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MODE OF LIFE OF GRAPTOLITES

Abstract.—The probable mode of life of the graptolites (crustoids, dendroids and graptoloids) is reconstructed from a logical interpretation of their rhabdosomal structures.

The readaptation of sessile colonial organisms to meet the requirements of a freely-moving existence in the plankton is regarded as the controlling factor in the evolution of the graptoloids.

It is suggested that the gradual reduction in the size of the colony in the dichograptids, biserial and uniserial graptoloids may have been a consequence of the undesirability of coloniality in the new environment, and that the graptoloids might have attained individuality, disappearing into the plankton at the time of their supposed extinction.

Much of the substance of this paper was read to the Symposium on Coloniality at Durham (Systematics Association) in 1976 and should be published shortly. This version contains some new ideas, however, and also many digressions to discuss points of outstanding disagreement. Since the broad outline of my theme will be familiar to graptolitologists, as was not the case for the Systematics Association, I trust that the digressions will be of use and interest in themselves, and, placed in parentheses, will not obscure too much my main argument.

It is generally believed that crustoids were encrusting, and the dendroids attached benthonic colonies. Their coloniality may have been an adaptation to the benthonic habit, which could have arisen by failure of asexually budded zooids to separate from the parent. By forming encrusting or tree-like colonies small zooids of comparatively simple organisation would have been able to establish themselves upon the crowded sea floor and avoid being overtopped by competitors. The Bryozoa constitute a very obvious modern analogue to these benthonic graptolites.

The periderm of the crustoids and dendroids has been shown (Urbanek and Rickards 1974; Urbanek and Towe 1974, 1975) to be made of increments whose cores of fusellar fabric were mainly responsible for extension round the growing zooids, and whose bounding lamellae and

cortical layers of parallel orientated fibrils contributed resilience and tensile strength in addition to that afforded by the stolons. The ability of the extrathecal tissue to continue to secrete successive cortical layers allowed the whole rhabdosome to be strengthened *pari passu* with its distal extension, and special colonial structures to be developed whenever and wherever they were required.

The crustoids may have been adapted to rather more exposed benthonic conditions than the dendroids, though their orientated autothecae suggest that they may have produced coordinated ciliary feeding currents enabling them to draw water from a greater distance and so abstract food from a larger volume of water.

The dendroids probably lived in less disturbed conditions and the treelike form seems to have been related to the need to obtain and maintain a foothold on a crowded substratum, and then overtop competitors and so secure a maximum share of food from the overlying water. It seems likely that distribution of these sessile colonies was first by the gametes liberated into the sea, and then by the mobile larvae which probably lived in the plankton for a time before settlement. After settling, incremental secretion beneath the extrathecal tissue permitted the growth and strengthening of the holdfast *pari passu* with the distal extension of the stipes bearing the zooids.

The conical rhabdosome of *Dictyonema* may have been a refinement of the tree-like form. The core of inward-facing, evenly spaced autothecae presumably served as an upward-widening plankton net into which the zooids drew down coordinated food-bearing ciliary currents. The stipes, sometimes forming acute cones, sometimes obtuse cones, would have been prevented from falling apart by the dissepiments, and the colony would have been supported partly by the buoyancy of the water and partly by the drag exerted by the ciliary action.

The illustrations shown by B.D. Erdtmann at this Conference seem to confirm this idea, and surprisingly show that large cones could be supported on thin stalks up to 50 mm long in the protected inter-reef lagoons.

Rickards' suggestion (1975: 413) that currents might have entered the cone sideways so that "some of the zooids would always be available to tap the current irrespective of its direction" I find unacceptable since some of the zooids would always have gone hungry. His suggestion that in still-water conditions the ciliary action "might have drawn in water from the outside of the cone and in effect expelled it upwards" I find even more improbable. In the more obtuse cones this would have drawn in nearbottom water already exhausted of its food-content by bottom-living neighbours, and the efferent current would not only have blown away the overlying water with its rain of food particles, it would also have tended to flatten the cone against the sea floor.

With regard to *Dictyonema peltatum* I would seek further elucidation. According to sections in Bulman and Richards (1966) the apertural shields are approximately equal in width to the stipes, and according to Bulman (1933) the stipes are about $\frac{1}{3}$ or $\frac{1}{4}$ the width of the spaces between them, so that the shields are prevented

from fusing sideways. Yet Rickards (1975: figs. 37, 38) draws the shields in lateral contact; one would like to know if this is a perspective effect, or if Bulman's observations are incorrect. In any case one must presume that the shields were protective, and they would only have shielded the apertures from large particles or organisms if the currents had impinged upon them before filtering between them to the thecal apertures i.e. if the afferent current had been drawn down into the mouth of the cone.

Since a coordinated, downward afferent current would have exaggerated the tendency for particles of unwanted debris to accumulate in the cone, I regard the bithecal zooids as having been cleaning individuals. Placed on the sides of the autothecae they would have been well placed to manoeuvre unwanted fragments through the meshes of the net on the outgoing current.

In *Dictyonema flabelliforme* the stout holdfast was replaced by the nema. This may have originated as an elongating tubular (Legrand 1974: pl. 1) holdfast, and the young colonies figured by Ruedemann suggest attachment by tissue enclosing the tip of the nema. The world-wide distribution of adult colonies of *D. flabelliforme* and their preservation in marine sediments often accumulated under anaerobic conditions, suggest that the colonies may have been liberated when quite young, possibly by resorption of the tip of the nema-prosicalae as described by Hutt (1974) in *Clonograptus tenellus*. The colony was presumably able to survive and complete its growth in the plankton by virtue of its balanced form and coordinated ciliary feeding currents. As a reaction to the downward afferent current the upward widening cone would have tended to rise slightly when actively feeding—probably at night, and to sink slightly with the rest of the plankton when less active during the day. The incremental mode of secretion of the periderm provided the means for increasing the resilient strength of the cone as the colony grew, and for the secretion of 3 stabilizing vanes at the proximal end of the rhabdosome. These could have helped to keep the apex of the cone down, and prevent rotation about its vertical axis.

So, by Tremadocian times, we have a colony which had been adapted to a sessile existence in the benthos taking up a mobile career in the plankton. As I see it, the graptoloids' spectacular evolutionary changes record the readaptation to a new, comparatively monotonous and very stable environment of a colonial animal that was initially unsuited to it.

The main requirement for existence in the plankton was to reconcile two conflicting needs: (1) the need to present the zooids as effectively as possible for the creation of ciliary currents and for the abstraction of food from them, and (2) the need to create a resilient supporting rhabdosome able to withstand the stresses resulting from the coordinated currents, but with the utmost economy of skeletal material so as to keep the overall density of the colony as close as possible to that of the sur-

rounding sea water. The graptoloids were able to reconcile successfully these conflicting needs by combining the sympodial budding of the colony with the unique incremental mode of secreting the periderm inherited from the dendroids. The zooids, so far as one can tell, underwent no important evolutionary changes at all.

Sympodial budding provided the possibility of constructing stipes of theoretically unlimited length and no more than two thecae in width, giving the zooids access to a large volume of water. At the same time incremental secretion beneath the extrathecal mantle afforded unique opportunities for the economical sharing of skeletal material, for the most mechanically effective use of the cortical "plies", and perhaps for reducing local or overall density by the inclusion of vesicles (Urbanek and Towe 1974; Kirk 1974b: 9).

The first evolutionary changes in the new environment were to reduce the resistance to the feeding rise resulting from the dense spreading form which had evolved to overtop competitors in the benthos. Progressive reduction of branching occurred, leading to a symmetrical but sparse rhabdosome. The dissepiments were lost as they were no longer required to hold up the stipes from the seafloor. A proximal web is found in some horizontal forms which may have supported the short branches of the young colony during its initially sessile stage of development on the seafloor following settlement by the larva. This web may have continued to develop to strengthen the proximal ends of the elongating stipes. But a proximal web would have been inadequate to hold up the long branches of a sessile adult colony, and the resorption of the tip of the nema prosiculae in *Colonograptus tenellus* (Hutt 1974) suggests how the colony might have been liberated at an early stage. Further growth of the adult nema may have occurred after liberation to produce a stabilizing structure, a kind of keel, and this became a solid rod in the graptoloids (Urbanek and Towe 1975; Kirk 1975). With the attainment of automobility the stolon system ceased to be sclerotized, possibly as a further economy in the use of dense skeletal material. And with the sparse branching unconnected by dissepiments, cleaning individuals became superfluous and the bithecae gradually disappeared.

The thecal gradient appears to be peculiar to the graptoloids (Urbanek, 1973) and probably evolved as a consequence of the sparse branching. In *D. flabelliforme* the frequent and rather regular branching of the stipes had resulted in an even distribution of the autothecae over the inside of the conical rhabdosome, giving the zooids as equal an opportunity as possible for the creation of currents and the abstraction of food. With reduction in branching the distal thecae became more widely separated. One wonders if their increasing size reflected larger and more vigorous zooids able to exploit the food in the larger volume of water available to them.

In colonies living in suspension with the sicular aperture facing upwards, a change in the inclination of the stipes to horizontal and 'reclined' could at first have been a passive response to gravity following the loss of dissepiments. As this change would have favoured the feeding rise, and would also have presented the proximal zooids more advantageously for the production of ciliary currents and for extracting food from them, the change in inclination became a positive evolutionary trend. Following larval settlement the young colonies may have been attached by the mantle surrounding the short nema until the 'reclined' thecae began to be secreted. At this stage the colony must have been liberated or, with further growth, the 'reclined' stipes would have impinged upon the sea floor. As a stabilizing nema would have been superfluous in a free-living colony with long 'reclined' stipes it was usually not developed further in the adult colonies.

Spirally twisted rhabdosomes first appeared among the 'reclined' graptoloids. They confirm, in my view, the supposition that the graptoloids moved relative to self-generated feeding currents (Kirk 1969). Had the colonies merely been carried in passive suspension by ocean currents, they would not only have rapidly exhausted the food in the water surrounding them, but they would have been carried along bodily whatever their form and posture — just as we are carried along by the earth's rotation — and the great variety and precision of form exhibited by the graptoloid rhabdosome would be unexplicable.

Rickards states (1975) that Bulman, in a personal communication, claimed that he had thought of automobility himself and then dismissed the idea. This could be so, but Bulman certainly never communicated the idea to me. And in discussion of my 1969 paper Bulman emphatically dissociated himself from my theory of automobility, maintaining that the graptolite zooid was too small to produce colonial automobility. This was not illogical, since Bulman believed that graptolite zooids were like pterobranch zooids, connected by stolons and only occupying a fraction of the space within the rhabdosome. He also seemed to believe that the ciliary action of the graptolite lophophore would necessarily have resembled that of *Rhabdopleura* or *Cephalodiscus*.

Spiral movement in the "reclined" rhabdosomes probably originated as a consequence of uneven ciliary pull by the zooids on the two stipes. As such movement would have given increased access to food, any irregularity in the rhabdosome reducing resistance to rotation would have tended to be selected. So the spiral action would have been gradually translated into spiral form.

In the branched graptoloids, and more especially in the non-spiral colonies, the drag exerted on the rhabdosome by the coordinated ciliary currents would have produced considerable stress at the origin of the stipes adjacent to the sicula. This would normally have been met by the more prolonged corticization over the oldest part of the rhabdosome —

a direct consequence of the incremental mode of distal extension and cortical thickening. In *Didymograptus pakrianus* (Jaanusson 1960) the peculiarly heavy secretion over the proximal part of the rhabdosome could have been a special device to withstand the considerable stress at the origin of the upright, forked colony. The complete or near closure of some of the most proximal zooids could have had little detrimental effect in this case, since such zooids would have been disadvantageously placed for both producing currents and obtaining food from them.

Another device to withstand stress at the origin of the stipes was the development of a number of crossing canals, leading to the evolution of the 'scandent', biserial rhabdosome.

In the biserial graptoloids the period of sessile development, following settlement by the larvae, was probably even shorter. The nema prosciculae was correspondingly reduced, to about $\frac{1}{4}$ the length of the proscicula (Hutt 1974). The adult nema is frequently regenerated from the broken proscicula, breakage presumably occurring upon detachment. This probably occurred at about the time the growth of the first two thecae changed direction from upward, facing the sicular aperture, to outward and downward — towards the sicular apex.

The compact development of the biserial rhabdosome permitted the maximum economy in the use of periderm, by elimination or sharing of interthecal walls, and by incorporation of the nema as a support within the rhabdosome (Kirk 1975). Stress at the origin of the colony was eliminated. The very compactness of the young colony may have led to difficulties of suspension by the feeding currents when only a small proportion of the zooids was sufficiently mature to produce effective ciliary action. The development of various balanced arrangements of proximal spines probably served to increase the frictional resistance to sinking at this stage, and the nema or virgula was relatively well developed, serving as a keel. In the older colonies, with a greater proportion of mature zooids working, the need for frictional spines was reduced and they are often confined to the proximal end of the rhabdosome.

In some climacograptids (Riva 1974) the proximal spines continued to be enlarged throughout the life of the colony, developing flanges connecting them with the proximal thecae. These may have served a counter-rotational role, like the winged spines in *C. ensiformis* and the large spines in *Lonchograptus*, but their exaggerated development could have been simply a gerontic effect. If vesicles had been included in the cortical increments they need not have made the proximal end of the rhabdosome unduly heavy.

At the other end of the rhabdosome 2 or 3 vanes were frequently developed from the projecting virgula, presumably again damping down any tendency to rotate about the virgular axis and helping to keep the proximal end uppermost.

By contrast some biserial graptoloids with attenuated periderm became extremely spinose throughout the length of the colony. These must have offered considerable frictional resistance to movement, so there would have been less tendency to sink when less actively feeding. The downward component of the ciliary currents could therefore have been reduced, allowing an increase in the lateral component. This would have been much to the advantage of zooids arranged in two vertical rows. These very spinose biserial graptoloids probably had an almost immobile existence in the deeper layers of the photic zone. (A specimen of *Holograptus mucronatus* var. *bimucronatus* figured by Elles and Wood (1901—1918: pl. 33: 8e) shows a long virgula with 6 triads of vanes which presumably maintained the spiny colony in vertical near-immobility with the sicula uppermost).

Other biserial graptoloids may have become adapted to life in the rather more turbulent, upper layers of the sea, though I suggest that these would still have been below wave base since the planktonic food supply becomes less abundant above that level. The small finite colonies of *Holoretiolites* had an inflated proximal end, and the reduced distal zooids formed an appendix. Sclerotization of the periderm was also reduced to the minimal framework of lists necessary to give the rhabdosome resistance to distortion. If the proximal end had been relatively buoyant and the appendix relatively dense, the strongly bipolar *Holoretiolites* colony would have rapidly returned to verticality whenever deflected from it, and would have been particularly adapted to withstand the more disturbed conditions and profit from the abundant food in the upper layers.

Adaptation to life at the food-rich higher level may have been the factor which enabled the holoretiolites to exist into Ludlovian times while the remainder of the biserial graptoloids almost died out in the Llandovery. This seems to suggest that although the biserial form provided the maximum opportunity for economical sharing of skeletal material, it may have failed to fulfill the other requirement for success in the plankton — the need to present the zooids most advantageously for the creation of feeding currents and for the abstraction of food from them. The success of *Holoretiolites* may have been due to the fact that the competition between its two rows of zooids was less of a disadvantage in the more turbulent but more food-rich upper layers of the sea.

In the calmer, somewhat lower layers of the plankton, the biserial graptoloids were replaced by uniserial forms, presumably because zooids arranged in a single row were able to produce more economic feeding currents.

In this connection the report by Jaeger, at this conference, of the finding of *Climacograptus* in the Devonian, has special interest. Since conditions for graptolite

abundance had existed throughout later Silurian and early Devonian times, the failure to find climacograptids among the many fossil uniserial rhabdosomes must have been due to the rarity of the biserial colonies. It hardly seems feasible that this could have been because they occupied some special niche—what niches are there in the plankton other than broad areas and layers of differing temperature and salinity? It seems unavoidable to conclude that the biserial climacograptids were simply unable to compete and coexist in any numbers with the more efficient uniserial feeding machines.

It seems likely that the uniserial colony was liberated from its attachment to the sea floor even earlier in its development than the biserial, since the nema prosiculae is even shorter, about 1/12 of the total prosicular length, and the prosicula was almost invariably regenerated after breakage—presumably the consequence of detachment. The early liberation would have been necessitated by the wholly downward-directed growth of the aperturally-budded first theca. The young colony probably rose with a spiral action due to the slight curvature of the uniserial rhabdosome. This would have benefitted zooids arranged in a single series, and the strongly curved and spiral rhabdosome probably evolved because it offered less resistance to a spiral feeding-rise and enabled its zooids to sweep a broader cylinder of water. Spiral movement implies coordinated and asymmetrical ciliary action along the curved stipe (Kirk 1969 and 1975: 15) and this is probably reflected in the thecal gradient and in the asymmetry of individual thecae, more especially of their apertural lobes. This reached its acme in the cucullograptids described and illustrated by Urbanek (1966). In the Cyrtograptidae the spiral form was augmented by the development of divergent cladia whose zooids presumably contributed a centripetal thrust to the spiralling procladium. It is suggested that these more complex rhabdosomes were adapted to exploit the more thinly-spread food-supply of the calmer, lower layers of the photic zone.

In 1964 Bulman suggested that spirally curved graptolites might have been caused to gyrate as a reaction to "any slight eddies in the surface waters", and in the 1970 Treatise this idea was repeated with the omission of the word 'surface'. But except near the surface and near the bottom of the sea there seem to be only relatively large, mass-movements of water, and an absence of those small-scale eddies which could have acted differentially on graptoloid rhabdosomes and caused gyration in spiral forms. While no one seems inclined to put adult graptoloids in the bottom waters, Rickards (1975) seems to follow Bulman in favouring the surface waters as their habitat. He maintains that the high percentage (60%) of broken rhabdosomes counted by Crowther indicates that graptoloids did live under turbulent conditions, and he figures his colonies as adhering to the underside of the waves (op. cit.: 427, fig. 68). However, I would point out that the 60% broken rhabdosomes were dead rhabdosomes. After death, the cessation of the feeding currents would have allowed the colonies to sink slowly until the gas bubbles created by decay caused them to rise to the surface. Here they would have been exposed to the destructive action of waves and currents, and it is probably this environment at this stage which

produced the damage recorded by Crowther, and some of the tangled skeins and accumulations figured by Hundt (1965). With further decay the gas bubbles would have been released allowing the graptolite "skeletons", often mixed with fragments of land plants which had been blown out to sea, to sink gradually to the sea floor where they might have been preserved as fossils under suitable anaerobic, low energy conditions¹⁾.

But if the graptoloid colonies had lived in the surface waters and become damaged during life as Rickards and Crowther suppose, then, as Dr. Bates pointed out to me, their 60% damaged rhabdosomes should show evidence of regeneration. Regeneration undoubtedly occurred in graptoloids, but I think it was not so frequent as to suggest that it was an adaptation to meet living conditions so strenuous that breakage was normal. Had graptoloids lived at the surface, as Rickards figures them, they would surely have shown a totally different range of adaptations, not the precise gradients and balanced asymmetries which makes them unique among colonial animals.

According to my concept of automobility, cyrtograptids probably rotated and rose with the sicula uppermost, only very slowly in response to their ciliary currents (Kirk 1969, 1976), as the stress at the cladial origins would otherwise have been very great. In the specimen of *C. linarssoni* (Rickards 1976: fig. 54), more than 1 metre in diameter and with stiffly radiating fine cladia, I would suppose that rotation only occurred in early growth stages represented by the spirally curved procladium, and that this movement gradually ceased as the cladia were budded. Such a colony, in my opinion, could only have lived in the very still, deeper layers of the photic zone, held in almost immobile suspension by the down-drawn component of the feeding currents. The widespread stipes would have presented the zooids to a large volume of water enabling them to subsist on a thinly-spread food supply.

I notice that the *Cyrtograptus* which Rickards attached (1975: fig. 68) to the underside of the waves is a particularly robust form, while the waves are singularly small. I wonder if he would expose his large specimen of *C. linarssoni* to surface conditions?

It is also necessary to point out that Rickards' interpretation of the change to reclined and scandent orientation of the stipes—as a manoeuvre to remove the downward-directed sicula and proximal zooids from the "most damaging surface environment"—would have placed in precisely that dangerous situation the unsclerotized growing ends of the stipes, and the tip of the virgula through which Rickards imagines the vital extrathecal tissue to have been exuded. In my view, most graptoloids, like most other planktonic organisms, avoided the brightly illuminated surface waters altogether and quietly ate their way through the rich broth a few metres down, safe from the vagaries of wind and waves.

I am also unable to find any consistency in Rickards' discussion of 'currents'. In some cases (Rickards 1975: 426—428) these seem to be unidentifiable providential food-carrying currents acting on the "efficient hydrodynamic shape" of stipe cross-section and virgella in *Monograptus* (op. cit.: figs. 70,71), though why these currents did not carry along the rhabdosomes bodily is not explained. In other cases (p. 413) his zooids seem to be generating the currents themselves as I would like mine to have done. But Rickards (Discussion of Kirk 1969) objected to such activity in mine, stating that in many Silurian graptolites the zooids had almost no access to the exterior, and in Hutt *et al.*, (1970: 10) he states that in *Monograptus cf. barrandei* "access to the exterior must have been quite difficult for the zooids". Personally

¹⁾ In some cases the foundered rhabdosomes seem to have become aligned by bottom currents, some taxa dragging at the proximal end, others at the distal end as figured by Rickards (1975: fig. 57).

I do not think that the protectively overhung and restricted apertures would have presented any problems of egress or withdrawal to the highly mobile and extensible lophophore structure as exemplified in a number of living phyla. But Rickards and Crowther now explain cortical tissue as the result of painting by zooids connected only by stolons and which could emerge bodily through those tiny openings and roam over the surface of the rhabdosome. I find these contradictory ideas very difficult to understand.

Adaptation to near immobility in the deeper layers of the photic zone was probably responsible for the radiating colonies of *Linograptus posthumus* and the branching colonies of *Abiesgraptus*. The virgellarium in the former possibly served as a buoyancy device to keep the heavily reinforced sicular aperture uppermost.

A rather different kind of evolution, from a mobile spiral ancestor, may have resulted in the almost immobile colonies of *Rastrites*. The widely spaced, threadlike thecae increased the frictional resistance to sinking and at the same time enabled the zooids to make the best use of the thinly spread food available at depth.

But the adoption of near-immobility in suspension by both biserial and uniserial graptoloids seems to have been relatively rare, perhaps because the food paucity of the deeper layers resulted in widely spaced colonies — leading to difficulties of cross fertilization between the gametes they liberated.

A totally different kind of immobility may have been attained by certain graptoloids. Thus the Corynoididae may not have become detached after larval fixation. While the prosicula is normal in shape and size, the abnormally long metasicula and adnate thecae could have been an adaptation to prolonged sessility on the sea floor. The small curved theca at the proximal end could have housed a cleaning individual responsible for protecting the attachment by the short nema as in certain dendroids — *Dictyonema cavernosum* and *Rhipidodendrum*.

The giant rhabdosomes found among the monograptids lead one to wonder if these also remained attached by the virgula at the distal end. It might be interesting to examine their prosiculae for signs of the breakage or resorption that normally accompanied detachment.

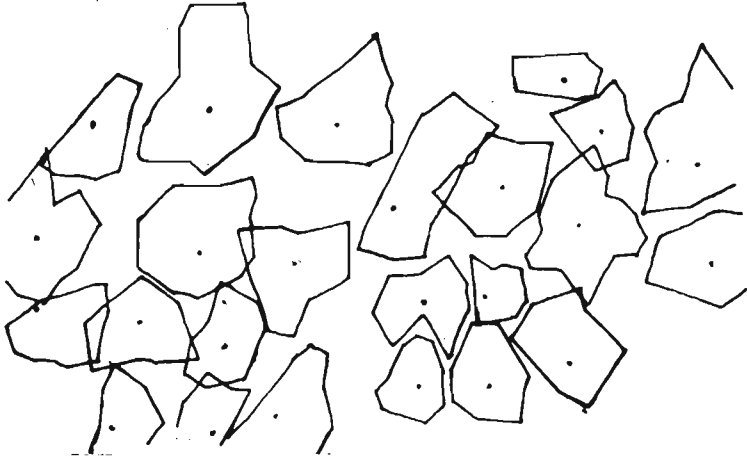
The synrhabdosomes found among both biserial and uniserial graptoloids seem to have been colonies of colonies. Dr. Bates' outline of the actual rhabdosomes composing the synrhabdosomes in Ruedemann's

Fig. 1. *Lasiograptus eucharis*. A natural group suggesting attachment of species bottom. Dolgeville Shale, Dolgeville, N.Y. (redrawn from Ruedemann 1947 and reproduced in Kirk (1969) and here with Ruedemann's caption); B the rhabdosomes of the synrhabdosomes in A have been outlined. The degree of overlap is seen to be very small in spite of flattening during fossilization; C the same synrhabdosomes as in A & B have been enclosed in circles of radius the longest rhabdosome in each colony association. This gives the impression of considerable overlap (reproduced from Rickards 1975: fig. 43).

A



B



C

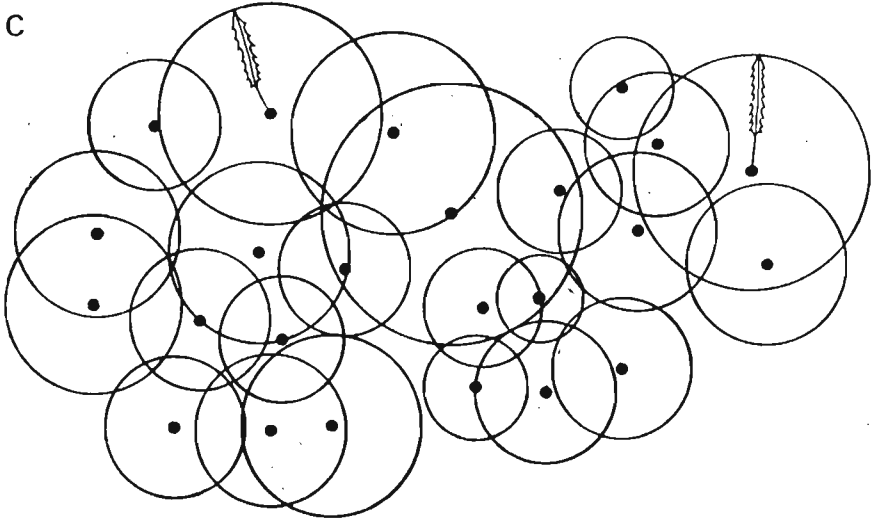


illustration (1947: pl. 81: 33) shows that even after flattening, there was virtually no overlap of the various colonies (fig. 1). The rhabdosomes seem rather to have fitted between one another, like a mosaic of leaves in a tree canopy. This would seem to suggest that the synrhabdosomes are in situ, having grown side-by-side on the sea floor, the more advanced rhabdosomes retarding the growth of the less advanced and so leading to the development of an interlocking mosaic. This seems to be consistent with Ruedemann's description of the Dolgeville shales as containing a mixed graptolitic and shelly fauna.

However, it is not absolutely impossible that dead synrhabdosomes could have occasionally settled on the sea floor in this orderly manner. The argument against their having been passively floating when alive is the same as the one applying to rhabdosomes: they would have starved when the food in the surrounding water became exhausted. But synrhabdosomes could have been automobile as a reaction to their feeding currents if the ciliary action of their constituent colonies had been coordinated. The rhabdosomes appear to be joined at the centre of a synrhabdosome by a tangle of threads. I cannot believe that this is a mass of tangled nemata as Rickards suggests (1975: 416), because on the previous page he describes the nema as a hard hollow rod. Nemata were undoubtedly resilient and, in my view, unlikely to have become entangled. I am inclined to favour Kozłowski's hypothesis, that the tangle of threads might be stolonal, which would imply an organic connection between the rhabdosomes in addition to that afforded by the mantle of extrathecal tissue collectively covering them. Coordination of the ciliary action between the constituent rhabdosomes would then present no greater problem than coordination between thecae. In this connection it is interesting to record that superficially similar radiating colonies of individuals joined by a tangle of threads are formed by the rotifer *Conochilus* (Hyman 1951; Buchsbaum 1938), and these colonies are described as having swum through the water as revolving spheres in response to their coordinated ciliary feeding currents. What is possible for the colonies of *Conochilus* should have been possible for the supercolonies of the graptoloids.

But evolution towards immobility in suspension, or perhaps towards a return to sessility on the sea floor, were only rare divergences from the main trend of graptoloid adaptation to life in the plankton. The main trend in the graptoloids, first in the branched dichograptids, then in the biserial and finally in the uniserial forms, has been towards smaller, simpler and somewhat more mobile colonies. This follows naturally enough if one accepts that coloniality, in the first place, had been an adaptation to a sessile habit on the sea floor. In that environment there was a distinct advance in the creation of large colonies by delaying the onset of sexuality.

In the plankton, on the other hand, except among the large colonies

which may have become secondarily almost immobile in the deeper, foodpoor layers of the sea, coloniality seems to have served no useful purpose at all, and was perhaps merely an inconvenient inheritance from the benthonic past. The repeated evolution in the direction of colonial smallness and simplicity perhaps records repeated 'attempts' at the elimination of coloniality.

Reduction in the size and complexity of the colony would have resulted in distinct advantages in the plankton. There would have been a better change of survival in the more turbulent, food-rich upper layers, and more colonies could have coexisted there without danger of entanglement on their feeding rides. With a shortened colonial existence resulting from accelerated attainment of sexual maturity, more colonies would have reached that stage before being destroyed by predation, and the chance of cross-fertilization between the colonies would have increased. The larvae would have had a better chance of settling on the floors of suitable shallow seas, and with the shortening of the life-cycle, the opportunities for mutation and evolution would have increased also.

If the evolution of the graptoloids has generally been towards reduction or even elimination of the colony, there seems little real basis for comparison with the physonectid siphonophores. These are relatively fast-moving macrofeeders whose ability to capture large prey and to avoid predation increased with the size of the colony. The graptoloids, in my view, moved only as a reaction to their coordinated ciliary micro-feeding, and I think it extremely doubtful if even the most stream-lined uniserial or biserial colonies could have directed their movements to avoid predation or to "swim away from environmentally uninhabitable water masses such as those of cold or toxic water" as suggested by Berry in his contribution to this Conference.

I doubt also if the budding from the enormously long physonectid oozoid could be compared with the sympodial budding of the graptoloids, and of course, in my opinion, an upward-opening sicula is an essential factor in a coherent theory of automobility on which graptoloid evolution might be explained. With this proviso, the verticality of the siphonophore and monograptid colonies could, I suppose, be compared.

At the time of the disappearance of the graptoloids from the fossil record in the Devonian, uniserial colonies had been reduced to rhabdosomes carrying only 20 or 30 zooids. If the tendency towards smallness had continued to the point where no blastozooids at all were budded, and the siculozoid became sexually mature, graptoloids represented only by siculozoids could have continued to inhabit the plankton. The sessile stage in development could have been omitted. With the elimination of the blastozooids as well, and with them the stress resulting from coordinated ciliary activity, even the secretion of a minimal sclerotized framework would have become superfluous.

So, by the time suitable conditions for graptolite preservation returned to those areas where they have last been found, the graptoloids may have been not extinct, but in the form of naked individuals no longer preserv-

able as fossils. Graptoloids may have continued to inhabit the plankton for much longer than is generally supposed. They could still be with us. The plankton is that relatively unchanging reservoir of food in which animals seem not normally to become extinct. But how could we recognise the graptoloid siculozoid without its uniquely constructed periderm?

The naked siculozoid would probably have been a coelomate animal between 1 and 10 mm in size. The conical form characteristic of the graptolite sicula have been an adaptation to sessility, and need not have been retained after the return to the plankton. The U-shape of the gut could in its turn have been an adjustment to the conical form, so that need not have been retained either. The 2 branched lophophore may have evolved to accommodate budding, and could have been replaced by a circular, spiral or lobed lophophore after the loss of coloniality.

So our new graptoloid would have been a very anonymous creature. Only somewhere among its chromosomes there would have been hidden a gene or a genius for the construction of unique collageneous architecture, now wholly obsolete. Such an animal would be very difficult for a zoologist, let alone a palaeontologist to recognise, but I doubt if we are justified in explaining away our difficulties by assuming that the graptoloids became extinct. There is also a possibility that the graptoloids vanished into the plankton more than once. In *Gothograptus nassa* the sclerotized sicular periderm had been reduced to a network — which might imply that the siculozoid metamorphosed in the plankton. In *Holoretiolites* the sclerotization of the sicula and thecae was even more reduced — to a sparse network of lists, and in *H. simplex* only 6 zooids were budded. Are we justified in supposing that these late-surviving and presumably highly successful biserial graptoloids then became extinct? If the siculozoid in *Holoretiolites* had become sexually mature the budding of the last six blastozooids could have been omitted altogether and the sclerotized framework could have disappeared. But the holoretiolite stock need not have become extinct.

Then if we go back to the branched graptoloids, we recall the progressive reduction which occurred there, leading ultimately to *Azygograptus*. Were these the graptoloids' earliest attempts to shed their coloniality? Did they also succeed in returning to invisible individuality in the plankton? ²⁾

²⁾ It was suggested by Professor Urbanek at this Conference, that graptoloids could have lost their coloniality as the result of a single mutation causing failure to bud, and that this would have been a simpler and more probable manner of attaining individuality than by the gradual reduction of coloniality which I had inferred from the broad evolutionary succession.

I do not dispute that such mutations could have occurred — many times — but they would have left no trace on the fossil record, except perhaps a diminution in the abundance of colonial forms competing with them. Also they would only have resulted in the establishment of a race of graptoloid individuals if the mutant siculozoids had been able to produce gametes.

Since the characteristic graptoloid periderm is likely to have been lost by any non-colonial descendants of the graptoloids, the search for those descendants inevitably involves the problem of graptolite affinities.

This problem was first discussed in detail by Kozłowski (1949) on the basis of his remarkable collection of isolated material from the Tremadoc of Poland. His conclusion, that the graptolites were fairly closely related to the Pterobranchia, was disputed by Bohlin in 1950 who favoured affinity with the Coelenterata. In 1972 I attempted to reconstruct the graptolite zooid by reference to the microstructure as then described, and in 1974a, on the basis of Kozłowski's descriptions and illustrations⁹⁾, I proposed that the Graptolithina fell naturally into two subdivisions. One included the sympodially budding, periderm-secreting crustoids, dendroids and graptoloids, the other the monopodially budding, coenoeicum — mortaring tuboids, camaroids and stolonoids which appeared to have closer similarity to the pterobranchs. These two broad subdivisions seemed quite distinct in spite of many similarities which could be attributed to convergent adaptation to a similar mode of life, but I suggested that they might still have been related by evolution from an ancestor not too remote to account for the unusual characteristics they had in common: the incremental mode of thecal extension, and budding from a black stolon. It was, of course, the unique association of these two peculiar characters which had led Kozłowski to include all the six orders within the Graptolithina, and which seemed to relate them most closely to the Pterobranchia as well as set them apart from the rest of the animal kingdom.

The suggested evolution from a common ancestor involved the extension of the secretory area in the crustoids, dendroids and graptoloids to the whole surface of the zooid and to the lining of the evaginated extrathecal tissue, and its localisation in the Pterobranchia, and perhaps also in the tuboids, camaroids and stolonoids, within a mobile preoral lobe. Whether such an evolutionary divergence is possible I do not know; I made the suggestion in the hope that it might be discussed by zoologists, rather than because I had any very strong belief in it myself. Perhaps also because I hoped that Kozłowski might still have been right in his close grouping of the six orders whose similarities and differences he had so admirably recorded.

The ultrastructural studies of the periderm of the crustoids, dendroids and graptoloids (Urbanek and Rickards 1974; Urbanek and Towe 1974 and

Gradual reduction of the colony implies increasingly early onset of sexuality, so that the coincidence of a cessation of budding with the attainment of sexuality by the siculozoid is perhaps more probable as a result of the method suggested by the evolutionary succession. This again could have happened many times without leaving any positive trace on the fossil record.

⁹⁾ The extreme accuracy of these illustrations made it possible to use them almost as if they had been the actual specimens. Dr. Bates and I would like to take this opportunity of thanking Prof. Urbanek who allowed us to examine Kozłowski's collection during our visit to Warsaw.

1975) confirmed the essential correctness of the zooidal structure and the relationship between extrathecal tissue and thecal construction which I had suggested in 1972, and Urbanek's description of the ultrastructure of the Pterobranchiates (1976) was in accord with the fundamentally different mortaring-mode of coenocidium construction to which Bohlin and I had tried to direct attention. However, Urbanek (1976: 28) does not seem to have appreciated my efforts (1972: 1—19; 1974a: 1—20) to draw the attention of palaeontologists to the "important differences which occur in the fusellar microstructure of rhabdopleuroid pterobranchs and graptolites" and attributes my supposed neglect to "an erroneous feeling that within closely related taxa 'striking differences of skeletal composition can also occur' (Kirk 1974a: 4)". However, a fuller and more adequate quotation from my p. 4 reads "I shall therefore pay particular attention to the fusellar structures (and their relationship to cortical layers), and to the style of budding. The scleroproteic composition of the periderm will not be discussed since such composition is not only of widespread occurrence among diverse phyla of the animal kingdom, but striking differences of skeletal composition can also occur within closely related taxa". Scleroproteic composition, of course, refers to chemical composition. Bulman (1970: V21) had emphasized the fact that the presence of serine, alanine, glycine etc., indicated a scleroproteic composition analogous to that of the cephalodiscid coenocidium and implied a close relationship to the pterobranchs, an argument that I found unconvincing for the reasons stated in the quotation above. Scleroproteic composition could not possibly refer to the skeletal structure of the graptolithina (the subject matter of my two publications) since this appears to be unique and is certainly not of "widespread occurrence among diverse phyla" etc.

Upon my suggestion that the contrasted modes of thecal construction might have evolved from a common ancestor by divergent modification of the secretory area (Kirk 1974a: 23, and pl. 2), Urbanek comments that by similar "radical transformations of the soft body and skeleton, one could derive the graptolites as easily from the Coelenterata or the Bryozoa". But could one? Is there anything in the Bryozoa to compare with the alternating secretion of fuselli in the graptolites, or anything in the Coelenterata to compare with the black stolon?

Urbanek seems not to attach as much importance to stolons as he previously did (Urbanek 1973: 441—514). He states (Urbanek 1976: 29) that "both morphogenetic role and relation of peridermal sheath of stolon to the thecal walls, are quite different in dendroid graptolites and pterobranchs" "These fundamental differences diminish considerably the morphological significance between internally placed 'black stolons' of Pterobranchia and Graptolithina. In spite of the above similarities they could hardly be considered homologous". But surely the critical difference in the relationship of stolonial sheath to thecal walls is due

to the fundamental difference in the nature of the thecal walls — a secreted skeleton in the dendroids and a mortared coenocium in the pterobranchs. The relation of these to the stolonal sheath was bound to be different, but this need not affect the possible validity of the homology of the stolons at all.

Because stolons and thecal walls were probably associated with different layers of the soft body, their relationships are more difficult to visualize and more open to alternative possibilities. This is why I omitted any detailed consideration of the stolons from my 1972 model of the graptolite zooid, leading, as Urbanek says (1976: 27) "to a more serious limitation to the value of the model suggested". Even with the sections of stolons provided by Urbanek and Towe in 1974, a reconstruction involving them must still be very tentative, and I offer one mainly with the idea of directing attention to particular problems and to the kind of investigation which might lead to their solution.

If daughter graptolite zooids became invested with extrathecal tissue (mantle) as they became separated by constriction from the aperture of the immature parent (Kirk 1975), previous to this they would have had no mantle 'arm-pit' in which arch-shaped increments could have been secreted. The 'internal tubes' recognised in dendroids proximal to their emergence from the parental theca, should therefore have had a different construction.

In the case of the internal bithecal tube and "the transparent-walled basal portion of the autotheca" (Bulman 1944—47: 15), the stolons appear to pass abruptly into the tubes which might be considered their prolongations. It seems likely that the crassal fabric of the stolons (Urbanek and Towe 1974: pls. 27—30) was secreted in laminae by living tissue within the narrowing lumen. This would account for the protuberances into the stolonal cavity seen in pl. 29 (op. cit.). It would also have allowed 'mesenchymal' cells within the autothecal zooid to secrete supporting fibrous material extending from the outside of the stolon to the inside of the incremental thecal wall.

The internal bithecal tube and transparent basal wall of the autotheca could also have been constructed of crassal fabric secreted from the inside. This would have made it possible for them, at their contact with the surrounding incremental autothecal wall, to fuse with the cortical lining similarly secreted from the inside by the epithelium covering the autothecal zooid.

In the case of the daughter autotheca, ('stolotheca' of previous authors)⁴ the problem is slightly different since the stolon extends into

⁴ I assume that since the idea of close analogy with *Rhabdopleura* has at last been abandoned, the unnecessary confusion occasioned by the practice of distinguishing the proximal part of an autotheca as a "stolotheca" can henceforth be avoided (see Kirk 1969 and 1972 b).

the internal tube which appears to arise from it "like the casing of a Liebig condenser" (Bulman 1944—47: 15). However, from the young growth stages figured by Kozłowski (1949: figs. 1D, 22B and 33A), it would seem that the internal tube of the daughter autotheca at first arose from the apex of the stolon as in the cases described above, and that the extension of the stolon into the internal tube occurred somewhat later.

The prolongation of the parent autothecal stolon beyond the node was not delayed in this way, and possibly preceded the development of the two daughter stolon buds. It almost certainly occurred slightly later than secretion of the parent autothecal wall which would have protected it, and after its expansion to form the "transparent-walled, basal portion" it could have fused with the lining of that incremental wall.

The internal tubes of bitheca and daughter autotheca appear to have occupied much of the parent autothecal cavity, fusing with the lining of its incremental wall. The "transparent walled, basal portion" of the autotheca is developed above the point of emergence of the daughter tubes, and could have formed a base to the 'visceral cavity' of the parent where the stolon tissue might have contributed to the zooid's internal construction.

The internal tube of the first theca arising from the base of the prosicula (Kozłowski 1949; pl. 3: 6, 7; fig 1) may have developed from stolon tissue situated there. The stolon within this tube again seems to have developed somewhat later, possibly as an extension from the stolon material at its base.

The tubular nema-prosiculae (cauda) and nema of *Clonograptus tenellus* (Hutt 1974) are considered (Kirk 1975) to have been a kind of elongated tubular holdfast. In *Dendrograptus* (Kozłowski 1949: fig. 1) the stolon is attached to the base of the prosicula, i.e. to the floor of the holdfast. Can one, therefore, logically assume that the nema-prosiculae in *C. tenellus* also contained a stolon? If so, the narrowing of the lumen of the nemal tube could have been the result of deposition, from the inside, of crassal fabric upon the lining of the incremental wall.

With the evolution of a solid nema with a core of fusellar fabric, as in *Didymograptus* (Urbánek and Towe 1975: pls 2, 3), it would appear that the stolon must have been excluded from the nema, and have become based instead upon the floor ("diaphragm") of the conus. In synrhabdosomes however, if Kozłowski was correct in supposing them to be the result of budding from stolons, the nemata might again have been hollow, containing stolon material which secreted a lining of crassal fabric from the inside.

While the black stolon in the Pterobranchia was probably thickened in a similar manner by secretion from living tissue within its diminishing lumen, the stolon itself could have evolved quite independently in

the pterobranchs and the dendroids as an essential prerequisite for budding in complex coelomate animals.

In the same way it is quite conceivable that the growth of thecae and coenoecia by a series of increments sometimes meeting in zigzag sutures could also have evolved independently in the two subdivisions, perhaps as an adaptation to feeding by a two-branched lophophore. It may be significant that the bithecae, which perhaps housed zooids equipped instead with a cleaning 'tentacle', have irregular increments without zigzag sutures in both dendroids and tuboids, while their autothecae have comparatively regular increments meeting in dorsal and ventral zigzag sutures. Nevertheless, in spite of these possibilities of convergence, the fact remains that two very unusual features are associated in the dendroids on the one hand and the pterobranchs, tuboids and camaroids on the other. It should not therefore have been so unexpected by Urbanek⁵⁾ that, in addition to enumerating the critical differences between the sympodial secreting and monopodial mortaring groups, I should also have considered the possibility of a common ancestry not too remote to account for the unusual features they share.

A very cursory examination of Kozłowski's collection has reinforced my belief that the tuboids and camaroids may have mortared their coenoecia. Such forms as *Idiotubus crassus* (Kozłowski 1949: pl. 4: 3, and pl. 14: 9, 10), *Conitubus siculoides* (op. cit.: pl. 15: 9) and *Calycotubus* (op. cit.: pl. 18: 1—6) are very reminiscent of rhabdopleurids. Also the section of *I. crassus* (op. cit.: pl. 4: 3b) shows a quite remarkable resemblance to the section of *Rhabdopleura* (Urbanek 1976: fig. 1A). It is, of course, conceivable that the above taxa are rhabdopleurids which have been included with the tuboids on the basis of their general similarity.

A critical examination, by electron microscope, of the camaroids and tuboids should go a long way towards solving the problem of their affinities with the dendroids on the one hand and with the pterobranchs on the other. In the meantime their general variability of form and size suggests freedom from the genetic control under which the dendroid and graptoloid rhabdosomes were secreted, and a more casual construction — perhaps by mortaring. Another factor of significance may be the striking difference in height of the prosicula, very constant around 0.6 mm in dendroids and graptoloids, only 0.2 mm in tuboids. Whether this reflects a fundamental difference in the larvae or merely the difference in shape is uncertain.

⁵⁾ Urbanek (1976: 28) also finds "a difficulty" in my reasoning. I suggested that the left and right growth of the zooid in dendroids and the left and right growth of the zooidal stalk in rhabdopleurids could have resulted in the secretion of semiannular fuselli in the former and the mortaring of semiannular increments in the latter. Urbanek has reversed my argument and therefore finds it unclear why "such different secretory organs should operate by different mechanisms to maintain the intermittent left and right advance of the ancestral zooid". But I never made such a suggestion.

With the possibility that the graptoloids returned to individuality in the Devonian, and the consequent uncertainty concerning their extinction, the problem of graptolite affinity with living animals takes on a new interest. While supposed affinity with *Rhabdopleura* was undoubtedly responsible for much misunderstanding about the structure of the graptolite zooid and the construction of the rhabdosome, it may still prove to be a living relative of that, in many ways, quite incomparable group.

Another possible relationship, suggested by the resemblance between *Conochilus* colonies and synrhabdosomes, is between the graptolites and the living rotifers. These animals have the kind of 'simple' body structure that one might expect of graptolites, and the absence of an extrathecal mantle and stolon system could be the result of the loss of coloniality. While the rotifers exhibit a great range of adaptations to fresh water and terrestrial habitats, a remnant remains of what might once have been an important marine group. Perhaps the scleroprotein pellicles of rotifers would repay a passing glance. It was the rotifer's mode of feeding and swimming which first suggested to me the possibility of graptoloid automobility.

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DISCUSSION

D. Erdtmann:

Comment on benthic life mode of sicular stages of biserial graptolites, *Corynoides*, and synrhabdosomes:

How could the "benthic" attachment model of the above graptolite forms be reconciled with the apparent anaerobic environments in which these are found? This is particularly difficult to envision for the very fragile synrhabdosomes which usually occur in abiotic black shales!

Ph. Legrand:

Quand on laisse tomber dans l'eau une partie proximale libre de *Dictyonema* e.g. *flabelliforme* (chaque branche primaire presentant 2 ou 3 authothèques) elle vient de poser sur le fond de récipient par l'extrémité de ses branches, la sicula restant au dessus (ceci est encore plus vrais s'il y a de la roche dissoute telle une vase au fond du récipient). Du point de vue mécanique l'observation de la chute montre que la sicula reste toujours vers le haut et on peut penser que c'est dans cette position seulement que rhabdosome de *Dictyonema* e.g. *flabelliforme* pouvait flotter. L'hypothèse de Kirk de voir un descendant de *Dictyonema flabelliforme* flotter, sicula vers le bas, après que la nema ait cessé de la fixer au fond de la mer apparait mécaniquement difficile.

A. Urbanek:

We all know how much Dr Kirk's views helped to revitalize the entire topic of the mode of life of graptolites. But I would like to refer to some of her suggestions which are immediately concerned with her lecture:

Coloniality as an adaptation to the benthic habit—though perhaps not a specific adaptation as Dr Kirk suggests, but rather a much more universal type.

In this connection let me remind you the XIX century idea of distribution of functions (labour) between the zooids in a colony. This may be core of adaptive significance in colonial organization.

Bithecal zooids as cleaning individuals—some most extreme benthic forms like some camaroids lacked bithecae. Therefore I would say a more complex and different function should be ascribed to thecal trimorphism. The main function of bithecae should have been more independent from environmental control than cleaning is.

Orientation of graptoloid rhabdosome—I am not against the “reversal” of graptoloid orientation as suggested by Dr Kirk, but slightly sceptical whether this is equally reasonable in each case. I was one of the first to put *Linograptus* “upside down” after reconsidering its structure. May be not all planktonic graptolites deserve to be reversed as compared with classical (anatomical) position. We cannot be sure as to their life orientation unless the statics of each pattern of rhabdosome has been studied and models constructed.

Reduction of coloniality in graptoloids—if it is an adaptive advantage in reduction of coloniality in graptolites, the reduction to a single zooid should be easily attainable by suppression of budding. Budding is a rather simple morphogenetic process and one could imagine ample mutations always present in the gene pool and capable to obliterate the budding or more generally to control it.

So the history of graptoloids seen as a struggle with their colonial past, from *Azygograptus* to Lower Devonian monograptids does not seem realistic to me. Graptoloids could always give a rather quick response if reduction of colony was needed.
