1–2. *Serpula lituiformis* Munster. A630, Oxfordian; Vaches Noires, Normandy, France. 1, × 1·5; 2, part of tube rim, × 8.

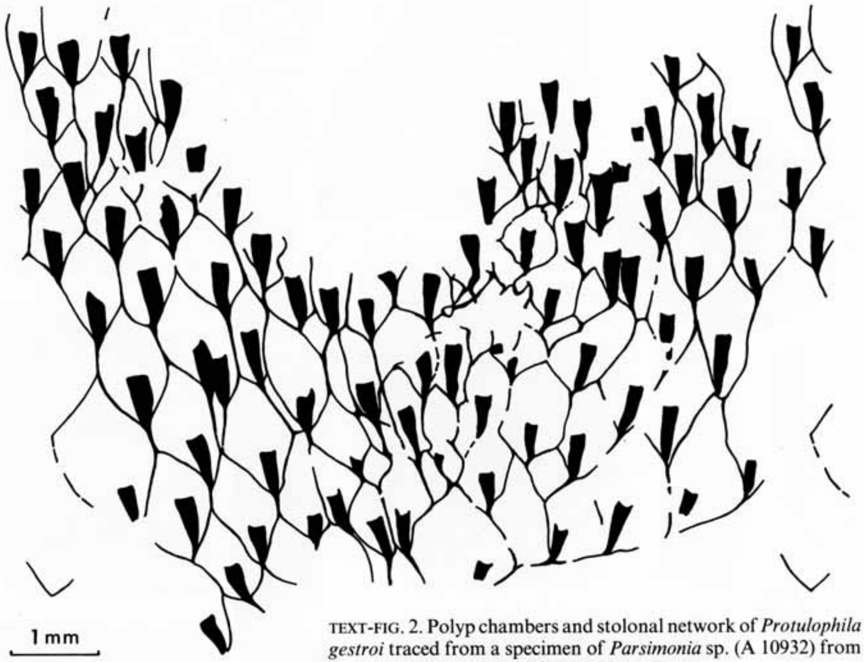
Figs. 3–5. *Serpula sulcata* Sowerby. A8367, Ampthill Clay, Corallian; Ampthill, Bedfordshire. 3, × 2·5; 4, × 8; 5, × 35.

Figs. 6–10. *Serpula sulcata* Sowerby. *Rhactorhynchia inconstans* Bed, Kimmeridge Clay; Osmington Bay, Dorset. Figs. 6–7, A10851; 6, × 2; 7, × 35. Figs. 8–10, A10850; 8, × 2; 9, × 8; 10, × 35.

Figs. 11–12. *Serpula tricarinata* Sowerby. A6641, Cornbrash; ?Callovian; Steeple Ashton, near Trowbridge, Wiltshire. 11, × 2; 12, × 8.



SCRUTTON, *Protulophila gestroi*



TEXT-FIG. 2. Polyp chambers and stolonal network of *Protulophila gestroi* traced from a specimen of *Parsimonia* sp. (A 10932) from the Gault Clay, Albian of Ford Place, Kent.

Thin sections and serial sections show that the growth-lines of infested serpulid tubes are deflected around both stolons and polyp chambers (Pl. 41, figs. 1–7). This is most clearly seen in serial sections of a tube of the strongly ornamented species *S. sulcata* (Pl. 41, figs. 1–4). In this specimen, tangential sections of the massive hood developed over an aperture show very clear growth-lines parallel to the margin of the

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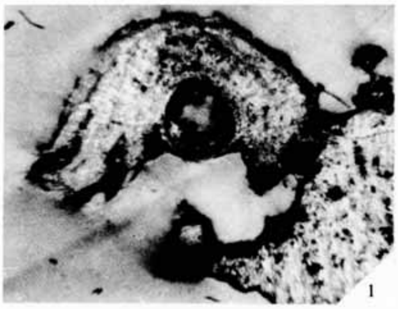
EXPLANATION OF PLATE 41

Figs. 1–4. *Serpula sulcata* Sowerby. A10853, *Rhactorhynchia inconstans* Bed, Kimmeridge Clay, Kimmeridgian; Osmington Bay, Dorset. 1–3, serial sections tangential to the tube surface through an aperture of *Protulophila gestroi*. Spacing of polished surfaces from exterior (fig. 1) of tube inwards, fig. 2 at 0·19 mm, fig. 3 at 0·33 mm, ×45. 4, longitudinal section through polyp chamber. The strong black line passing diagonally upwards from the tube exterior to the base of the polyp chamber is a crack in the tube and is not part of the stolonal network, ×45.

Figs. 5–7. *Parsimonia* sp. *H. orbignyi* Subzone, Gault Clay, Albian; Ford Place Clay pit, Wrotham, Kent. Figs. 5–6, A10920; 5, tangential polished section through apertures of *Protulophila gestroi*, ×45. 6, longitudinal section through polyp chamber, ×45. 7, A10915, cross-section through peripheral part of serpulid tube with stolons and polyp chambers. The pyrite filled tube sectioned at upper right centre and within the peripheral ring of stolons and chambers is a boring and is not part of *Protulophila*, ×70.

Fig. 8. *Immergentia*? *lissajousi* Walter on *Serpula* sp. cf. *S. lituiformis* Munster. Colln. Dep. Sci. Terre, Fac. Sci. Lyon 28970 (holotype), Oxfordian; Hurigny, Saone-et-Loire, France, ×8.

Fig. 9. *Sclerostyla perforata* Wrigley. A6983 (holotype), London Clay, Eocene; Wokingham, Berkshire, ×8.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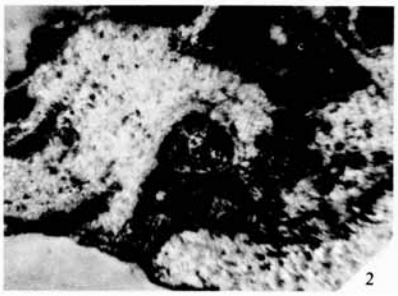
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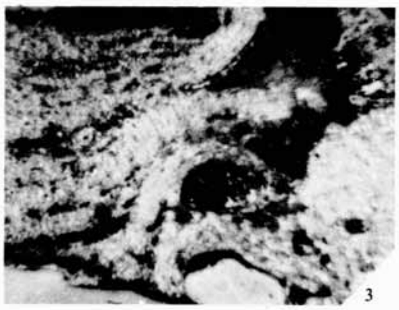
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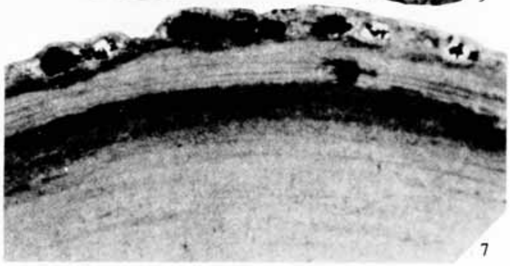
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SCRUTTON, *Protulophila gestroi*

polyp chamber, confirming the impression given by the external appearance of the hoods in this species (Pl. 40, figs. 3–10). In longitudinal section (Pl. 41, fig. 4) the growth-lines are particularly strongly deflected in the hood and can be clearly seen to overlap against the walls of the polyp chamber. The same relationship can be seen, though less clearly, in the serial sections of a tube of *Parsimonia* sp. in which the stolons and polyp chambers are less deeply buried (Pl. 41, figs. 5–6). The cross-section of another tube of this species shows that the growth-lines in the tube interior to the network are somewhat less distorted around the stolons and chambers than those in the external part of the tube (Pl. 41, fig. 7).

In serpulids such as *S. sulcata*, in which a discrete pipe may be secreted at the aperture, the substance and structure of the pipe appear to be continuous with that of the associated hood (Pl. 41, figs. 1, 2).

DISCUSSION

The evidence strongly suggests that the polyp chambers and stolonal network were formed by the incorporation of the symbiont into the host tube during calcification and were not primarily the result of boring activity. Externally, the manner in which the outer tube wall is moulded over shallowly buried chambers and stolons clearly indicates that calcification took place around the body of the symbiont (see particularly Pl. 39, fig. 10; Pl. 41, fig. 8; Pl. 42, upper part of fig. 8). The morphology of the apertures and hoods as well as the deflection of growth-lines in the serpulid tube and the manner in which they overlap against the walls of the polyp chamber all support this conclusion. The symbiont occupied a position in life encircling the serpulid at or very close to the rim of its tube (see text-fig. 5). During calcification, polyps and stolons were gradually incorporated into the host tube and the stolonal system extended and new polyps differentiated to maintain the colonization of the advancing tube rim. Presumably calcification did not take place over the advancing ends of the stolons, perhaps because they were able to inhibit precipitation at the point where their tips appeared at the rim of the tube. Well-preserved tube rims are rare, however, and even on the best of these (Pl. 40, fig. 2) the surface is sufficiently irregular to make the identification of the tiny stolonal orifices uncertain.

EXPLANATION OF PLATE 42

Figs. 1–10. Variation in the polyp chambers and stolonal network of *Protulophila gestroi* on some exfoliated Cretaceous and Tertiary serpulid tubes.

Figs. 1–2. *Parsimonia* sp. A10932, *H. orbignyi* Subzone, Gault Clay, Albian; Ford Place Clay pit, Wrotham, Kent. Both ×8.

Figs. 3–4. *Protula firma* Seguenza. SV.-I-LF/805–806 Pal. Colln., Univ. Genoa (lectotype of *Protulophila gestroi*), Pliocene; Albenga, Liguria, Italy. 3, ×2; 4, ×8.

Figs. 5–6. *Protula protensa* (Lamarck). A229, ?Miocene; Latakia, Syria. 5, ×2; 6, ×8.

Figs. 7–10. *Parsimonia* sp. *H. orbignyi* Subzone, Gault Clay, Albian; Ford Place Clay pit, Wrotham, Kent. Figs. 7–8, A10923; 7, ×2; 8, ×8. Figs. 9–10, A10892; 9, ×2·5; 10, ×8.

Figs. 11–12. Two infested tubes of *Serpula conformis* Goldfuss growing commensally on the pedicle valve of *Cererithyris intermedia*. A10450, Jurassic; Wiltshire. 11, ×1·5; 12, close up of apertures of *Protulophila gestroi* on one of the serpulids, ×8.

PLATE 42


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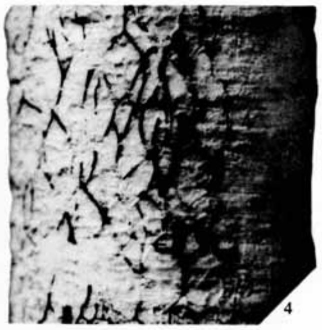
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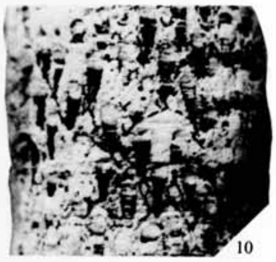
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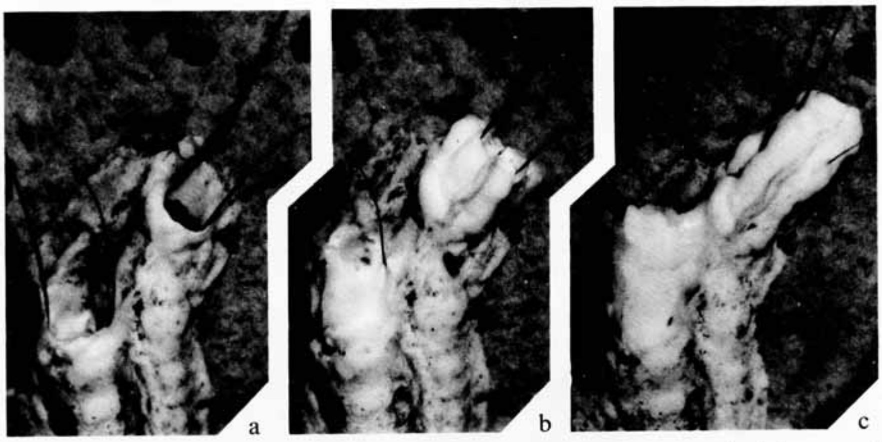
SCRUTTON, *Protulophila gestroi*

An experiment was set up to determine if the peristomial collar of a living serpulid, which acts as a template for the addition of calcium carbonate layers to the tube rim, is sufficiently flexible to envelop polypoid individuals orientated vertically on the tube rim in the manner envisaged here. Thin hairs to represent the polypoid form (eyelashes were found to be of appropriate size) were cemented to the rims of tubes of the adnate serpulid *Pomatoceros triqueter* collected from mean low-tide level in Cullercoats Bay, south-east Northumberland (text-fig. 3). Two tubes on the same small boulder were kept in the laboratory in standing sea water, changed twice weekly, at a temperature of 15–20° C. The new tube growth, after a moderately strong discontinuity, had a sharper, more pronounced keel and remained much whiter than the tube formed prior to collection. Observations made when the serpulids were expanded showed that their peristomial collars were able to fold round the base of each hair. The hairs were thus incorporated into the newly formed tubes, in one case with the formation of a small keel over the buried part of the hair but in the three other cases with perfectly smooth exterior tube surfaces over the hairs. The growing edges of the tubes formed small projections along the hairs and where they diverged outwards from the plane of the tube wall small calcareous cones formed around the bases of the projecting hairs (text-fig. 3*c*, see particularly the right-hand hair).

During the experiment the tubes were extended by 1·8 to 2·0 mm in the first 12 days, and by 1·7 mm in one case and 2·9 mm in the other in the following 76 days during which the experimental conditions were much less rigorously maintained. Neither of these sets of figures may reflect very accurately the growth rates under natural



TEXT-FIG. 3. Tubes of *Pomatoceros triqueter* mounted with hairs (*a*) which are progressively incorporated into the tubes during subsequent growth (*b*, *c*). *a*, hairs on the left-hand tube were fixed using Bostik quick-set epoxy adhesive and those on the right-hand tube with paraffin wax. *b*, appearance after 12 days during which tubes were constantly covered with sea water, changed twice weekly. *c*, appearance after a further 76 days during which the tubes were uncovered for part of the time and the sea water less regularly changed. All ×6.

conditions which vary significantly in several respects, particularly temperature, water movement, and tidal exposure, from the laboratory conditions.

No attempt was made to modify the orientation of the hairs during the experiment. In the fossil material described here, however, it appears that during the later stages of investment of an individual polyp, it changed its orientation relatively suddenly from a vertical to a more or less lateral aspect. This presumably represents a response to the calcifying activity of the serpulid, triggered by the stimulation of the tentacular crown of the polyp by the serpulid's peristomial collar, through which the polyp avoided complete incorporation into the host tube. Thus it seems likely that the chamber length bears a direct relationship to the length of the polyp. The formation of apertures suggests that the polyp was active until at least this stage of tube growth and the hood represents a callus formed by the serpulid in response to the presence of the symbiont.

Variation in aperture and hood morphology seems to reflect differences in the calcifying activity of the various species of serpulid hosts. This would tend to mask any changes in the character of these structures which might reflect slight morphological differences in the symbiont itself and in fact no such changes have been detected within the material studied.

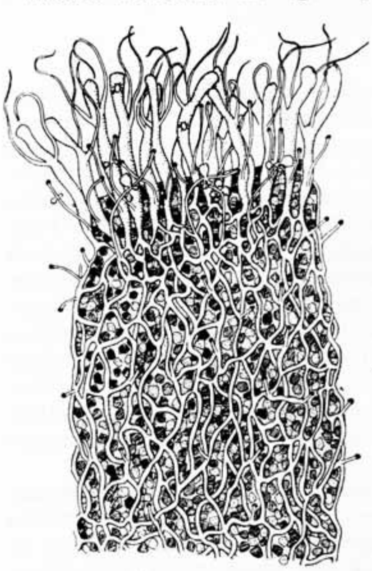
Affinities of the symbiont

Having established the morphology and the mode of origin of the polyp chambers and stolonal system, the identity of the symbiont can be discussed. Previous workers have considered the symbiont to be a ctenostomatous bryozoan, either adherent (Rovereto 1901) or boring (Walter 1965). The stolonal network described here, however, has no really close comparative among the stolon systems developed by living or fossil stoloniferous ctenostomes (see, for example, Prenant and Bobin 1956, pp. 176–335; Brien 1960, pp. 1177–1189; and Bassler 1953, pp. 32–37) and the only similar relationship with a tube worm is that shown by *Hypophorella*. In this case, *Hypophorella* initially ramifies over the inside of the tube of the polychaete *Chaetopterus*. As the worm continues to line its tube, the bryozoan colony becomes embedded and the zooids regain access to the tube lumen by rasping through the lining (Ryland 1970, p. 80). In the case of the present symbiosis, however, the apertures face outwards from the tube and are clearly not the result of burrowing through from within. *Hypophorella* itself does not closely resemble the symbiont described here (see Prenant and Bobin 1956, p. 273).

A closer comparison can be drawn between the present symbiosis and that between the hydroid stage of *Proboscidactyla* (formerly *Lar*) and various sabellid polychaetes (text-fig. 4). This symbiosis is well known and aspects of it have been described by several workers (Uchida and Okuda 1941; Hand and Hendrickson 1950; Hand 1954; Hirai 1960; and Campbell 1968*a* and *b*). Species of *Proboscidactyla* have a reticulated stolonal hydrorhiza which is adherent on the outside of the tubes of particular sabellid species. Gastrozooids are present in a ring around the rim of the tube whilst gonozooids occur in a whorl behind them and sparsely scattered over the immediately subjacent area.

Although the life style of *Proboscidactyla* can be usefully compared with that of the fossil symbiont, colony development in this hydroid appears to be unusual and is inconsistent with the pattern preserved in the fossil material. Campbell (1968*b*) has described how in *Proboscidactyla flavicirrata* the gastrozooids themselves migrate up the growing sabellid tube to maintain their position at the tube rim; the stolon system is developed behind them. This pattern of development is only known so far in *Proboscidactyla* and other hydroids extend the colony by stolon growth followed by the differentiation of new hydranths in peripheral areas. For example, the growth of *Tubularia* in culture reported by Mackie (1966) matches the pattern of growth preserved in the fossil material very closely. He described how new hydranths differentiate at stolon tips with the formation usually of two new diverging stolons at the base of the hydranth (Mackie 1966, fig. 2). This mode of growth on a suitable surface, with anastomosis of the stolons, would produce a hexagonal stolon network as pointed out by Braverman (Mackie 1966 discussion, p. 411) and although Mackie did not record anastomosis in his experiment both Thiel and Rees (Mackie 1966 discussion, p. 411) considered it a common phenomenon in hydroid cultures. It is also illustrated in natural material of *Tubularia* and other hydroids (for example *Proboscidactyla*, see text-fig. 4).

Mackie considered the regular pattern of colonial growth obtained in his glass-slide culture to be rare in nature because of the ease with which growing hydroid stolons are deflected by surface irregularities. The 'substrate' offered by the lip of a growing calcareous serpulid tube, however, with stolon growth keeping pace with tube elongation, is probably sufficiently uniform to explain the relative regularity of the stolonal network in the fossil material.



TEXT-FIG. 4. The hydroid *Proboscidactyla flavicirrata* Brandt growing on the sabellid polychaete *Potamilla myriops* (after a text-figure by Uchida and Okuda (1941) based on living material from Akkeshi Bay, Hokkaido, Japan), approximately × 15.

Although no direct comparison can be drawn between a particular living hydroid and the fossil symbiont there seem to be sufficient points of general similarity to favour its identification as a hydrozoan colony. The polyp chambers are interpreted as formed around the proximal (subtentacular) parts of hydranths rising directly from the stolonal network and the dimensions of the stolons and polyp chambers preserved in the serpulid tubes are of the same order as those of comparable structures in living hydroids. There are no structures in the fossil material which can be specifically identified as occupied in life by reproductive individuals. Gonophores may have been carried on the hydranths, however, or blastostyles developed from hydranths to occupy already formed polyp chambers. In either case the appearance of the polyp chamber would be unmodified.

Character and history of the association

The hydroid-serpulid symbiosis seems to have enjoyed considerable success to judge by its geological history. The fossil material spans the period Middle Jurassic (Bajocian) to Pliocene, approximately 170 m.y., with several different genera and species of serpulids involved, including straight and coiled, adherent, and free living tubes. Only limited data are available on the status of the symbiosis at any particular time and place. For example, from the *Rhactorhynchia inconstans* Bed in the Kimmeridge Clay of Osmington Bay, Dorset, seventeen out of thirty-six tubes of *Serpula sulcata* show signs of the infestation and on some of these (for example, the specimen figured on Pl. 40, fig. 6) apertures are sparse and irregularly distributed. Two other common serpulids from the same bed (*S. variabilis* and *S. tricarinata*) show no signs of the symbiosis at all, suggesting that the hydroid was host specific in that assemblage. A much higher percentage infestation was found in a large sample of the tubes of *Parsimonia* sp. from the *H. orbignyi* Subzone of the Gault Clay (Lower Cretaceous) of Ford Place, Kent, in which 174 out of 183 specimens were infested. Several hundred additional tubes from the same horizon were judged to be too worn to retain any trace of the symbiosis.

In the early stages of the fossil association it is likely that the calcareous tube of the serpulid was little more than a favourable substrate for growth. Hydranths closer to the worm's crown of brachial filaments, however, would have enjoyed a feeding advantage by poaching from the worm's feeding currents and this may have encouraged growth of the colony towards this source of nutrients. Once hydranths had established themselves on the growing margin of the serpulid tube, they would tend to become incorporated into the tube during calcification, giving rise to the system of stolons and polyp chambers described here.

Once this pattern of growth was established, all new hydranths would have differentiated at the growing margin of the serpulid tube. There is little direct evidence to suggest how dependent the hydranth may have become on its site at the serpulid tube rim, or indeed whether the hydrozoan colony was eventually unable to develop other than in association with a serpulid host. The living *Proboscidactyla*-sabellid symbiosis is probably sufficiently similar, however, to give an indication of the likely character of the relationship. The hydrozoan colonies of *Proboscidactyla* are known only on the tubes of sabellid worms (Campbell 1968*a*). Hand and Hendrickson (1950, p. 83) have described in some detail from their observations of living material how the gastrozooids use their tentacles to capture food particles from the sabellid's feeding currents and to take particles from the brachial groove, or the lips and palps of the worm. Furthermore, Hirai (1960) has shown experimentally that the removal of the sabellid from its tube causes the degeneration of the gastrozooids and gonozooids even though an adequate diet is maintained. Thus the dependence of *Proboscidactyla* on its sabellid host seems to be complete. If a similar degree of dependence evolved in the fossil symbiosis, there is a possibility that active gastrozooids may have been confined to the upper parts of the serpulid tube, close to the crown of the worm, in the manner shown in text-fig. 5.

The existence of a commensal relationship in the fossil material seems clear, but the advantages may not have been all one way. Batteries of nematocysts on the

TEXT-FIG. 5. Reconstruction of the possible appearance of *Parsimonia* sp. in the Lower Cretaceous Gault Sea. *a*, general appearance of serpulids. *b*, head of a tube with serpulid expanded showing relationship with hydroid gastrozooids. The peristomial collar of the serpulid has been omitted and the brachial filaments on the near side of the worm are not shown in full, approximately ×8.

hydranths of the hydrozoan colony may well have conferred protection on the serpulid host although there is little evidence in the fossil record to suggest that such a mutualistic relationship was particularly advantageous. The 95% infestation of *Parsimonia* sp. may or may not prove to be significant; otherwise infested and non-infested serpulids, both of the same and different species, could apparently exist equally successfully in the same environment. The possibility that the *Proboscidactyla*-sabellid symbiosis might be mutualistic does not seem to have been investigated.

Two examples are known where infested serpulids themselves enjoyed a commensal relationship. In both cases the serpulids' hosts were specimens of the Jurassic terebratulid *Cererithyris intermedia*. In the better example two specimens of *Serpula conformis* originate on either side of the umbo of the pedicle valve. They both grow anteriorly close to the commissure, following the left and right flanks of the valve respectively until they meet at the median sulcus (Pl. 42, figs. 11, 12). On the other brachiopod, only one serpulid belonging to the same species is present, following the commissure to the median sulcus on the left lateral side of the pedicle valve. From the orientation of the serpulid tubes on the brachiopods there can be no doubt that this was a living rather than a post-mortem relationship, with the serpulids tapping at first the inhalant currents and later the exhalant current of the brachiopods and the hydroids in turn poaching from the serpulids.

The question naturally arises as to whether several different species of hydroids were involved in the fossil symbiosis as 170 m.y. seems a long time for a single species to survive associated with different serpulids at various times and places. At least five species of *Proboscidactyla* are known as symbionts with sabellid worms at the present day. These living hydroids are clearly selective in their choice of hosts but species that are host specific in one area may have two different host species in another (see, for example, Uchida and Okuda 1941, p. 431 and Hand 1954, p. 56). Thus, the existence of a range of host serpulid species in the past does not in itself prove the presence of more than one hydroid species. In fact the basic morphology of the symbiont is so similar over its known range that even if several hydroids were involved the evidence would suggest that they were congeneric, or at least members of closely related genera. The effects of interspecific differences in serpulid tube calcification on the appearance of hoods and apertures, however, would tend to mask any slight modifications of these structures induced by different but related hydroid symbionts. At the present time, therefore, there appears to be no way in which the fossil material can be reasonably subdivided and all the known examples of this symbiont are placed in a single species here.

It is tempting to speculate that the fossil symbiont could be ancestral to *Proboscidactyla*. Subtentacular hydranth length, shape, and stolon thickness in species of the latter match the dimensions of the polyp chambers, and stolonal network very closely. The life-styles of the two organisms are considered very similar and *Proboscidactyla* appears to be unique among living hydroids in its highly developed symbiosis with sabellid polychaetes. The major difference between the two is in the manner of colony development in *Proboscidactyla*. This appears to be specifically adapted to the continuously elongating tubiform substrate provided by its hosts and these highly specialized hydroids presumably evolved from an ancestor with a more basic pattern of colonial growth. The fossil symbiont would seem to be a reasonable candidate. Whether or not the fossil symbiont infested sabellids as well as serpulids in the past will almost certainly never be established from the fossil record but it is possible that the symbiosis with serpulids is still continuing at the present day, although as yet unrecorded.

SYSTEMATIC PALAEONTOLOGY

Class HYDROZOA Owen, 1843
Order HYDROIDA Johnston, 1836
Genus PROTULOPHILA Rovereto, 1901

1901 *Protulophila* Rovereto, p. 223.

Diagnosis. As for species.

Protulophila gestroi Rovereto, 1901

1901 *Protulophila gestroi* Rovereto, p. 223, pl. 28, fig. 7*a–c*.
1965 *Immergentia*? *lissajousi* Walter, p. 286, figs. *a–c*.

Diagnosis. A system of stolons and polyp chambers preserved by overgrowth of a hydrozoan colony in the outer layers of the calcareous tubes of certain serpulid worms. The stolonal network, consisting of tubes 0·04–0·05 mm diameter, is diamond- to hexagonal-shaped when regularly developed but is often less well ordered. Polyp chambers, compressed, conical, 0·24–0·40 mm broad by 0·76–1·20 mm long, arise at or close to the base points of polygons in the stolonal network. At their densest they are spaced 0·58 mm apart laterally and 0·83 mm apart vertically. The polyp chambers have access to the exterior of the serpulid tube through semicircular to sub-circular apertures, 0·10–0·20 mm high and 0·18–0·40 mm broad. Hoods of variable prominence are developed above the apertures which may be produced in some cases as short pipes.

Lectotype (here chosen). SV.-I-LF/805–806, Palaeontological Collections, University of Genoa. Pliocene; Albenga, Liguria, Italy.

Distribution. Middle Jurassic (Bajocian) to Pliocene of Europe; ?Miocene of Syria.

Discussion. Unfortunately Rovereto's figured material of *Protulophila gestroi* was lost in the floods of 7–9 October 1970 which severely damaged the palaeontological collections of the Department of Geology, University of Genoa (Mastrorilli 1970). By good chance, I had three of Rovereto's unfigured syntypes on loan from Genoa at that time and it is one of these which is here designated lectotype for the species.

There is no doubt that Walter's material should be placed in *P. gestroi.* Although Walter (1965, p. 286) described his examples as lacking stolons, they are present but partly obscured by the density of the polyp chambers and their very shallow burial in the tube wall which has diffused the outline of the stolon and chamber system (Pl. 41, fig. 8).

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APPENDIX

This list of the serpulid species acting as hosts to *Protulophila gestroi* is arranged in ascending stratigraphic sequence. Only material deposited with museums and examined by the author is included here. Register numbers refer to specimens in the Department of Palaeontology, British Museum (Natural History) unless otherwise stated.

JURASSIC

Serpula sp. Bajocian. A541 Inferior Oolite; locality unknown.

Serpula intestinalis Phillips. Bathonian. A8769 White Limestone, Honeycombe Leaze, near Fairford, Gloucestershire; A1380–1381, Forest Marble, Fairford, Gloucestershire.

Serpula conformis Goldfuss on *Cererithyris intermedia*. A10407 Bathonian, Lower Cornbrash, Sutton, Wiltshire; A10450 Jurassic, Wiltshire.

Serpula tricarinata Sowerby. A6641 ?Callovian, Cornbrash, Steeple Ashton, Wiltshire.

Serpula lituiformis Munster. A618, A630, A693, A696 Oxfordian, Vaches Noires, Normandy, France.

Serpula sp. cf. *S. lituiformis* Munster (material described by Walter 1965). Colln. Dep. Sci. Terre, Fac. Sci. Lyon 28970 (holotype of *Immergentia*? *lissajousi* Walter), 28971–28975 Oxfordian, localities in Ain, Jura, Saone-et-Loire, and Calvados, France.

Serpula sulcata Sowerby. Oxford Clay. A520 St. Ives, Huntingdonshire; A6738, A6741 Ludgershall, Wiltshire; A6147 Jordan Hill, near Weymouth, Dorset.

Corallian. A6644 Coral Rag, Shotover Hill, near Oxford; A6743 Oakley Beds, Ashenden Junction, Buckinghamshire; A8352 Headington, Oxfordshire; A8367–8369 Ampthill Clay, Ampthill, Bedfordshire; A5107 Nattheim, Germany.

Kimmeridgian. A8529 Weymouth, Dorset; A10850–10866 *Rhactorhynchia inconstans* Bed, Osmington Bay, Dorset.

CRETACEOUS

Rotularia phillipsi (Roemer). Neocomian. A402, A2528, A5039, A5042, A5448–5449, A5051, A10410–10419, A10425 Speeton Clay, Speeton, Yorkshire; A196 Guerum, near Brunswick, Germany.

?*Rotularia* sp. Albian. A100, A446, A934, A1481–1482, A10443, A10445–10449 Gault Clay, Folkestone, Kent.

Parsimonia sp. Albian. A10886–10984 Gault Clay, Ford Place, Kent.

Parsimonia antiquata (Sowerby). Albian. A604, A5194, A7625, A10084 Red Chalk, Hunstanton, Norfolk; A2525 Red Chalk, Speeton, Yorkshire.

Rotularia umbonata (Sowerby). Albian. A271, A1390, A10349–10351, A10386–10387 Red Chalk, Hunstanton, Norfolk; A10394 Upper Greensand, Devizes, Wiltshire.

Cenomanian. A512 Cambridge Greensand, Cambridge.

Glomerula gordialis (Schlotheim). Albian. A10398 Upper Greensand, Blackdown, Devon.

Rotularia sp. A. Cenomanian. A31, A116, A119, A7486–7487, A10429, A10438 Grey Chalk, Dover; A2605 *S. varians* Zone, Burham, Kent; A8387 North Buxbury pit, Wiltshire.

Coniacian. A10391 East Cliffs, Dover.

Upper Cretaceous. A10399 Chalk, Dorking, Surrey.

Proliserpula ampullacea (Sowerby). A10393 Chalk, near Weymouth, Dorset.

Serpula macropus (Sowerby). Senonian. A7425 *M. coranguinum* Zone, Northfleet, Kent.

Serpula sp. Cenomanian. A1673 Chalk Marl, Cambridge.

Coniacian. A10390 East Cliffs, Dover.

EOCENE

Sclerostyla perforata Wrigley. London Clay. A6983 (holotype), A9512–9513 Wokingham, Berkshire; A9141–9143, A9146 London Clay, Amen Corner, Berkshire.

MIOCENE

Protula protensa (Lamarck). A358, A10622 Tortona, Italy; 52346, A10657–10658 Piedmont, Italy; A229, A10664–10665 ?Miocene, Latakia, Syria.

PLIOCENE

Protula protensa (Lamarck). Plaisancian. A44, A10641, A10645 Bordighera, NW. Italy.

Protula firma Seguenza. Pliocene. SV.-I-LF/805–806 Pal. Colln., Univ. Genoa (lectotype of *Protulophila gestroi*), Albenga, Liguria, Italy.