



Soft-bottom tube worms: from irregular to programmed shell growth

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Like other secondary soft-bottom dwellers, serpulid and sabellid tube worms used particular strategies in order to cope with their earlier loss of mobility. This is expressed by the transition from irregular to genomically programmed morphologies of their calcareous shells that guarantee a stable horizontal resting position. In contrast to permanent recliners, however, this attitude was probably only the starting position for active resurrection after the muddy tail of storm sediments had settled on top of the displaced animal. □ *Countdown programmes, functional morphology, Sabellidae, secondary soft-bottom dwellers, Serpulidae.*

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In a recent review on secondary soft-bottom dwellers (Seilacher 2005), tube worms have been mentioned only in passing. New material now makes it possible to deal with this theme in more detail. Serpulid and sabellid annelids, like many other groups of marine invertebrates, have given up mobility and the ability to actively burrow when they became sessile filter feeders. Crucial in this transition was a calcareous tube, into which the worm can quickly withdraw and close the aperture with an operculum attached to a specialized tentacle. Being calcitic, this tube has a much higher fossilization potential than any other annelid remains. We deliberately do not include *Ditrupa*, because it had never been a truly sessile organism and, therefore, does not qualify as a secondary soft-bottom dweller. Yet, and despite the rich geological record, fossil worm tubes fail to attract the interest of collectors and biostratigraphers. This is because in most species the tube is firmly cemented to the substrate, the irregularities of which control growth at every stage. The resulting morphological variability makes determination difficult. In contrast, the present study focuses on the much more regular shell shapes of soft-bottom species and on the question, to what extent they are still ecophenotypic or genomically controlled. This is done without considering the taxonomic consequences. Repositories for figured specimens include the Peabody Museum of Natural History (Yale University (YPM), New Haven, CT, USA), Geologisch-Paläontologisches Institut,

Universität Tübingen (GPIT), Tübingen, Germany, and Centro Austral de Investigaciones Científicas (Ushuaia, Argentina).

Morphogenetic background

In contrast to mollusc and brachiopod shells, worm tubes are not secreted by a mantle, but by a soft collar extending from the head. As the animal can move freely in its tube, the construction process resembles the building of adobes, in which the lamellae deposited on the outside of a structureless inner tube slope back. Consequently, there is no continuous protective coating (periostracum) on the outside of the shell and hollow spaces may be left open between successive calcareous increments for lightweight purposes. In typical serpulids, one side of the tube remains cemented throughout life to hard substrates (including shells). If the substrate provides inclined surfaces (for instance, echinoid tests from Cretaceous chalk), the tubes may be slope-oriented with the apertures pointing up, so that orientation of the dead substrate on the sea floor can be reconstructed.

In contrast to the 'serpuliform' species, 'spaghetti-form' tubes (*Filograna* and *Glomerula*) are longer and have a smooth surface. According to their ultrastructure (Jäger 2004; Vinn *et al.* in press) *Glomerula* belongs to the Sabellidae, which are better known by the horny tubes of *Sabella*. Both are smooth

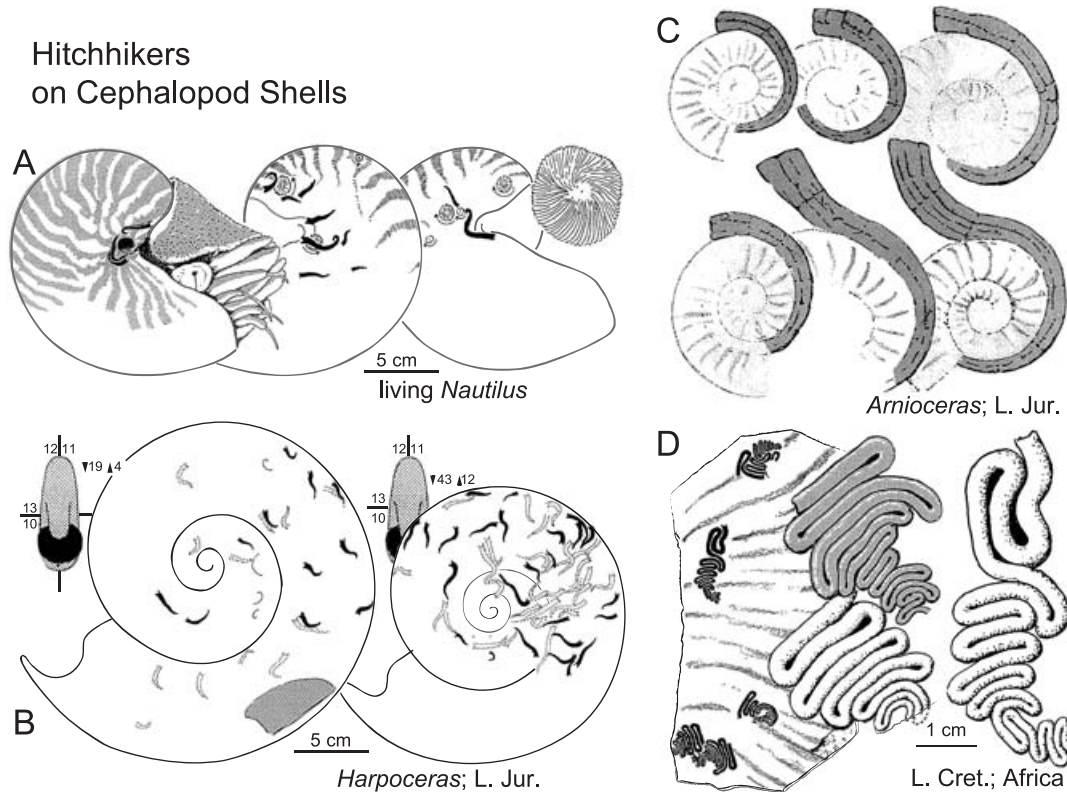


Fig. 1. □A. On modern *Nautilus* shells, serpulids face the forward motion of the host and follow its spiral growth. Associated acorn barnacles probably attached in the necroplanktonic stage, because they turn in the opposite direction. □B. Slope orientation predominates on large ammonites, probably because they moved mainly up and down (from Seilacher 1982). Counts show approximately equal numbers of individuals on either flank of the shell, but a preference for the upper half. □C. A single serpulid (rarely two) is regularly associated with these small ammonites from a Lower Jurassic oil shale. It followed the keel as long as the host's growth continued and turned away after it had stopped. Attitudes are uncertain, because the aragonitic ammonite shells are preserved only as vague phantoms (from Seilacher 1982). □D. Lack of alignment suggests that these meandering sabellids (*Glomerula serpentina*) settled on a dead ammonite shell at the sea bottom (Wiedmann Collection, Universität Tübingen).

because they produce only the inner tube without adding an outer layer. Members of this group also have the ability of asexual reproduction as a means to form colonies and bypass the dangerous state of the juvenile form (Pernet 2001).

Piggybackers

The preference of larvae to settle on live hosts and to maintain preferred orientations is observed in *Serpula olifex* (Fig. 1C) that lived commensally on small ammonites in the lowermost Jurassic of southern Germany, particularly in a Sinemurian bituminous shale. In this facies, the aragonitic ammonite shells became diagenetically reduced to a flattened periost-racal foil, while the calcitic shells of epizoans are preserved. In some cases, the worms settled first on the flanks of the host shell and then grew towards the ventral keel, where they continued upward growth.

Thus, the tubes (sometimes a couple) kept growing spirally ahead of the advancing ammonite shell, which successively immured the rear parts of the worm tube. In a few specimens, however, the worm tube turns sharply away from the ammonite shell in its terminal section. Probably, the host had stopped growth before the worm, which preferred to grow on as a chimney rather than further contouring the ammonite in a head-down attitude. It died when the dead ammonite sank to the toxic ocean bottom. In this case an apparent morphogenetic countdown resulted from the behavioural response to the terminal growth of the host shell.

Serpulids are also found on both flanks of larger cephalopod shells; so it can be inferred that they settled when the host was still alive or at least necroplanktonically afloat. In modern *Nautilus* from a shell shop, epizoans from several shells were mapped on a single outline (Fig. 1A). The serpulids preferentially grew in the direction of the host's aperture,

Hitchhikers on modern Scallop

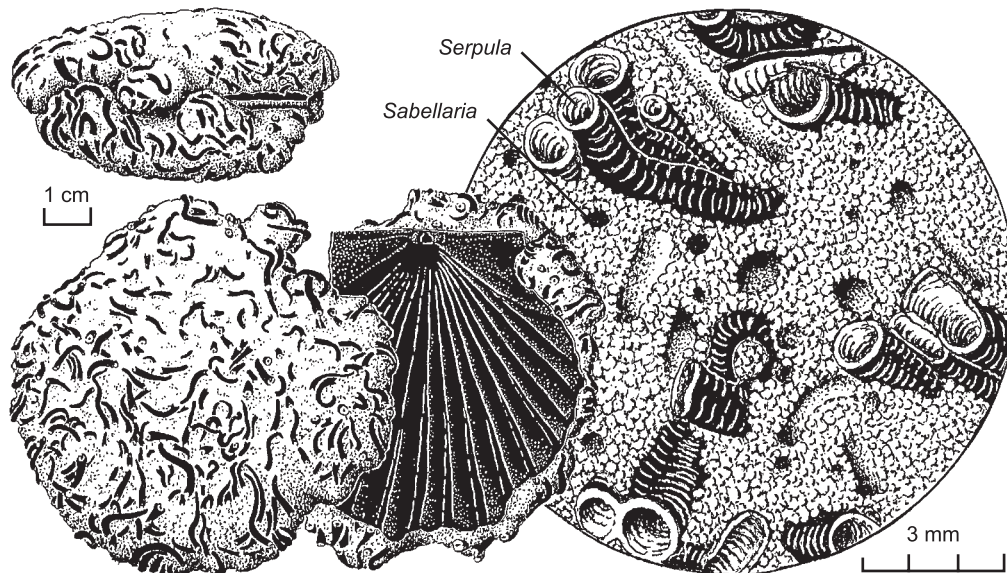


Fig. 2. This heavy overgrowth consists of the calcareous tubes of a serpulid and the agglutinated tubes of a sabellariid species. Nevertheless, they did not kill the pectinid host (Yale Peabody Museum (YPM) No. 37281, Division of Invertebrate Zoology).

in order to profit from its forward swimming. Older worms also turned to adjust for the rotation of the growing substrate. Associated basal plates of acorn barnacles also show a twist, but strangely in the opposite direction. These cirripeds possibly settled only on necroplanktonically drifting shells that rotated opposite to growth rotation as air chambers became gradually waterlogged. In ammonites from the Lower Jurassic Posidonia Shales (Fig. 1B), serpulids settled on both shell flanks while the host was still alive. Nevertheless, there is no uniform growth pattern.

Small spaghettiiform tubes (*Glomerula serpentina*) on a large Cretaceous ammonite (Fig. 1D) also lack uniform orientations. Instead, they developed tight sinusoidal meanders, the amplitudes of which increased with the age of the individual. This behaviour resembles that of 3-D glomerulate soft-bottom dwellers of the same time (Figs 4–6), except that the loops follow the plane of the host shell.

Another case of ‘piggybacking’ is documented in commercially harvested scallops from Cape Cod, Massachusetts (Fig. 2). Despite the heavy encrustation, the host was still able to open its shell, but it probably could not swim any more. Strangely, the calcareous tubes of the serpulids appear to be embedded in a sandy matrix. Only under magnification can one detect the openings of *Sabellaria*, another sedentary worm that produces an agglutinated rather than a calcareous tube. Thus, this is a minute reef, in which *Serpula* grew together with *Sabellaria* as the framebuilder.

Colonial aggregates

Fascicular mudstickers

In some muddy environments (e.g. the Berriasian Serpulite of northern Germany; ten Hove & van den Hurk 1993), tube worms became the dominating benthic element, seemingly without depending on suitable hard substrates. By comparison, corals grow up with sedimentation and tend to become solitary *sediment stickers* (Seilacher 2005), in which the abandoned apical part of the corallum serves as an anchor. Thin-walled serpulids and sabellids used the same strategy in a colonial mode. The spaghettiiform individuals in such a colony remain very slender, have thin walls without longitudinal ribs, and widen so slowly that in fragments one cannot tell apart apical and apertural ends (Fig. 3A). Larger bundles are easier to orient, because they develop ascending branches, like staghorn corals (Fig. 3C–D). Nevertheless, the muddy sediment makes it clear that these colonies lived on soft bottoms. It is also significant that reclining shield-shaped colonies, which are so common in asexually budding recliners (various corals and bryozoans), have never been found in serpulids. Nevertheless, asexual reproduction, as described by Pernet (2001), probably played an important role. As these animals can move freely within their tube, they are able to bud off the posterior end as a new individual. As soon as it has moved to level of the escape hatch produced by the parent, the offspring pops open the loose attached disk by which

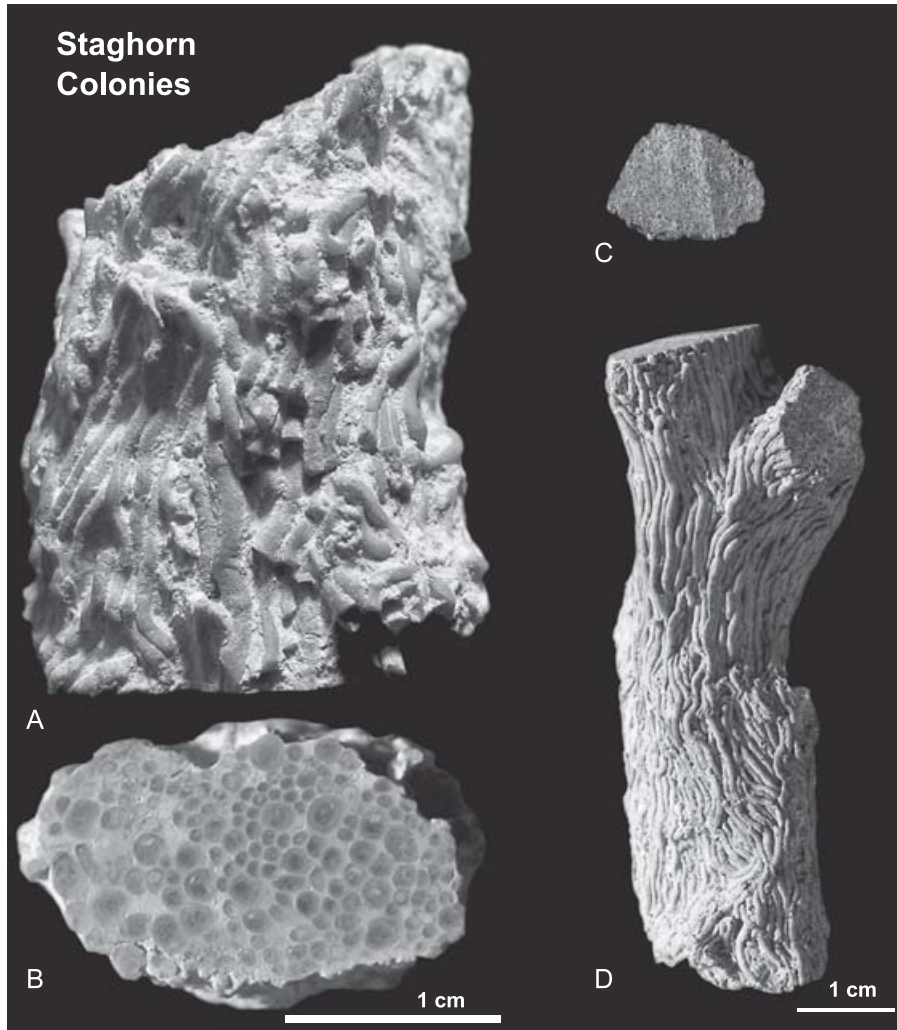


Fig. 3. Because tube diameters remain constant, the orientation of the first bundle (□A–B. *Glomerula plexus* from the Upper Cretaceous Greensand, Melbury Hill, England; YPM 207059) remains uncertain. Its cross-section shows halves of younger individuals around the older ones. Branching in the second specimen (□C–D. Geologisch-Paläontologisches Institut 1911; *Filograna socialis* from the German Middle Jurassic) suggest that these fasciculate colonies grew upright like staghorn corals.

it was originally sealed. It is possible that the majority of the fascicular colonies developed in this mode.

Colonial reeflets

Serpulid and sabellid colonies require that the larvae prefer attachment to tubes of their own kind after a starter substrate has been successfully colonized. In spaghetti-form species, further growth of the thin-walled tubes produces a body ('reeflet') heavy enough to rest stably on a soft bottom. Otherwise each species follows its own programme. Mud-sticking *Filograna* colonies (Fig. 3C–D) did it by parallel upward growth. Ovoid (rather than shield-shaped) reeflets could probably roll during storms. They consist either of spirals with connecting straight sections or of glomerulate meanders (Fig. 4A–C). As tubes hardly become

wider towards the surface in cross-sections, several generations appear to be involved in the formation of such reeflets.

Reeflets of spiral tubes

In the attempt by spaghetti-form sabellids to build colonies stabilized by their own weight, spiral growth was an effective strategy for weight distribution (Fig. 4D–E). The turban-shaped encrustation in Figure 5A–B consists of four stacked spirals (I–IV) on a globular starter substrate (now perished). They increase in size and tube diameters from the lower to the outer layers. All four spirals have continuous attachment scars on the lower side. While spirals would originally start from the center, the arrows show that they could also grow inward. The entire structure may in fact have been produced by a single tube worm.

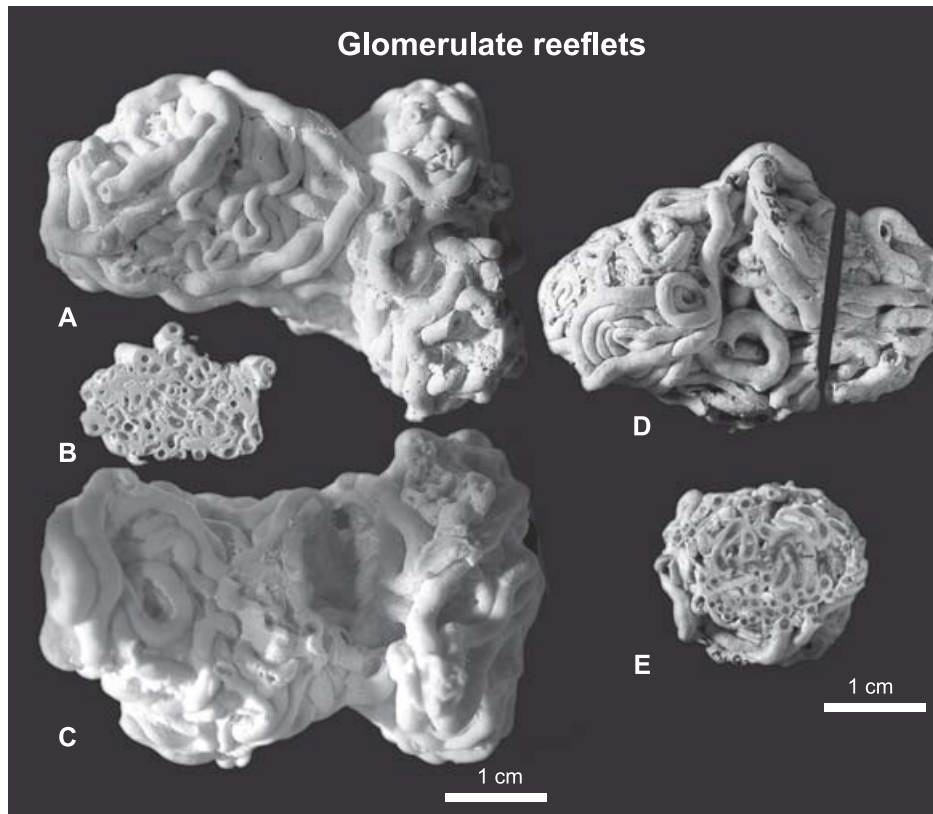


Fig. 4. In the two colonies of *Glomerula plexus*, the first one (A–C) started to grow on a now perished starter substrate (hole at base), but soon became stabilized by its own weight. Only a few generations were probably involved (Upper Chalk, Great Britain; YPM 207084). The second specimen (D–E) has a similar ovoid shape, but used spirals for incrustation (Gault, Folkestone, Great Britain; YPM 206932).

Glomerulate reeflets

A more flexible, but behaviourally more complex mode of encrustation is by *meanders*. Glomerulid reeflets are not as tightly meandering as those in Figure 1D. Their three-dimensionality also makes it difficult to disentangle the Gordian knots without sectioning (Fig. 5A). Yet, the consistent increase of the tube diameters from the base to the top suggests that only a few individuals were involved. Larger reeflets (Fig. 4A–B) were probably made by more than one generation, but still show the cavity left by the perished starter substrate. To what extent spiral versus meandering behaviours should be taxonomically separated depends on their stratigraphic separation or co-occurrence.

Solitary glomerulids

Solitary soft-bottom dwellers show more organized growth programmes. *Glomerula* from Cretaceous chalks occurs in great numbers in sieved samples (Fig. 6A–D). It first produced a Gordian anchor of spirals and meanders and then a straight chimney. As stated in the diagnosis, individual coils are not cemented together

(Howell 1962; see also Savazzi 1999). Yale Peabody Museum specimens also have a tubercular surface texture unknown in any other tube worms. They are preserved as silicified internal casts and the texture can be attributed to the silicification process (Beekite rings). With the calcareous walls reconstructed, the tubes were as densely coiled as in other glomerulid species. In a similar form from the Upper Jurassic (Fig. 6E–J), the wall is preserved, but the growth programme is very different. It starts with a straight tube that provided an axis for the following coils. These two programmes make no sense, unless they were combined with a regular sequence of asexual budding (Pernet 2001), in which the parent either placed the escape hatch at the end of the old chimney or at its base, so that it could be used as a guide for the following coils. In this case, the offspring had to produce its own chimney, but could use the old escape hatch as a preformed fracture point.

Iterative countdown programmes

In molluscs (heteromorph ammonites, muricid gastropods), deviations from the ordinary growth programme that provide more comfortable morphologies are not necessarily restricted to the terminal parts of

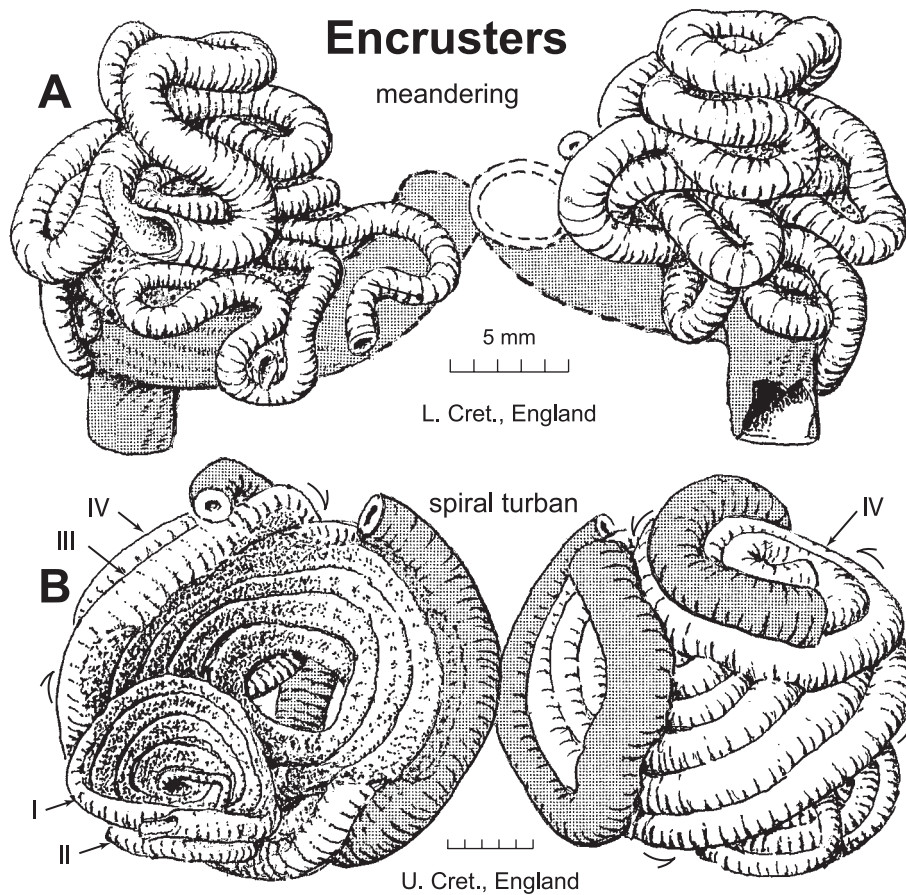


Fig. 5. Single individuals of the spaghettiform *Glomerula* could form their own reeflets, in which tube diameters increase in subsequent layers. □A. Gordian meanders on larger serpulid tube (YPM 208196). □B. Pancake spirals on globular starter substrate now perished (YPM 36194).

the shell. Once introduced, they may be rhythmically repeated throughout ontogeny. In such *iterative count-down* programmes, periods of normal shell growth are regularly interrupted by heteromorph stages. In muricid gastropods and the ammonite *Nipponites*, this implies that shell growth is halted for a while, before it proceeds more quickly in the normal mode to the next stop. The specimens illustrated in Figure 7 (from Jäger 1983) show that iterative programmes evolved in serpulids as well as sabellids.

The three knots of *Glomerula* (Fig. 7D) were unattached, because an encrusting tube could hardly coil this way. They are connected by straight portions, each of which served as a chimney before the next knot was built. As there is no increase in diameter, the original 'string of beads' may have been even longer and increased the snowshoe effect of the whole system by its zigzag course. This opens the possibility that the specimens shown in Figure 6 are parts of such strings that became actively broken. Asexual reproduction by breakage is also common in fungiid

corals (*Cycloseris*) and lunulitid bryozoans (O'Dea *et al.* 2004). In this way they bypass the minute post-larval stage, which is at particular risk in secondary soft-bottom dwellers. In this perspective, the strange behaviour of the Jurassic *Glomerula gordialis* (Fig. 6E–J) becomes understandable: its straight core is possibly a former chimney that became overgrown by the next coil and then broke off at the base.

This model cannot be readily applied to the multiple spirals of *Spiraserpula* (Fig. 7A–C), because they were attached (Jäger 1983). In Figure 7A and B, the lateral flaps of the overlapping spirals also contribute producing a flat plate. This plate could have acted as a snowshoe if the substrate perished during the lifetime of the worm. In a fabrication sense it is also noteworthy that the sense of coiling (arrows) tends to switch in subsequent spirals, thereby avoiding a linear arrangement. Significantly, iterative countdown never occurs in *Rotularia* (see below), the larvae of which settled on a minute starter substrate and produced only a single spiral with a terminal chimney.

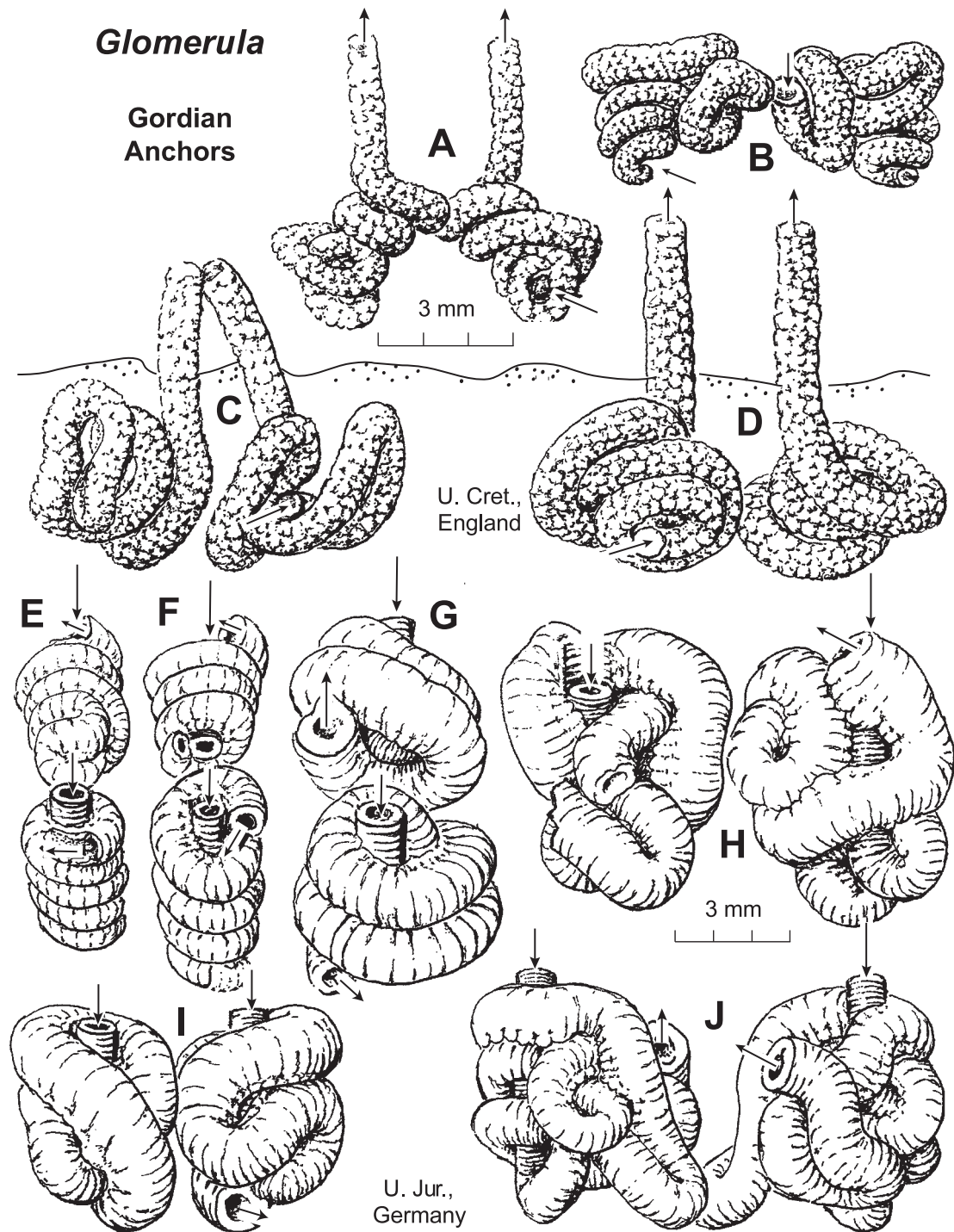


Fig. 6. By using countdown growth programmes, solitary *Glomerula* can produce compound structures with a Gordian anchor and a straight chimney. □A–D. Silicified internal moulds; *Glomerula serpentina*, Upper Cretaceous, England. □E–J. *Glomerula gordialis*, Upper Jurassic, northern Germany. Instead of being the terminal structure, the ‘chimney’ was made first and the anchor grew around it in a corkscrew or meandering fashion. This and the lack of an initial tube suggest that one deals with autotomized fragments of a more complex structure (Fig. 7) (YPM numbers: A, 208198; B, 208200; C, 208199; D, 208197; E, 208202; F, 208203; G, 208201; H, 208206; I, 208205; J, 208204).

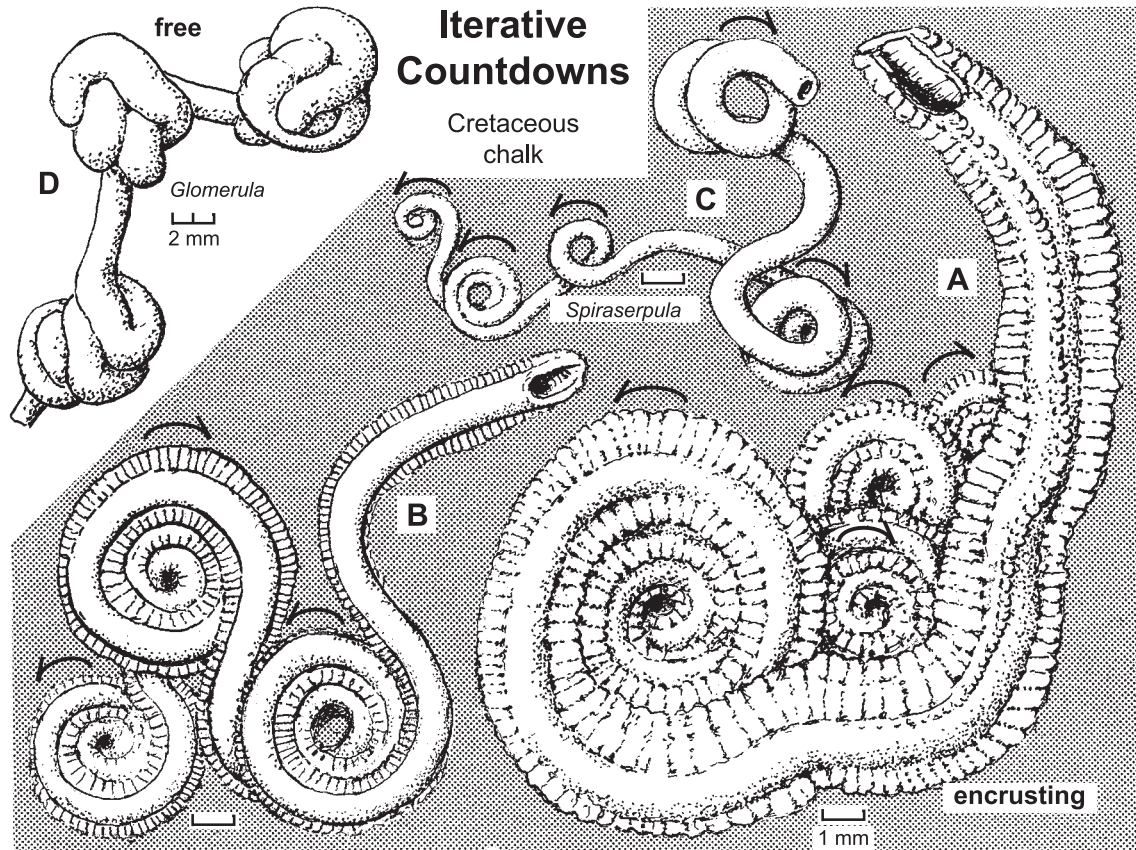


Fig. 7. In Cretaceous tube worms, the iterative change of growth programmes served different functions. In encrusters (A–C) it enlarged the potential resting surface in case the substrate perished. In the free-living *Glomerula serpentina* (D) it may have allowed fragmentation into functional units (Fig. 6A–D) in asexual reproduction. Note changes of coiling directions in A–C. All specimens drawn from Jäger (1983).

Walking stick resurrectors

While ‘spaghettiform’ soft-bottom dwellers build excessively long, but unsculptured, tubes for stabilization, the tubes of soft-bottom Serpulidae remain relatively short. Accordingly, they increase stability by modified tube geometries and ornamentations. Horn-shaped growth, for example, keeps conical shells from rolling. *Hamulus* and other serpulids (Fig. 8) followed this strategy; but, unlike the similarly shaped horn corals, they lack the high profile necessary to produce an upcurrent scour. Nor is there any differential weighting of the convex side that would have assisted passive implantation into a terminal position with the aperture pointing up. To the contrary, longitudinal ribs (Fig. 8D) and intermittent transverse shell thickenings (Fig. 8A and C) helped maintain the lateral position. Neither did the broad wings of a Cretaceous form (Fig. 8B) facilitate passive implantation. In a waning storm, such tubes would have ended up in a horizontal position after the coarser sediment had settled and would have become buried in this attitude under the mud settling from suspension.

This paradox may be solved in analogy to *Sowerbyella rugosa* (Dattilo 2004). After a storm, this Ordovician brachiopod came to rest with the concave ventral valve down and the commissure piercing into the sediment. This stable (but uncomfortable) attitude, however, was only temporary. As soon as the mud had settled from suspension, the animal righted itself by flapping its unequal valves and thereby rotating around the long hinge line. In this way, it restored the vertically implanted life position even though it was unable to actively dig. If hamuliform species used their tentacular opercula in a similar way, they would fall into the guild of *resurrectors*, while one would classify them as a *recliners* from shell morphology alone. We shall come back to this strategy when discussing *Rotularia*.

Helicoidally coiling climbers

In contrast to the planispiral coiling of spaghettiform species, *trochospiral* growth of serpuliform species may be induced by winding the tube around an

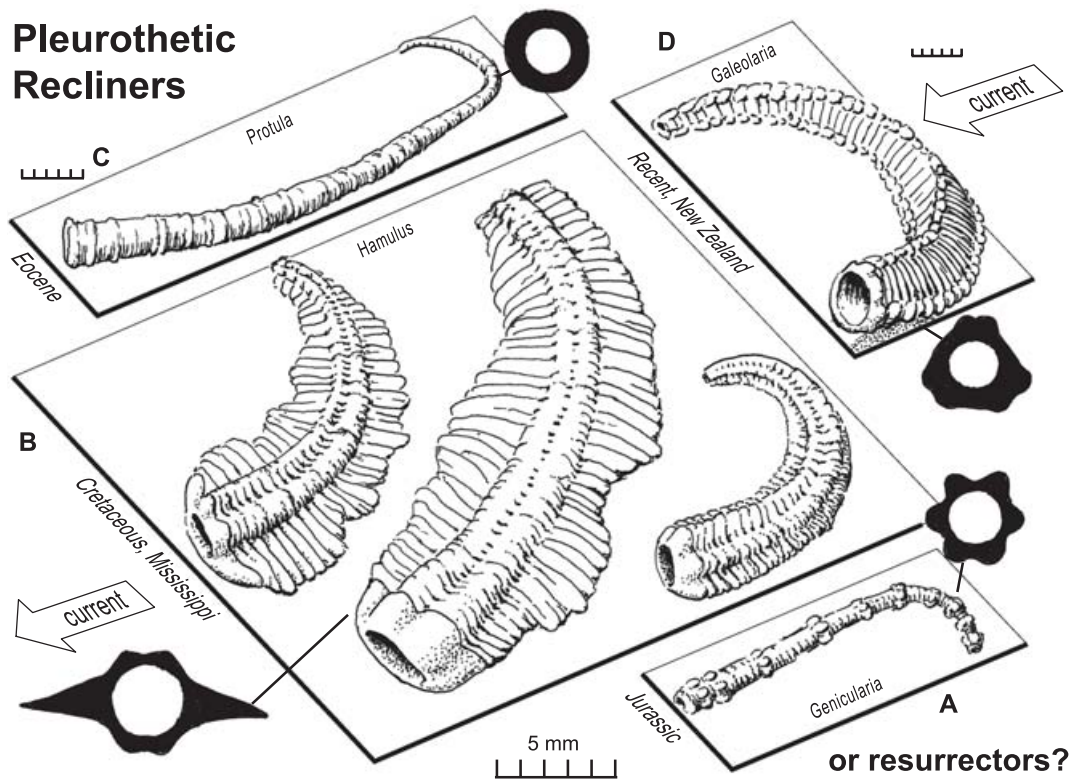


Fig. 8. In free conical shells, the simplest mode of stabilization is horn-shaped growth in a single plane. Examples shown evolved independently in different lineages. In a filter feeder, the passive resting position makes sense only if combined with active resurrection. Spaghetiform species never use this strategy. □A. *Genicularia ornata*, YPM 207081; □B. *Hamulus onyx*, YPM 208208 (left), YPM 208207 (middle), YPM 208209 (right) and YPM 208211 (cross-section); □C. *Protula* sp., YPM 207085; and □D. *Galeolaria hystrix*, YPM 206966 and YPM 206962 (cross-section).

upright host stem. In Figure 9A, one individual started to spiral when climbing the vertical tube of another serpulid. Subsequently younger individuals joined in. At mid point, the whole bundle of encrusters switched from sinistral to dextral coiling. Eventually they reached the same level as the initial host, forcing it to grow on with the same coiling.

In another specimen (Fig. 9B), the original stem substrate has perished. On its mould one recognizes a first bundle of small dextrally coiling serpulids, followed by a sinistral bundle that later opened into a fan-like structure by insertion of additional individuals. As seen in the enlarged view of the lower side, this fan provided a substrate for the sinistraly coiled tubes of another small serpulid (*Spirorbis*).

Serpula convoluta from the Middle Jurassic (Figs 10–11) resembles trochospiral species of *Rotularia*, except that sinistraly and dextrally coiled specimens occur in the same population. However, median sections show a cylindrical cavity, indicating that the animal grew around stems of a perishable stem, perhaps kelp. Modern serpulids are known to encrust seagrass and to alter their coiling angles, based on the elongate axis of the grass blade (Hickman 2005). In Figure 11A, two individuals settled next to each other around the

same stem and grew in opposite directions in the shape of an hourglass. In another group (Fig. 11B), only one individual grew trochospirally, while the other two wound around it like wrestlers. Nevertheless, all three lived at the same time, as shown in cross-section by the mutual attachment of coils.

Serpula convoluta was clearly an encruster, but its walls are overly thick for such a lifestyle. There are also specimens (Fig. 10F–G) that did not grow around a cylindrical stem. This is indicated by a wide conical umbilicus. It is possible that this species evolved to outlive perishable substrates. The heavy shell would then have allowed it to live on as a free recliner.

Solitary mudstickers and recliners

Prototypes of mudstickers are solitary rugose corals (Seilacher 2005). After having outgrown a minute starter substrate, their basal disks grow upwards and keep pace with sedimentation by accreting circular growth rings of increasing diameters. The result is a conical theca anchored by its own weight and a rugose surface. In tube worms, the basic approach to the mudsticker paradigm is to grow helicospirally, with coils of

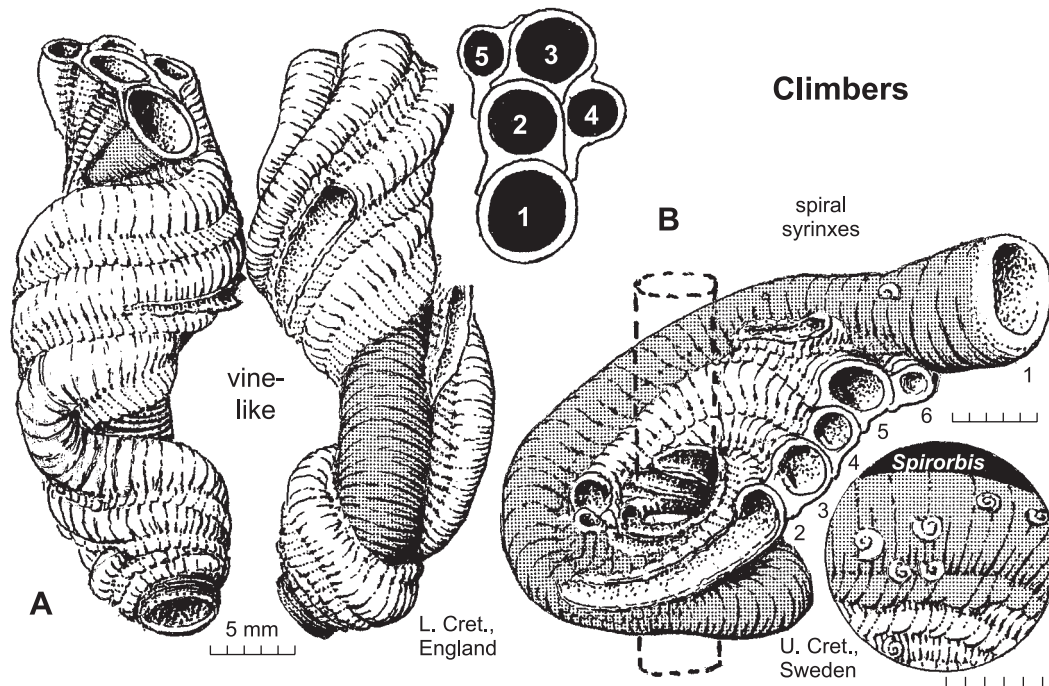


Fig. 9. Coiling of *Dorsoserpula* around upright stems of other organisms plus colonial settlement of new members leads to strange growth forms. Note upward growth in all examples. □A. Coiling changes from sinistral to dextral and eventually involves the large host (YPM 206930). □B. In both colonies (first one seen inside hole left by perished stem), new settlements occurred sequentially inside the older coils. Enlarged picture shows a smaller serpulid (*Spirorbis*) on the lower side of the fan (YPM 207002).

increasing diameters firmly attached to each other. Resulting growth forms (*Orthoconorca*; Jäger 1983) resemble high-spired gastropod shells, except that the body cavity is narrower, while a massive core provides the necessary ballast. In most cases, the sense of coiling varies not only between individuals. It may also switch after incidents (Jäger 1983).

Other species in this group (e.g. *Conorca trochiformis*; Jäger 1983) have a lower spiral, fitting passive reclining rather than mudsticking. They resemble *Rotularia leptostoma* (Gabb, 1860) from the Paleocene of New Jersey, of which a large sample has been available (Fig. 12). It shows about equal proportions of trochospiral versus planispiral and of sinistrally versus dextrally coiled individuals within the same population. This variability is lost in *Rotularia*, the shells of which not only followed stricter growth programmes, but also became much larger and heavier and developed a straight chimney in the adult stage.

Cretaceous *Rotularia* from Antarctica

Lifestyle

Seymour Island and other islands north of the Antarctic Peninsula have been the targets of many

geological missions. In the folded, 1190-m thick Cretaceous mudstones of shallow marine origin (Macellari 1984), *Rotularia* (*Austrorotularia*) is locally the most abundant fossil (Fig. 13A). Various species have been distinguished for stratigraphic purposes (Macellari 1984). All studied specimens are sinistrally coiled and share considerable size, a heavy ballast skeleton, knobby spiral ribs, and a lenticular shape making them fit for passive reclining. Adult individuals also developed a long chimney, but instead of elevating like the head of a cobra snake, it extends in the plane of the original spiral. As this attitude contradicts the functional paradigm of a reclining suspension feeder, Savazzi (1995) proposed that *Rotularia* had become a sediment feeder, the 'chimney' of which increased stability.

In fact, shells are horizontally embedded in the lag horizons at Seymour Island, where most collections have been made (Fig. 13A). Isolated shells dispersed in silty sediments, however, have an edgewise position with the chimney pointing upward (Fig. 13B). How can the two conflicting observations be accommodated in terms of lifestyle?

In general, heavy recliners have a higher fossilization potential than other shells. Therefore, they commonly become reworked and accumulated into lag deposits. Their actual life position, however, is more likely preserved in isolated specimens. In *Rotularia*, a vertical attitude could only be obtained by active

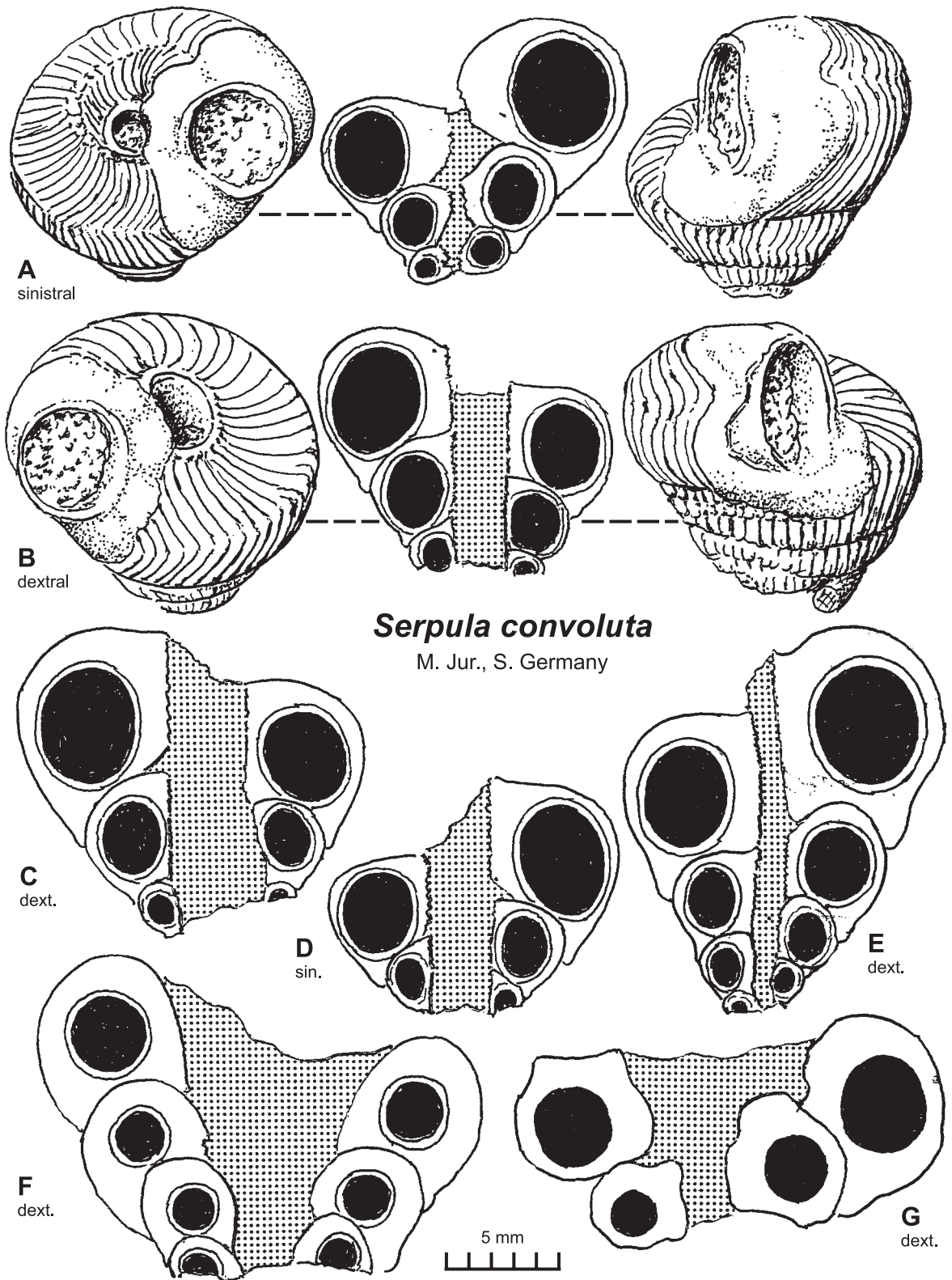


Fig. 10. □A-E. Normally, this species lived solitarily, coiling around a now perished cylindrical stem (probably seaweed) in an either sinistral or dextral sense. Its walls, however, were unnecessarily thick and made it a potential recliner when the host's stem perished. □F. and □G. The species developed the same gastropod-like shape despite having no cylindrical core (YPM numbers: A, 206914; B, 206913; C, 206905; D, 206912; E, 206901; F, 209680; G, 206906).

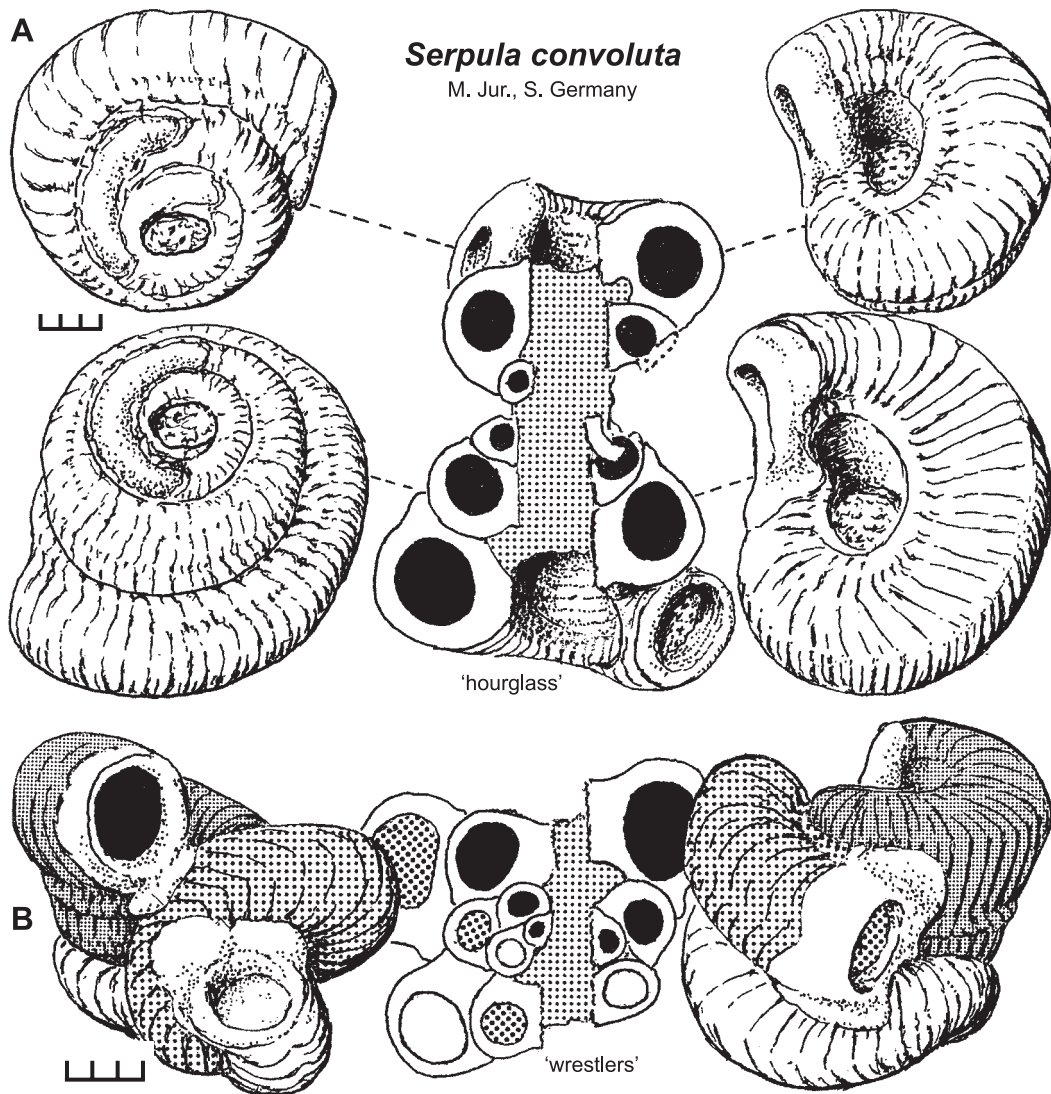


Fig. 11. □A. In the two specimens (both dextral) growing around the same stem, one must have spiraled downwards (YPM 206909). □B. Intertwined group of three individuals, of which only one grew around the stem in the proper helicospiral (YPM 206910).

resurrection (see above). An edgewise life position is also corroborated by naticid bore holes, which are concentrated on the top part of the spiral (Fig. 13C).

Morphogenetic programmes

Another problem is the increasing genomic control on the developmental programme of the shell. The first species, *Rotularia* (*Austrorotularia*) *fallax* from the basal López de Bertodano Formation of Snow Hill and Seymour Island (Maastrichtian), is recognized by five rather sharp longitudinal ribs (Fig. 14C and P–U). As seen in cross-sections, it shifts gradually and relatively early from the initial trochospiral to a planispiral mode, in the outer whorls. A second

developmental shift is marked by the terminal straight chimney (Macellari 1984), which has been lost in specimens available for our study.

In the second species, *R. (Austrorotularia) tenuilaevis* from higher up in the López de Bertodano Formation at Seymour Island (Fig. 14B and J–O), the spiral ribs are reduced to three. In cross-section, the wall is thicker than the diameter of the inner cavity, expressing the ballast function of the thick outer shell layer. Coiling is always sinistral [Luther (1999) found only one dextral shell in 174] and again starts in a trochospiral mode. The switch to planispiral or hyperstrophic coiling is abrupt and takes place at the same point in ontogeny in every individual. From outside, the trochospiral part can hardly be seen in adult shells, because it is covered

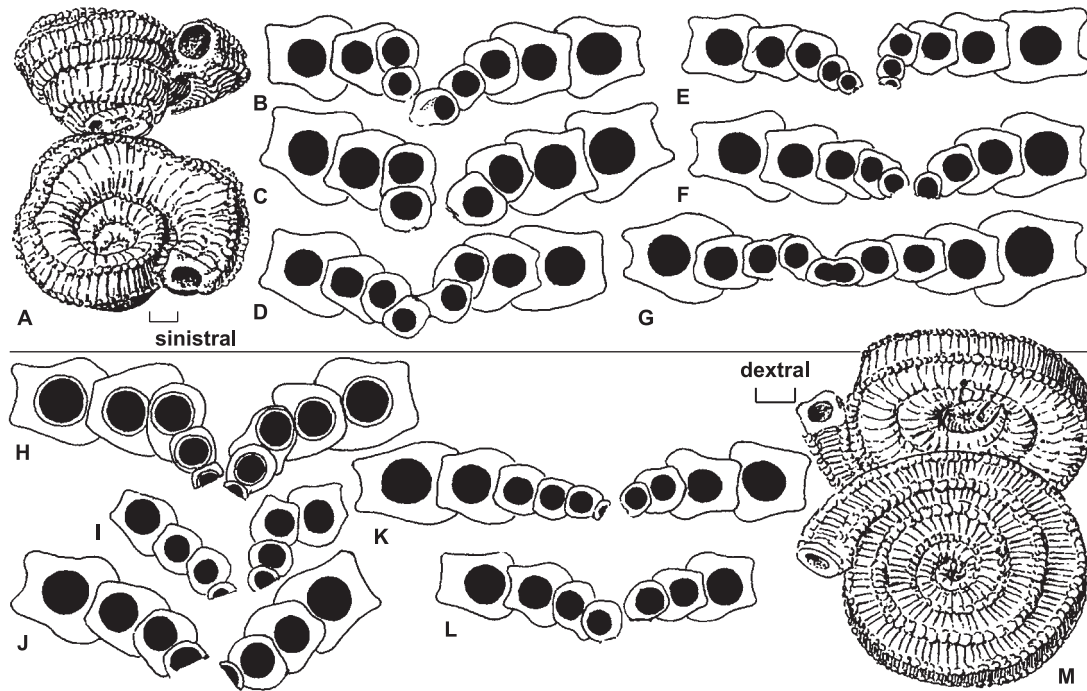


Fig. 12. The small shells of this species (*Rotularia leptostoma*) from the Paleocene of New Jersey indicate a free recliner that needed only a minute starter substrate. Nevertheless, individuals varied between sinistral and dextral, as well as trochospiral and planispiral coiling, with about equal numbers (YPM numbers: A, 207053; B, 213785; C, 213796; D, 213797; E, 213789; F, 213786; G, 213794; H, 213790; I, 213793; J, 213791; K, 213787; L, 213792; M, 207052).

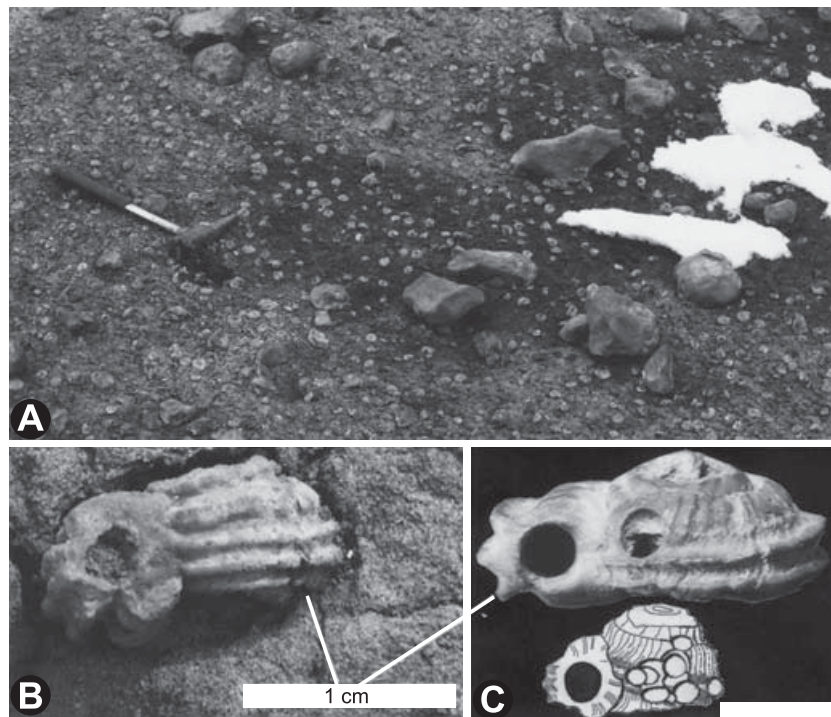


Fig. 13. In lag deposits (A), shells of *Austrorotularia* are always horizontally embedded. A vertical life position with the chimney on top is documented by field observations of isolated individuals (B) and the borings (C: superimposed from 12 specimens in Ushuaia collection) of naticid gastropods that always attacked the top of the shell. The vertical attitude could only be obtained by active resurrection.

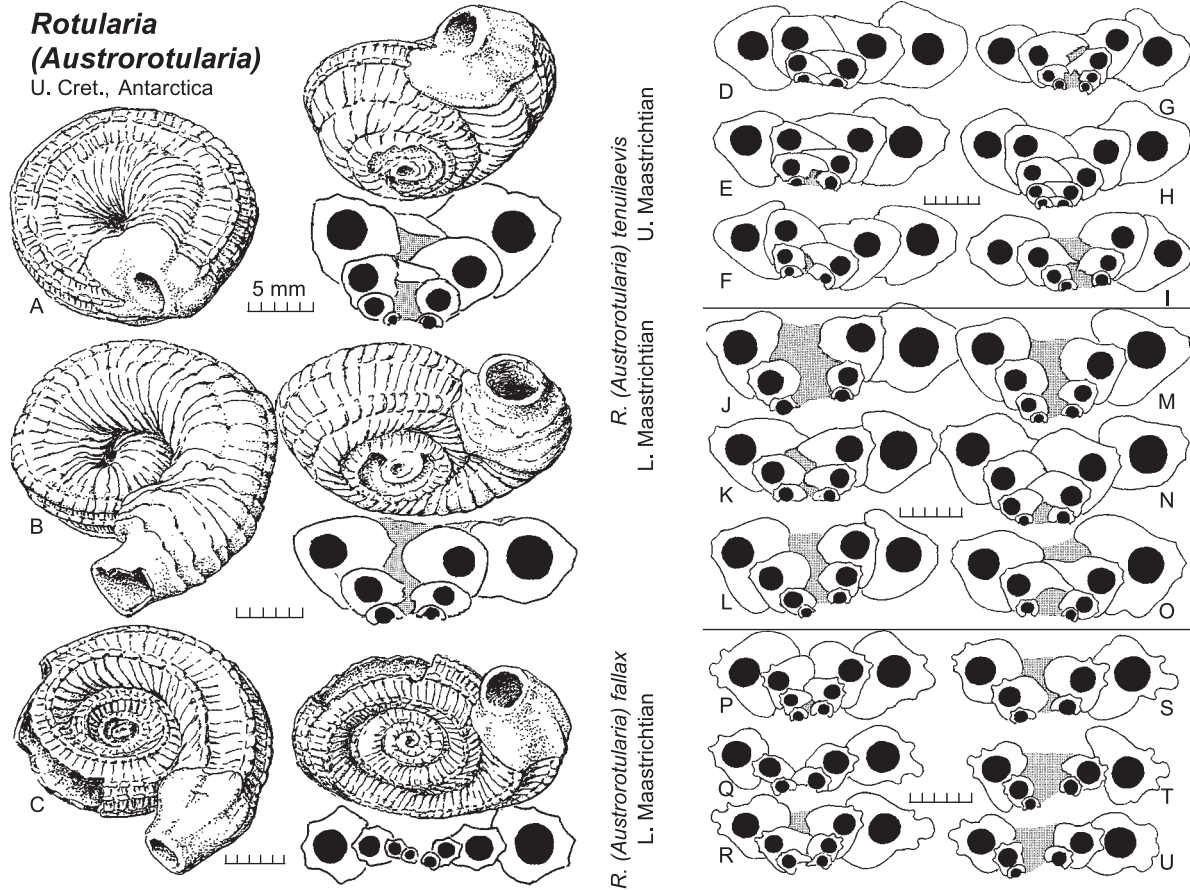


Fig. 14. In Antarctica, *Austrorotularia* is always sinistrally coiled and cross-sections reveal a three-stage countdown programme. It starts with a switch from trochospiral to planispiral growth and ends with an uncoiled chimney (lost in figured specimens). As the wall is very thick and whorls overlap, the shell was relatively heavy (YPM numbers: A, 206956; B, 206957; C, 206964; D, 206944; E, 206942; F, 206941; G, 206948; H, 206945; I, 206947; J, 209128; K, 209126; L, 209129; M, 209127; N, 209132; O, 209133; P, 209117; Q, 209120; R, 209112; S, 209115; T, 209118; U, 209113).

by the involute outer whorls. Adulthood is signalled by the formation of a straight terminal *chimney*.

In analogy to the uncoiled body chambers in adult heteromorph ammonites, this feature may be called a morphogenetic countdown. These departures from the original mode allow for functional commodities unavailable during spiral growth (Seilacher & Gunji 1993). The argument (Savazzi 1995, 1999) that the chimney served mainly for enlarging the resting surface is also contradicted by its shape. For effective stabilization, it should have a thicker wall than the rest of the shell, so that the animal would have come to rest after a storm with the filter fan pointing upcurrent. Instead, the wall of the chimney is always thinner and lacks ribs, which would have provided ballast and have increased the purchase on the sediment, as in the coiled part of the shell. A stable horizontal position, however, was also necessary for active resurrection into the edgewise life position after the tempestitic mud had settled on top.

Eocene *Rotularia*

The highly specialized *Rotularia* is probably a form genus that developed in various lineages after the end-Cretaceous mass extinction. The Eocene *Rotularia spirulaea* (Fig. 15A–H) followed the trend of Cretaceous forms by developing only a single massive keel that effectively shifted additional ballast to the outer margin of the disk. Countdown features, such as the switch from trochospiral to involute planispiral coiling and the addition of a smooth chimney, were retained.

Rotularia bognoriensis from the Eocene London Clay (Figs 15I, 15J and 16) also developed a long chimney in the adult stage, but lacks the planispiral portion, as well as the ballast ribs. Instead, the tube remains smooth throughout, reminiscent of the smaller 'spaghettiform' serpulids. As planispirality and spiral ribs would have improved stability in the reclining phase, it is unlikely that these features have been

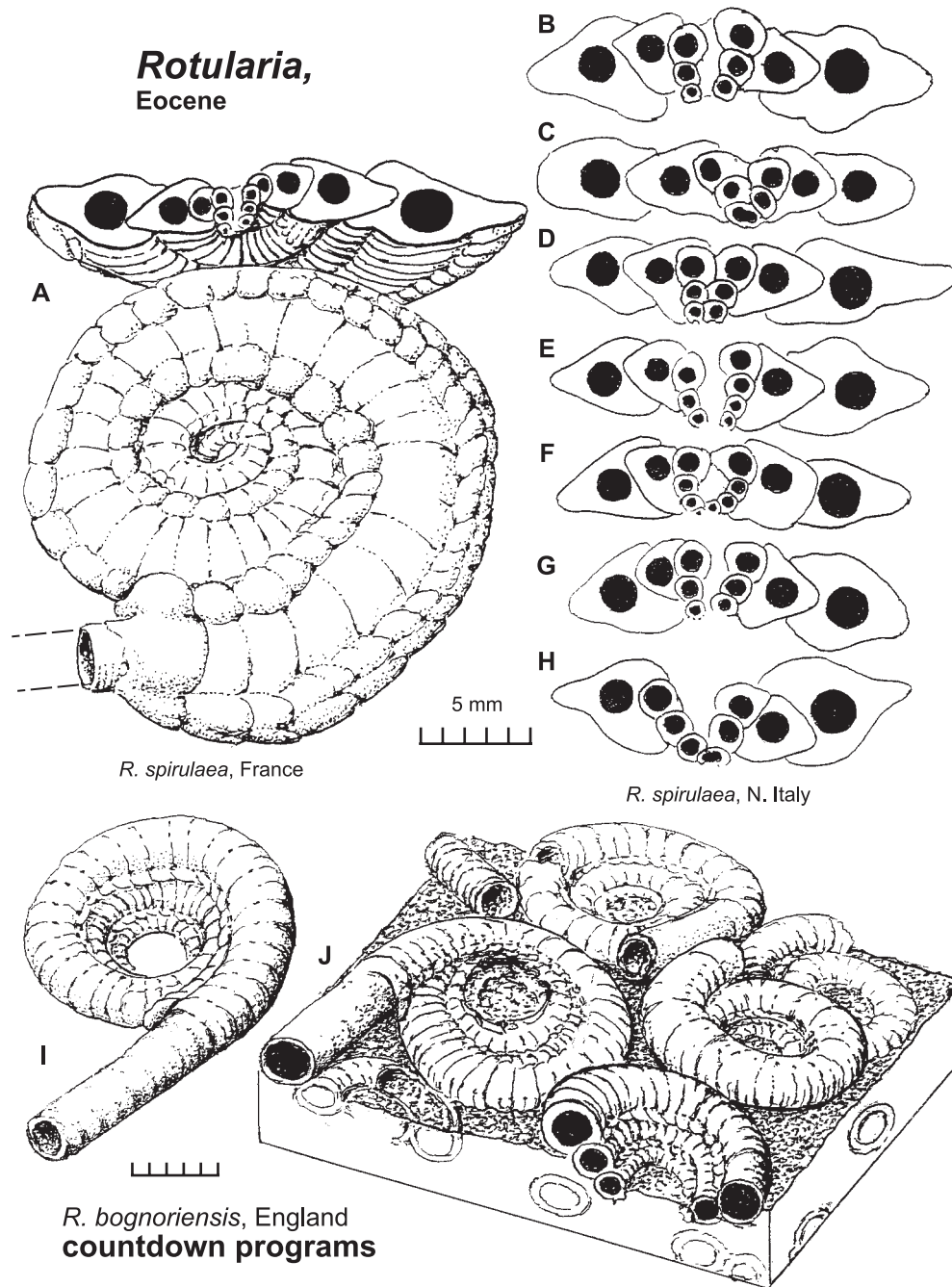


Fig. 15. □A–H. After having survived the end-Cretaceous extinction, Tertiary *Rotularia* became so involute that the initial trochospiral part is hidden by the planispiral and heavily keeled outer whorls (YPM numbers: A, 206973; B, 206993; C, 206990; D, 206994; E, 206995; F, 206989; G, 206991; H, 206992). □I–J. This ladle-shaped species from the Eocene London Clay (YPM 206971) possibly evolved independently, because it is relatively thin-walled, lacks ornamentation and does not switch to planispiral coiling. Nevertheless, the long chimney made the animal come to rest in a horizontal position, from which it could actively resurrect after the suspended mud had settled on top of the initial tempestite layer. Part of hand specimen (see Fig. 16), in which reworked shells ended up horizontally and became fixed by concretionary cementation.

secondarily lost. More probably, *R. bognoensis* represents a convergent approach to the same paradigm: a ladle-shaped shell that after a storm came to rest with the convex side up and the chimney pointing downstream – an uncomfortable position indeed for

a filter feeder. Rather than making it a deposit feeder (Savazzi 1995) we suggest that *Rotularia bognoensis* was, like many other soft-bottom serpulids, a ‘resurrector’ that could right itself up with the help of its tentacular operculum.

Rotularia bogneriensis
Eocene, U.K.

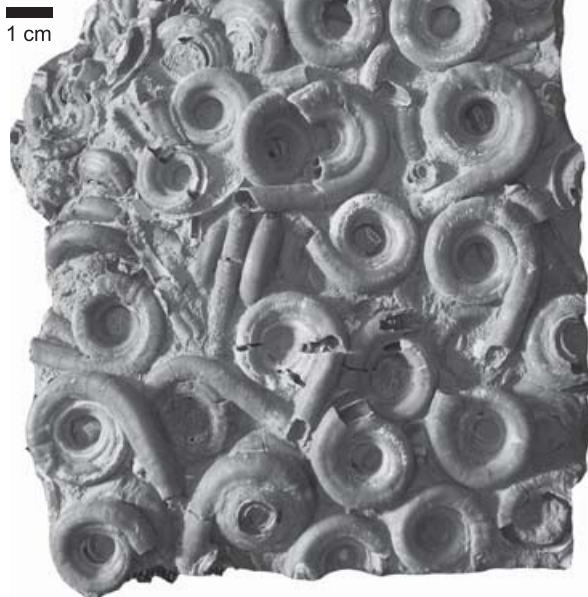


Fig. 16. Taking concave-down positions in the first layer as a geopetal criterion, this lag deposit represents a sole face. The terminal chimneys are preserved in many shells, indicating minor transport (YPM 206971).

Conclusion

Secondary soft-bottom dwellers are particularly suited for comparative evolutionary studies, because they evolved independently in a broad range of marine animals (Seilacher 2005). They all derive from ancestors that had become sessile filter feeders on hard or rocky substrates. When descendants were about to colonize the vast areas of oceanic soft bottoms, this step turned out to have been an evolutionary mistake: as the original mode of attachment did not work on soft and mobile substrates and because evolution is an irreversible process (Dollo's Law), alternative modes of stabilization had to be 'invented' to deal with the problem.

As it turns out, there is only a limited number of 'strategies' that secondary soft-bottom dwellers can use. But due to historical limitations and licenses, the same adaptive peaks were approached from different sides in every case. Therefore, the ecologic guilds, or paradigms, are less characterized by convergent morphologies than by the sedimentational, hydrodynamic, and behavioural processes involved.

Serpulid tubes are a special case, because they are domiciles rather than shells and because their walls are

built inside-out by lips extending behind the animal's head region. Also, their colonies rarely grow by budding, but require selective settlement of the larvae.

Nevertheless, tube worms successfully entered the niches of hitchhikers on ectocochleate cephalopods, of mudstickers, and of stable recliners in various lineages. All the more surprising is the lack of features that would have assisted passive implantation. Therefore, it is hypothesized that stable reclining was only a stage in a sequence followed by active resurrection after the muddy top of a tempestite had settled from suspension. The extendible operculum may have been instrumental in this process. *Rotularia* specimens sticking edgewise in the sediment and the positions of naticid bore holes support this assumption. Taking advantage of the graded deposition after a storm, the displaced animals ended up implanted in the muddy top layer without having to burrow. The ultimate life position was vertical with the aperture elevated above the sea floor, while horizontal attitudes found in lag deposits probably resulted from the reworking of dead shells, in which the chimneys are mostly broken off.

From a morphogenetic point of view it is interesting that these transformations led from irregular growth to increasingly rigid growth programmes in a structure that was not an integral part of the body. In a strict sense, its growth was controlled by behaviour, rather than development.

Future research should try to verify this scenario by observation of live serpulids, flume experiments, and the comparison of opercular morphologies in hard-bottom versus soft-bottom species. Furthermore, it would be interesting to test 'recliners' in other phyla for the possibility of active resurrection. The serpulid model might also be helpful in the interpretation of problematic taxa, such as the hyolitids, the stiff appendages (helens) of which may have been used for resurrection as well as stabilization, while the 'rocking profile' in many forms (Malinky 2007) resembles that in the suspected rugose resurrector *Calceola* (Seilacher 2005).

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