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A CONTRIBUTION TOWARD UNDERSTANDING THE RELATIVE INTEGRATION OF GRAPTOLITE COLONIES

Abstract. — Transmission electron microscope investigation of ultrathin microtome-sections of graptoloid graptolite periderm forming nema and virgula walls in a didymograptid, an orthograptid, and monograptids indicates that these structures had certain similarities as well as differences in ultrastructure. Similarities include: An internal canal that is partly hollow and partly filled with loosely woven fibrous material, layered walls, layers in the walls formed of electron dense, homogenous sheet fabric bounding compact fabric formed of densely-packed fibrils, and holes or vesicles that perforate the compact fabric.

Two aspects of colony growth may be recognized among graptolites. One is extension of those tissues related to nema or virgula formation, and the other is zooidal budding. The two growth aspects appear to be little, if at all, related in didymograptids and other graptolites with a nema. They may or may not be related in orthograptids and other biserial scandent graptolites. Study of peridermal ultrastructure suggests that they may have been closely related in monograptids because the outer layers of the virgula wall develop into thecal wall growth increments.

Graptolite colonies, particularly uniserial graptolites, resemble physonectid siphonophores in certain gross morphological aspects as well as in having two similar aspects of colony growth. Physonectid colonies are highly integrated. Physonectids may provide a model for use in suggesting potential graptolite colony function and degree of colony integration. The close relationship between the two growth aspects in monograptids suggests that they could have been the most highly integrated graptolite colonies. Members of the colony may have acted together to generate efficient flow of water currents past the zooids for feeding and waste disposal. Perhaps, too, tissues related to virgula development were connected with buoyancy and mobility, by analogy with the functions of the physonectid nectosome. Inasmuch as uniserial graptolites essentially replaced biserials, and the biserials replaced many graptolites with a nema, these developmental steps may have been those leading toward increasingly greater degrees of colony integration. Ultrastructural studies thus may provide insights into not only colony function and integration, but also into graptolite evolutionary adaptive strategy.

INTRODUCTION

Examination of graptolite peridermal ultrastructure using electron, particularly transmission electron, microscopy not only has led to recognition of fundamental peridermal ultrastructural elements, but also it

has provided certain insights into graptolite phyletic relationships (Urbanek 1976). Potentially, graptolite colony function and colony integration may be addressed in the light of knowledge of graptolite peridermal ultrastructure.

Graptolite peridermal ultrastructural elements have been recognized as being fibers or fibrils woven compactly or loosely to form different types of fabrics (Urbanek and Towe 1974, 1975; Towe and Urbanek 1974; Berry and Takagi 1970, 1971, 1973; Berry 1974). Thin, membrane-like sheets or pellicles that are electron dense and homogeneous and mark surfaces of certain growth discontinuities have also been recognized (Urbanek and Towe 1974, 1975; Berry 1974).

Peridermal fabrics commonly appear to be porous and to have a spongy aspect, suggesting the possibility that the periderm could have been internal and not external to the soft tissues of the zooids or polyps (Berry 1974; Hutt 1974; Urbanek 1976). Long fibers have been observed in the outer parts of graptolite thecal and metasicular periderm (Berry and Takagi 1970, 1971, 1973; Berry 1974; Urbanek and Towe 1975; Urbanek 1976). The length, degree of overlap, and angle made by groups of these fibers in one peridermal layer with those in subjacent or superjacent layers (see Berry 1974:fig. 2) suggest that the fibers provided the periderm with a high degree of flexibility as well as strength.

Observations of peridermal ultrastructure may be considered in addition to those of colony form and a knowledge of the evolutionary development of colony form to suggest potential colony integration and colony function.

Although peridermal ultrastructure of certain dendroid as well as some graptoloid graptolites has been investigated, the designation "graptolite" herein and the organisms considered herein are members of the Order Graptoloidea. They appear, from both their biogeographic and biofacies distributions, to have been prominent zooplankton of the Ordovician, Silurian, and Early Devonian. Many of them seem to have lived in surface or nearsurface oceanic waters; others may have lived at modest depths within the oxygenated waters of Early Paleozoic oceans. Because graptolites were relatively large zooplankton, it is possible that different methods were employed by different taxa to maintain buoyancy and to control position within the oceanic water column. Bulman (1970:V93) discussed potential mechanisms, stating "in a wide range of biserial graptolites the distal prolongation of the virgula into a so-called "float" suggests that a truly planktonic mode of life was quite common." Bulman (1970:fig. 70) illustrated several different graptolites that had apparent "floats" or other structures possibly related to buoyancy of the colony. Bulman (l.c.) suggested that certain structures found in the proximal part of the rhabdosome as well as structures such as apparent "floats" found in the distal part of the rhabdosome could have been associated

with buoyancy. Bulman (*op. cit.*: V93) went on to indicate that inasmuch as the graptolite periderm may have been an internal skeletal feature, external tissues "may have played some part in the buoyancy of graptolite rhabdosomes, more plausibly, perhaps, through the occurrence of gas bubbles in this tissue than a development of fat bodies." Indeed, the porous aspect of the graptolite periderm revealed by studies of the ultrastructure indicates that tissues did ramify through the periderm. Such tissues could have formed and held air or gas bubbles at almost any position in the colony. The presence of relatively large vesicles near the borders of fabrics and their bounding membranes (Urbanek and Towe 1974, 1975; Berry 1974) suggests that these vesicles could have been loci of gas bubbles within the periderm.

The size of the graptolite colonies and some aspects of their structure indicate that comparisons of them with certain modern large zooplankton potentially could lead to speculations concerning possible colonial integration and function. It is the intent herein to draw attention to those studies of graptolite peridermal ultrastructure that may lead to an increased understanding of colony integration. These ultrastructure studies will be considered in the light of changes in the graptolite colony through time to suggest potential colonial function and certain adaptive strategies that graptolites may have followed.

Valentine (1973:257—263) discussed potential adaptive strategies that organismal populations could have followed in the course of their evolutionary development. Valentine (*l.c.*) stated that adaptive strategies are "the ways in which populations have adapted to patterns of environmental variation." He pointed out that "the term 'strategy' is not intended to suggest that populations plan ahead, but merely that natural selection adapts them to certain eventualities, such as seasonal environmental fluctuations." As Valentine (*op.cit.*) described, "patterns of environmental variation occur in both spatial and temporal dimensions." Some changes in graptolite colony form may have been the consequence of an adaptive "strategy" that was called into focus by changing conditions such as those of temperature or food resources, through time.

ASPECTS OF GRAPTOLITE PERIDERMAL ULTRASTRUCTURE

Graptolite colonies develop from an initial individual that was housed or enclosed in the sicula. Bulman (1970:V57) described graptolite colony development as follows: "The sicula gives rise laterally to a single initial bud from which ultimately the entire rhabdosome develops, and the apex of the sicula is prolonged as a slender thread known as the nema (or virgula in scandent forms)." Bulman, went on to point out that "the relation between direction of growth of the branches of the rhabdosome

and the nema has afforded a basis of subdivision among the Graptoloidea."
Bulman noted that "a general tendency in the history of the group"
had been "toward attainment of a scandent direction of growth." As
Bulman (op.cit.) described, a general trend in the evolutionary history
of the graptolites is from those graptolites in which a nema extends freely
above the sicula apex and the branches or stipes extend at some angle
from the lower part of the sicula to those graptolites in which two stipes
are arrayed in a scandent position and the virgula extends from the
sicula apex through the thecate part of the rhabdosome and freely above
it, to those graptolites that were scandent but uniserial in which the
virgula is enclosed within the dorsal wall of the periderm but extends
away from the thecate part of the rhabdosome. Among uniserial scandent
rhabdosomes, the single stipe may be curved or coiled. In a few of them,
cladia, which Bulman (op.cit:V58) described as "second- and higher-order
rhabdosomes," developed from modified thecae on the main rhabdosome
or from the sicula aperture.

As Bulman (op.cit.) noted, the nema and virgula have long been re-
cognized as significant parts of the graptolite rhabdosome, and their func-
tion appears to have been related to buoyancy of the colony. The possibil-
ity that the nema and virgula may have been associated with colony
buoyancy, which was, of course, important to the livelihood of the colony,
and that the change in position of the stipes in relation to the position of
the nema/virgula may have played a significant role in colony function
and integration.

Berry (1974) indicated some aspects of the ultrastructure of an ortho-
graptid virgula. Berry (op. cit.) and Urbanek and Towe (1975) described
the ultrastructure of monograptid virgulae, and Urbanek and Towe
(op.cit.) recorded the ultrastructure of a didymograptid nema. These
recorded observations as well as new observations of the orthograptid
studied by Berry (op.cit.), and Monograptus of the M. priodon type vir-
gulae form the basis for the descriptions and comparisons of virgulae
made below.

Ultrastructure of a didymograptid nema

Urbanek and Towe (1975) described the nema in a *Didymograptus* sp.
as being essentially a tubular structure that extends freely away from
the sicula apex. The nema has an internal canal that is about 15μ in
diameter and is filled with a "loose mat of delicate fibrils" (Urbanek and
Towe, 1975:4). The loose mat of fibrils in the center of the internal canal
passes without hiatus into the fibrils of the innermost layer of the nema
wall. Urbanek and Towe stated that "the wall of the nema is
a distinctly layered structure" and that "the layers are deposited con-

centrically and the majority of them are continuous around the circumference, with only a few tapering at places." Urbanek and Towe (*op.cit.*: 4—5) went on to point out that "each layer is delimited by sheets composed of densely reticulated material continuous with the ground substance between the cortical fibrils within the layer." Intrasheet vesicles are relatively common. Urbanek and Towe (*op.cit.*: 5) note that each intrasheet vesicle is "provided with its own pellicle." They emphasized the "distinct cortical appearance" of the fabric within each layer and noted that the major part of each layer is formed of "ordered and highly packed fibrils." Each layer of the nema wall is thus bounded by a thin sheet and is composed of relatively closely packed fibrils. These firbils may, as they do in passing from the innermost layer into the central internal canal, pass into relatively loosely woven sets of fibrils close to the join with the sheet bounding the next inner layer.

Virgulae in Orthograptus sp., (*O. quadrimucronatus type*)

Virgulae in specimens of *Orthograptus* sp. (of the *O. quadrimucronatus* type) examined are tubular structures which appear to have a narrow internal canal that is hollow for short distances separated by relatively longer intervals in which its center is filled with porous, spongy material. Examination of many transverse ultrathin microtome sections of the virgula indicates that the hollow and filled parts of the center may repeat along the length of the whole structure. The only difference between the hollow and filled parts of the virgula is in the presence of the loosely-woven fibrous material in the internal canal.

In all virgulae examined, the wall is a distinctly layered structure. Most layers are arranged concentrically around the entire structure. Some, however, extend only part-way around, tapering and pinching out against the next inner layer. The layers are separated by an electron dense, homogeneous sheet fabric. The greater part of most layers is formed of compact material that appears to be composed of tightly woven fibrils. The compact material is bounded by sheet fabric and is commonly provided with numerous elongate to subround holes. Most of these holes are markedly elongate and are situated close to the join of the compact material with sheet fabric. The compact material becomes notably less tightly woven near its contact with the sheet fabric of the next inner layer. In some layers, particularly those in the inner part of the virgula, most of the layer may be composed of loosely-woven fibrils. These layers have a distinctly spongy appearance. The layers are slightly wider in the inner part of the virgula than in the outer. The greater width of the inner layers appears to result from the presence there of loosely woven material in addition to compact material.

Virgulae in two monograptids

Urbanek and Towe (1975) examined ultrathin microtome sections of the nema/virgula in *Pristiograptus dubius*. They (*op.cit.*: 5) described the virgula as being "a thick-walled tubule" parts of which are "provided with a narrow internal canal" that is hollow and other portions of which have the central part "filled with a porous material." They noted that "examination of a number of transverse ultrathin microtome sections indicates that portions of the hollow and the filled nema may repeat along the thread." They (*op.cit.*: 6) pointed out that "the only difference between the hollow and filled nema is in the development of the loosely packed fibrous material of the internal canal.".

Urbanek and Towe (*op.cit.*) showed the *P. dubius* virgula to be distinctly layered, and they noted that "each layer seems to be composed of a rather compact material, provided with numerous irregular, sometimes angular, sometimes rounded, or elongated holes." They (*op. cit.*: 6) stated that "the concentration of these holes seems to increase toward the center and the layers surrounding the internal canal are thus porous." Each layer of the *P. dubius* virgula is bounded by "electron-dense and homogeneous sheet fabric".

Urbanek and Towe (*op.cit.*) described a relatively complex ultrastructure of the main fabric in each *P. dubius* virgula layer. Their study revealed the presence of two major components of the main fabric. One of the two includes "electron-lucent, rounded areas" that are "diffuse in outline", and the other is an "electron-dense material filling the spaces between the lucent areas and continuous with the sheet fabric separating particular layers" (*op.cit.*: 6). They suggested that the "whole assemblage of ultrastructual features recognized within the nema of *P. dubius*" be "regarded as virgula fabric."

Berry (1974) cited some features of the virgula wall ultrastructure in specimens of *Monograptus* of the *M. priodon* type. Those observations and others made since by examination of a number of ultrathin microtome sections cut both across and along the virgula reveal that the virgula wall is a tubular structure composed of a number of layers. Each layer is bounded by electron dense, homogeneous sheet fabric. Each layer is composed primarily of tightly woven fibrils that form a compact material. That compact material may have a few to many elongate to subrounded holes in it. The holes commonly are located near the boundary of the sheet fabric with the compact material. In some layers, the compact material passes into relatively loosely woven material near the join with the sheet fabric of the next inner layer. Most of the layers pass around the entire virgula. Some, however, go only part of the distance around, tapering to join the adjacent inner layer.

The virgulae in *Monograptus* of the *M. priodon* type specimens ex-

amined appear to have a hollow internal canal for most of their length, but parts of the central canal of the virgulae are filled with loosely-woven material that has a spongy appearance. The loosely-woven fibers of that spongy-appearing material appear to pass into the fibrils that form the compact material of the innermost layer of the virgula wall.

Several concentric layers about the internal canal form the major part of the virgula wall. Certain outer layers become elongate, however, and form a part of the thecal wall. The sheet fabric and compact material of these layers clearly form a border for a large amount of spongy-appearing material formed from loosely-woven fibrils. Berry (1974: pl. 8) illustrated the development of layers around the virgula and the expansion of the outermost layers into the thecal walls. Thecal walls are formed primarily of loosely-woven, spongy material bounded by a relatively thin border of compact material and sheet fabric. The peridermal ultrastructure of a theca appears to be made up of two or three essentially V-shaped "packets" (op.cit.) of spongy material bounded by compact material and sheet farbic. Interwoven, long fibers appear to be present on the outer side of thecal walls (op.cit.: fig. 2). Because the outer layers of the virgula wall appear to become a part of thecal walls, Berry suggested that development of the virgula wall in monograptids might be closely related to the development of thecal walls and that the peridermal growth increments could include a component that developed along the virgula and a component that developed as a part of a thecal wall. The suggested growth relationships are indicated diagrammatically in figure 1.

Comparison of the nema and virgula ultrastructure

The nema and virgulae studied in ultrathin microtome sections to ascertain peridermal ultrastructure are essentially hollow or partly hollow tubules. The internal canal may be partly filled with loosely-woven spongy-appearing material. The tubules have layered walls. The layers are bounded by sheet fabric and include a certain amount of compact material formed from tightly-woven fibrils. Numerous elongate to sub-rounded holes or vesicles are present in all virgulae and the nema examined. Although certain details of the ultrastructure differ from taxon to taxon, the general construction of the walls of the nema and virgulae and their interior canals are closely comparable. The layers of the virgula walls of the monograptids are more closely spaced and formed of more compact material than are the layers in the orthograptid virgula and the *Didymograptus* nema. The monograptid virgulae, therefore, appear to be more compact, relatively solid structures than do the virgulae in the orthograptid and didymograptid nema. The presence of more holes or vesicles and more loosely-woven material in the virgulae of the orthograptid and the didymograptid nema than in the monograptid virgulae
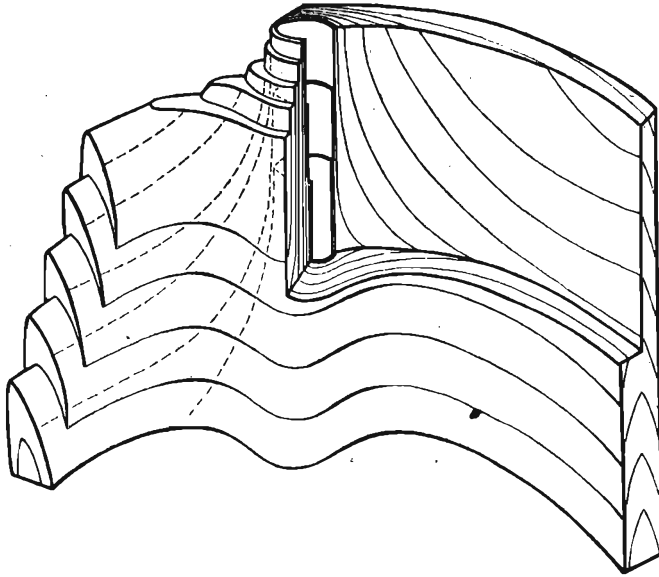
Fig. 1. Schematic diagram of dorsal part of thecal wall in a *Monograptus* of the *M. priodon* type indicating relationship between virgula wall layers (interpreted as virgula wall growth increments) and thecal peridermal layers (interpreted as thecal peridermal growth increments).

suggest that these structures were more porous and perhaps had more tissues ramifying through them than did the virgulae in monograptids. Examination of many ultrathin microtome sections of virgula wall periderm of the orthograptid and monograptid of the *M. priodon* type suggests that each layer has an elongate, tubular form and that the addition of each layer creates an extension of the virgula beyond the thecate part of the rhabdosome (see schematic diagram of fig. 1). Extension of the virgula wall in the monograptid appears to be closely related to development of thecal periderm. The relationship between extension of the virgula and thecal peridermal development in the orthograptid is uncertain. Among didymograptids, extension of the nema from the sicula apex may not have been related to thecal budding and thecal peridermal development because development of thecal periderm and thecal budding was taking place in a direction different from that of extension of the nema.

SUGGESTIONS CONCERNING THE NEMA AND VIRGULA

Urbanek and Towe (1975: 7) noted that the diameter of the internal canal in the *Didymograptus* sp. nema and the "fibrous loose nature" of the thin membrane or diaphragm that separates the apex of the prosicula from the nema in *Didymograptus* sp. "do not preclude the presence of a cord of soft tissues obtaining nourishment via the prosicula." Urbanek

and Towe pointed out that the diameter of the internal canal in the *P. dubius* virgula is so slight that the former presence of tissues in it "seems improbable." Urbanek and Towe suggested that the internal canal in the nema and virgula was most likely "primarily a structural space," and that "it probably served no special physiological function." They concluded that "the nema and virgula were most probably formed by soft tissues enveloping them from the outside, the deposition of each successive layer being external."

Berry (1974) implied that the spongy, porous aspect of the virgula wall periderm, the presence of many holes or vesicles in the virgula wall periderm, and the small diameter of its internal canal indicated that soft tissues probably enveloped and ramified through the virgula wall periderm. Berry (*op.cit.*: 139) speculated that "the possible hormonal substances suggested as controlling colony development by Urbanek (1960, 1963) could have been conducted" by tissues related to the virgula.

In the didymograptid, orthograptid, and monograptids, tissues may well have extended from the sicula along the nema or virgula. The function of those tissues is uncertain, but they may have played some role in maintenance of colony buoyancy or in orientation of the colony.

Of note in consideration of the development of soft tissues from the sicula is the recognition that not only did tissues apparently extend from the sicula apex away from the thecate part of the rhabdosome, but also that budding developed from the metasicula. Colony growth thus seems to have had two aspects. One was the extension of tissues from the prosicula to envelope the nema or virgula. The second was the development of zooidal budding. Bulman (1970: V72—V89) reviewed many potential budding patterns among graptolites.

As already noted, the aspects of colony growth may not have been related in the didymograptids. The two probably were not in other graptolites with a nema extending away from the main direction or directions of budding. The ultrastructural studies of the monograptid suggest, however, that a relationship between development of the virgula and of the thecae did exist in these graptolites.

A general trend in graptolite evolution was from the didymograptids and other graptolites with the nema extension apparently unrelated to the budding aspect of colony development to orthograptids and other biserial scandent graptolites in which some connection between these two growth aspects may have been possible, to the monograptids and other uniserial graptolites in which a relationship between the two aspects of colony growth does seem to have existed. That trend suggests that the probable close relationship between the two aspects of colony growth seen in uniserial graptolites may have had an adaptive significance. Indeed, the apparent evolutionary development toward a close relationship between the two aspects of colony development may have been an "adap-

tive strategy" (in the sense of Valentine 1973). The general evolutionary trend to the uniserial colony with close relationship between the two aspects of colony development may indicate that those tissues related to the virgula did have a significant function in the development of the colony.

SIPHONOPHORES: A POTENTIAL FUNCTIONAL ANALOGUE

Some modern zooplankton may be examined to ascertain if form and function in any of them might be used as a model with which to compare the graptolites and form a basis from which to speculate on the potential function or functions of the tissues related to the virgula. When modern, relatively large zooplankton are reviewed with the intent of ascertaining which of them might serve as a model useful in understanding graptolite colony function, consideration of the morphology of certain siphonophores may be appropriate. Siphonophores are a relatively diverse group of large zooplankton. They are colonial; the colonies include a number of different types of individuals. The colonies are, despite the diversity of types of individuals present, highly integrated. Some siphonophores float on or close to the ocean surface. Others swim and may be found at great depths. Certain siphonophores are a part of the "deep scattering layer" of the oceans, swimming upward from depth to near-surface waters in the evening and returning to the depths in the daylight hours. Siphonophores have left no fossil record, being composed of soft, fragile tissues that commonly are ripped apart shortly after death of the colony.

Totton (1965) summarized existing knowledge of the anatomy and organization of many siphonophores and commented upon siphonophore colony organization. He (op.cit.: 20) described the fully developed siphonophore colony as being "essentially an over-grown oozoid polyp that remains juvenile and asexual, but which carries round with it large numbers of other unseparated, asexual juvenile polyps (gastrozooids, palpons, bracts) as well as sexual adults (medusoid gonophores) and asexual adults (medusoid nectophores), all budded from the original and often much elongated oozoid, or from other juveniles." Totton went on to note that "the examination of the younger growth stages reveals three general patterns of organization, at first sight very complex, but in essence closely resembling each other in the very youngest stages." The three general organizational patterns form the basis for recognizing three main types of siphonophores. The three are the cystonectids, the physonectids, and the calycophorids. Of the three, the physonectids appear to bear certain general morphological similarities to graptolites.

Physonectids commonly are elongate colonies that may achieve lengths of up to 50 meters. A central tubular structure extends through the

colony. Different types of zooids bud from it. Although the central tubular structure extends the length of the colony, two distinct growing and budding zones may be identified. One of the two develops upwards and the other downward from a zone of minimal growth. The upward developing tubular structure is termed the nectosome. Globular, adult, asexual nectophores bud from the nectosome. The youngest nectophores are located along the uppermost part of the nectosome. The nectosome is terminated by a float sac. Nectophores function as aids in colony buoyancy and colony propulsion.

The other part of the physonectid colony is centered about the downward-developing, tubular siphosome. The original larval polyp is located at the downward terminus of the siphosome. Larval polyps that give rise to cormidial groups of polyps arise from the siphosome. Cormidial groups consist of gastrozooids, palpons (gastrozooids with simple tentacles that function as feelers and tasters), and gonophores with bracts (palpons modified by an enlarged mesoglea to have a buoyancy and protective function).

The siphosome and nectosome are hollow, elastic tubes that carry muscle and nerve fibers. Most members of the colony bud from either the siphosome or nectosome, and the hollow canal of each polyp is continuous into the hollow internal canal of the siphosome or nectosome. As Totton (1965) emphasized, the fully grown physonectid colony may be quite long, but the long axis is essentially a "larval nurse-carrier" that bears several different types of individuals, both asexual and sexual. The upper terminus of the colony is a float sac at the top of the necto-some. The lower end of the colony is the downward-facing original polyp, the oozoid.

Totton pointed out that, despite their high degree of polymorphism, physonectid colonies are highly integrated. He (op.cit.: 29) noted that although "various polyps and medusoids may move or feed independently, or groups of them may break away and lead a free existence, yet there is a co-ordination of the whole" colony. Totton drew attention to the physonectid *Athoryphia* which "can swim up to the surface by co-ordinated movement of its paddling bracts" as well as to other physonectids which "swim by co-ordinated movements of the series of necto-phores."

Although the many dissimilarities between physonectid siphonophores and graptolites preclude more than generalized comparisons, certain similarities may be identified, particularly among the uniserial scandent graptolites and the elongate physonectids. In both physonectids and graptolites the larval individual remains at the downward-directed end of the colony. Both graptolites and siphonophores have in common two aspects of growth: the budding of polyps and the extension of a tubular structure away from the oozoid. Clearly, in some graptolites (see Bulman,

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1970: fig. 70), the tubular virgula bears a float sac at its upper terminus. In comparison, physonectid siphonophores have a float sac at the upper terminus of the nectosome. Urbanek (1973) drew attention to the changes in thecal shape as well as proportions of length to width in thecae from proximal to distal parts of many different graptolite colonies. These thecal size and shape differences may be taken to suggest that zooids or polyps having different functions (perhaps in reproduction) were present in the colony. Graptolites may have been somewhat comparable with siphonophores in this character, although it appears that graptolite colonies could not have had as many different types of polyps as do siphonophores. If soft tissues enveloped the graptolite nema and virgula, then those tissues potentially could have had some relationship to buoyancy and even mobility of the colony, as the nectosome and nectophores do in physonectid siphonophores.

These relatively crude, generalized comparisons between physonectids and graptolites suggest the possibility that graptolite colonies may have functioned in a similar manner to physonectids. Perhaps the evolutionary change from graptolites with nema to the uniserial scandent forms in which a close relationship appears to have existed between extension of the virgula and development of thecal periderm is indicative of change toward more closely integrated colonies. Monograptids may have been relatively the most highly integrated graptolite colonies. If so, then the change in colony form seen in the evolutionary development of the graptolites suggests that increasing degrees of colonial integration in the course of graptolite evolution provided the more highly integrated colonies with an advantage in selection and that uniserial graptolites, with the most highly integrated colonies, could have carried on some functions similar to those of certain physonectids. If they could have performed similar functions to some physonectids, then certain graptolite polyps may have been able to act together to provide propulsion to escape predation or to migrate diurnally. Coordinated action among polyps could have resulted in water flow about the colony that promoted efficient feeding and waste disposal for the entire colony. If minute currents could be generated about the colony such that the currents passed feeding polyps and then flowed away from the colony with appropriate flow patterns to take away wastes, then the two vital operations of feeding and waste disposal could have been separated and yet efficiently conducted.

Coordinated polyp action also could have permitted those colony gyratory motions Bulman (1970) indicated might have taken place in some graptolite colonies. A certain degree of colony integration probably would have been a prerequisite to the concerted polyp action necessary to effect gyratory motion of the whole colony.

A relatively high degree of colony integration would have permitted an entire colony to react not only to predatory attack, but also to onset of unfavorable environmental conditions. Perhaps certain graptolite colonies could have moved efficiently enough to permit them to swim away from environmentally uninhabitable water masses, such as those of cold or toxic waters.

Ultrastructural studies thus suggest the possibility that a general trend (indeed, an "adaptive strategy") among graptolites was toward colonies in which a relatively high degree of colony integration was achieved. Ultrastructural studies of the graptolite periderm also suggest that the tissues related to the virgula could have had a significant role in colony integration, perhaps carrying not only muscle fibers and nerves, but also hormonal substances that controlled colony growth.

In conclusion, in view of the suggestion made herein that some graptolites may have functioned, at least in principle, in a manner analoguous to certain siphonophores, perhaps the following quotation from Mackie's (1963) discussion of the significance of siphonophores may not be altogether inappropriate, particularly in the light of Urbanek's (1976: 30) statement that graptolites may represent "a rather separate phylum among the Coelomates." If nothing else, this quotation should at least generate a degree of amusement among graptolite specialists. Mackie (1963: 336) commented: "No one would suggest that the siphonophores are 'higher animals', but they are the most complex coelenterates and the only ones to have explored fully the possibilities of colonialism. They have developed colonialism to the point where it has provided them with a means of escaping from the limitations of the diploblastic body-plan. The higher animals escaped these limitations by becoming triploblastic and using the new layer, the mesoderm, to form organs. The siphonophores have reached the organ grade of construction by a different method — that of converting whole individuals into organs. It is interesting to speculate that, had it not been for the invention of mesoderm in some remote, diploblastic era, the highest animals on earth might now be, if not the Siphonophora, something similar to them in principle."

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