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PART V, SECOND REVISION, CHAPTER 6: PALEOECOLOGY OF THE PTEROBRANCHIA (CEPHALODISCIDA AND GRAPTOLITHINA)

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INTRODUCTION

The Pterobranchia is a widely distributed group of marine colonial organisms with its acme in the early Paleozoic and a few surviving, extant members. The modern taxa are all benthic and live in waters ranging from shallow-coast to deep-marine environments. Consequently, they are of limited use for interpreting the ecology of the extinct planktic Graptoloidea. Nevertheless, the living pterobranchs provide us with important information on the soft-body anatomy of the Pterobranchia that is not available from fossil taxa. The comparison with the modern pterobranchs enables us to reconstruct graptolites as living entities and better understand their biology, including their feeding and tubarium secretion.

Most of the work on graptolite ecology has been directed towards the planktic faunas, and little is known about benthic graptolite ecology. This imbalance sources from a primary focus on the planktic taxa because of their exceptional biostratigraphic utility and the fact that benthic faunas are rarely found in their original environments. The following account is based largely on Cooper and others (2012).

LIFE MODE

The Pterobranchia can easily be differentiated into benthic (sessile) and planktic taxa, and interpretation of their lifestyles is based on this knowledge. Benthic taxa have an elongated dome as the initial part of the colony, as in *Rhabdopleura* or *Epigraptus* (Fig. 1.1–1.2) or a tubular sicula with a flat base for attachment, as in *Dendrograptus* and related taxa (Fig. 1.3,5). In encrusting taxa, the ventral parts of the tubarium adhere to the substrate, whereas the erect, bushy, or treelike colonies have a specialized structure—a holdfast of varied shape. However, the attachment mode is known from relatively few taxa. In erect-growing Graptolithina, the attachment structure may be rootlike or disc-shaped, but it is invariably a surface attachment feature (Fig. 1.4) and does not extend into the sediment as a root system. All nematophorous graptoloids can be interpreted as planktic (Bulman, 1970; Fortey & Cooper, 1986). They possess a free nema and do not show any indication of attachment (Fig. 1.6).

Since benthic graptolites are rarely found *in situ* with their attachment intact, the attachment mechanism is little understood. The erect *Mastigograptus* aff. *tenuiramosus* (Walcott, 1883) is known to have overgrown calcitic shells, as can be shown from the features of an attachment disc (Bates & Urbanek, 2002), which indicates the need for a solid surface for attachment. Also, the benthic *Rhabdotubus johanssoni* Bengtson & Urbanek, 1986, is often attached to shell, adhering to the phosphatic shells of the small brachiopods *Acrothele* and *Dictyonina*, and, more rarely, to trilobite fragments. Rarely, benthic encrusting taxa have been found *in situ* (e.g., Mitchell, Wilson, & St. John, 1993). Most examples of encrusting material

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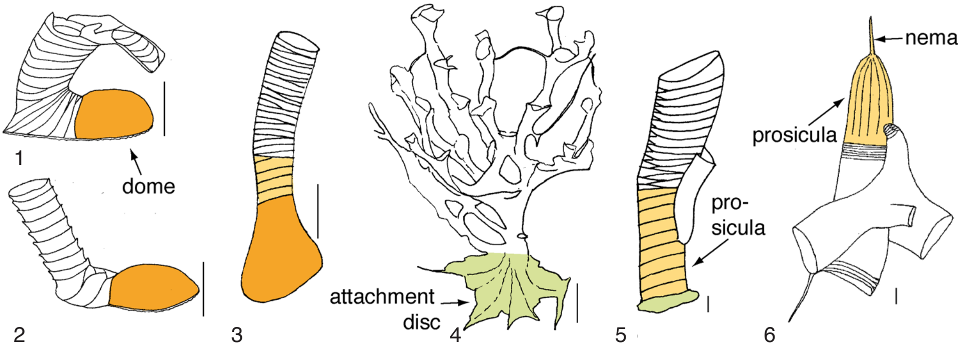

FIG. 1. Sicular development and attachment. *1, Epigraptus* sp. (adapted from Kozłowski, 1971, fig. 1); *2, Rhabdopleura compacta* (adapted from Stebbing, 1970, fig. 3); *3, Kozlowskitubus erraticus* (KOZŁOWSKI, 1963) (adapted from Kozłowski, 1971, fig. 5); *4, Dictyonema cavernosum* with attachment (adapted from Wiman, 1896, pl. 1, fig. 1); *5, Dendrograptus communis* KOZŁOWSKI, 1949, tubular prosicula (adapted from Kozłowski, 1949, fig. 1); *6, Xiphograptus* sp., showing prosicula with free nema (new). Scale bars, 0.1 mm in *1–3, 5–6;* 1 mm in *4*.

have been obtained from chemically isolated material (e.g., KOZŁOWSKI, 1949). ERDTMANN (1976) described dendroid faunas supposedly preserved *in situ* in the Mississinewa Shale of Huntington, Indiana, as occurring under low-oxygen, low-energy conditions within the photic zone (less than 60 m deep). Some of the specimens appear to be in growth position, but others clearly indicate at least minor transport because of their lateral orientation on the shale surfaces.

The Graptoloidea, as a planktic group of the Graptolithina, have long been recognized as an important component of the Paleozoic plankton (e.g., LAPWORTH in WALTHER, 1897; BULMAN, 1964, 1970; and many others). However, interpretation of the graptoloid habitat within the Paleozoic oceans has proved difficult, and a variety of habitat models have been proposed (see COOPER & others, 2012). Fundamental to all models is the observed distribution of graptoloids in a range of bio- and lithofacies representing all depositional depth zones, from shallow shelf (inshore) to open ocean. Evidence from morphology, inferred feeding mode, and facies preference suggests that graptoloids were able to control the depth at which they lived in the water column, either actively or passively by buoyancy adjustment (RIGBY & RICKARDS, 1989). In other respects, however, graptoloids were largely passive occupants of the water mass in which they lived, and drifted with the ocean currents, both seasonally and as part of the ocean circulatory system. Thus, new species were able to disperse widely and rapidly around the world and establish themselves in new regions.

LOCOMOTION

Benthic graptolites obviously were not actively moving, but their dispersal by means of planktic larvae in extant taxa (e.g., *Rhabdopleura*, *Cephalodiscus*) provides a mechanism for their wider geographical distribution. In graptoloids, tubarium structures such as spines, vesicles, or nematularia, and a disc-shaped or netlike colony form have been interpreted as hydrodynamic drag structures and evidence for a passive mode of life (RICKARDS, 1975; FINNEY, 1985; FINNEY & JACOBSON, 1985). However, ecological models for the planktic graptoloids now generally assume that they were able to move relative to the water mass in which they lived, particularly for feeding efficiency. Among the movement mechanisms suggested are turbulence, buoyancy control, and active swimming. Wind turbulence was no doubt significant for graptoloids living in the surface waters of the ocean (RICKARDS, 1975), but it is unlikely that all species lived in this zone.

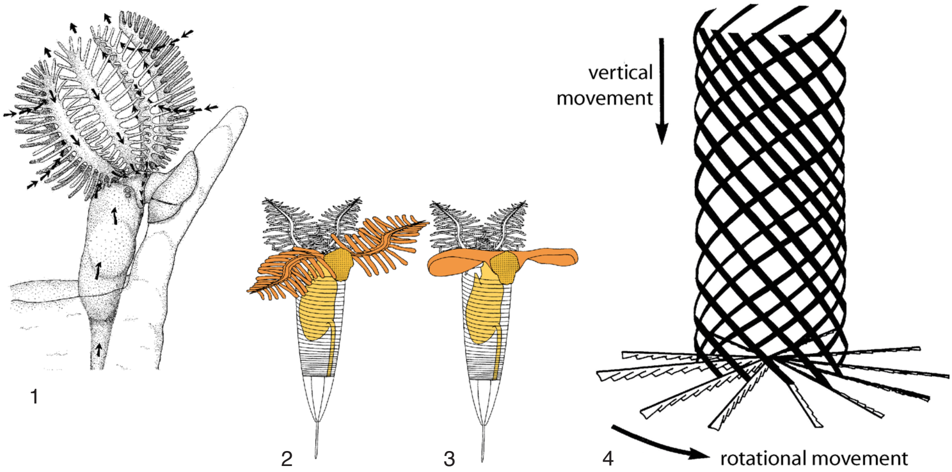

FIG. 2. Feeding and locomotion of graptolites. *1, Cephalodiscus* sp., *arrows* indicate movement of food particles along the arms of a cephalodiscid zooid (Lester, 1985, fig. 3); *2–3,* zooidal reconstruction of MELCHIN and DEMONT, showing enlarged arms (*2*) and possible wing-like muscular extensions of the cephalic shield (*3*) for locomotion (Melchin & Demont, 1995, p. 117, fig. 1); *4,* diagram showing rotational movement of multiramous colony (adapted from Rigby & Rickards, 1989, fig. 4).

Models of movement by buoyancy control through gas buildup require extrathecal soft tissue (BULMAN, 1964; RICKARDS, 1975; FINNEY, 1979), which is incompatible with the pterobranch zooid model (CROWTHER & RICKARDS, 1977). Automobility of the tubarium by ciliary propulsion was suggested by KIRK (1969, 1972a, 1972b) and BATES and KIRK (1985. BATES (1987) also suggested that the negative buoyancy of the tubarium could have been at least partly offset by low density fats within the fibrous fusellar tissue. MELCHIN and DEMONT (1995) suggested a new model of automobility of the colonies using putative winglike extensions of the cephalic shield for rowing (Fig. 2.2–2.3), as they considered passive buoyancy control unlikely due to the size, architecture, and phylogenetic history of the graptolites. RIGBY and RICKARDS (1989) and RIGBY (1991, 1992) modeled graptoloids in relation to rotation and feeding efficiency during passive sinking.

All considered, however, there are significant problems with all locomotory mechanisms proposed for the graptoloids (COOPER & others, 2012)**.** The topic remains one of the major questions in graptoloid ecology.

FEEDING

The example of the living pterobranchs can be used to infer the feeding mechanisms of fossil benthic graptolites. The extant *Cephalodiscus* and *Rhabdopleura* use their ciliated arms to extract food from the water column. The cilia on the tentacles move water into the center of the basket formed by the arms of the zooid (Fig. 2.1). Food particles are separated and collected in the median canal of each arm. The food is then transported into the mouth (LESTER, 1985).

While it is generally agreed that the zooids of fossil benthic graptolites fed by sampling water that passed through the colonies (as seen in extant taxa), just how the feeding mechanism might have worked is mostly conjecture. KIRK (1969, 1990, 1991) suggested that in conical forms, afferent flows entered through the central opening and efferent flows passed out through the mesh. This is in conflict with the observations of similarly organized organisms such as modern sponges and bryozoans. Modeling by MELCHIN and DOUCET (1996) showed that afferent flows through the sides and efferent flows through the top of the colonies was more likely. Different colonial morphologies may also be related to the paleoenvironmental conditions under which the graptolites lived (Rickards, Baillie, & Jago, 1990; Melchin & Doucet, 1996).

Modeling of planktic graptoloid colonies and water tank experiments (Rigby & Rickards, 1989; Rigby, 1991, 1992) suggested that flat, horizontal colonies as well as conical to umbrella-shaped colonies may have maintained a stable horizontal orientation in the water and were able to rotate during ascent and descent to improve water sampling and feeding efficiency (Fig. 2.4). Straight axonophorans are sometimes found on bedding planes with their long axes aligned; this is interpreted to indicate the direction of bottom currents (Moors, 1970; Rantell & Rigby, 2002). Modern analogs may help to infer details of the feeding strategies. Some filter-feeding euphausiids in the Humboldt Current of the eastern Pacific migrate from the surface to the oxygen-minimum zone at 300–400 m deep in the daytime to harvest microplankton and avoid predators (Antezana, 2009).

The fluid-dynamic models of Rigby and Tabor (2006) suggest that water flowed towards the thecal apertures in taxa with simple thecae; however, the complex development of the thecal apertures in many taxa and the development of the external lacinia and ancora sleeve in axonophorans suggest that this model has limited applicability.

PARASITES, EPIBIONTS, AND PREDATORS

Examples of parasites in modern pterobranchs are extremely rare despite the fact that records go back more than a hundred years. However, a few parasites have been found in the following extant species. Calman (1908) described the parasitic copepod *Zanclopus cephalodisci* (Figs. 3.1–3.5) from the stomach of *Cephalodiscus gilchristi* Ridewood, 1906. Calman (1908) referred *Z. cephalodisci* to the family Ascidicolidae (now Enterognathidae; Boxshall & Halsey, 2004; Ohtsuka, Kitazawa, & Boxshall, 2010, p. 689). Calman recognized *Enterognathus comatulae* Giesbrecht, 1900, a species infesting the echinoderm *Antedon*, as possibly the closest relative of *Zanclopus*. A second species of the genus *Zanclopus*, *Z. antarcticus* Gravier, 1912b, was found in the stomach of *Cephalodiscus anderssoni* Gravier, 1912a. Also, Ridewood and Fantham (1907) described the protozoan *Neurosporidium cephalidisci* from the nervous system of *Cephalodiscus nigrescens* Lankester, 1905, as a parasite.

Parasitism has been recognized in well-preserved, chemically isolated material of the fossil record of various benthic graptolite groups and in the graptoloids but is limited to instances in which it resulted in a response by the zooids to the parasite. The parasites themselves have not been preserved. For example, anomalous outgrowths formed from fusellar and cortical tissue are thought to indicate response to infestations by parasites (Kozłowski, 1970; Maletz, 1997). The best examples of these infestations include the tubothecae described by Kozłowski (1970) (Fig. 3.8), tubular growths from cortical material attached to the tubaria in a number of benthic graptolites (e.g., Wiman, 1901; Skevington, 1963; Urbanek & Mierzejwski, 1982). These tubes do not show any internal communication with the tubaria to which they are attached. Kozłowksi (1970) and Conway Morris (1981) concluded that tubothecae resulted from graptozooids secreting cortical tissue over the parasites (perhaps annelids) living on the graptolite colonies.

In describing possible parasitism in Graptoloidea, Bates and Loydell (2000) differentiated between open-ended tubes and closed blisters of various shapes (Fig. 4). The structures include mostly round or oval blisterlike protuberances (Jackson, 1971; Bates, 1994) on the obverse and reverse side of the colonies (Figs. 4.3–4.4,6). The most spectacular features are eight tubular outgrowths on a proximal end of *Geniculograptus typicalis* (Bates & Loydell, 2000) that might have considerably changed the hydrodynamic behavior of the colony, but

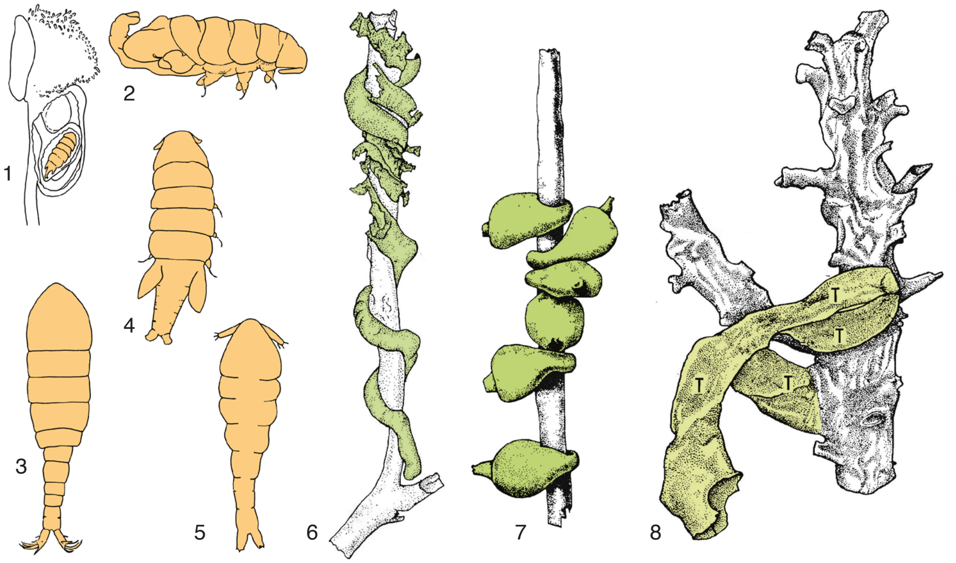

FIG. 3. Pterobranch epibionts and parasites: *1–5,* extant, *6–8,* Middle Ordovician, upper Darriwilian. *1, Cephalodiscus gilchristi* RIDEWOOD, 1906, showing the position of the parasite *Zanclopus gilchristi* CALMAN, 1908 in its stomach; *2–5, Z. gilchristi, 2, 4,* female in two views; *3,* male in 5th copepodid stage, appendages omitted; *5,* earliest known larval stage (*1–5* adapted from Calman, 1908, pl. 18–19); *6, Helicotubulus dextrogyra* (KOZŁOWSKI, 1967), holotype of fragment of *Mastigograptus* sp. (adapted from Kozłowski, 1967, fig. 7); *7, Clistrocystis graptolithophilius* KOZŁOWSKI, 1959 (adapted from Kozłowski, 1965, fig. 1); *8,* tubotheca (*T*) on *Acanthograptus* sp. (adapted from Kozłowski, 1970, fig. 5).

were apparently non-lethal (Fig. 4.1–4.2). Abnormalities in Silurian monograptids are extremely rare. URBANEK and TELLER (1974) and TELLER (1998, 1999) described a few unusual features in monograptids, but none of these are similar to the blisters and tubes found in Ordovician taxa.

Although called parasites, these outgrowths could alternatively be interpreted as indications of epibionts, organisms growing on the graptolite tubaria without harming the colony. Other possible epibionts include *Clistrocystis graptolithophilius* KOZŁOWSKI, 1959, an organic-walled microfossil, invariably attached to the stipes of *Mastigograptus* (Fig. 3.7). KOZŁOWSKI (1965) interpreted this fossil as possible eggs of cephalopods. Another enigmatic fossil is *Helicotubulus dextrogyra* (KOZŁOWSKI, 1967) (see MIERZEJEWSKI & KULICKI, 2003), originally referred to the Phoronida (Fig. 3.6). MARKHAM (1971, fig. 5) illustrated a number of possible folliculinid ciliates on an empty tube of the extant *Cephalodiscus* (*Orthoecus*) *densus* ANDERSON, 1907. Small phosphatic brachiopods have been found as epibionts (WANG & others, 2012) on the possible pterobranch *Malongitubus quangshanensis* HU, 2005, an erect, multibranched fossil identified as an alga in the past.

Graptoloids may represent primary consumers (UNDERWOOD, 1998) and have been placed close to the base of the Paleozoic food web. It is possible that they also formed an important food source for other marine organisms, but there is very little evidence of predation on graptolites (UNDERWOOD, 1993; LOYDELL, ZALASIEWICZ & CAVE, 1998). However, UNDERWOOD (1993)described possible fecal packages of Silurian monograptids and interpreted accumulations of biserial colonies as fecal accumulations, which could support predation. On the other hand, BATES and KIRK (1985) have suggested that the fusellum of the graptolites might have been too tough for ingestion and that the soft tissues might have been poisonous.

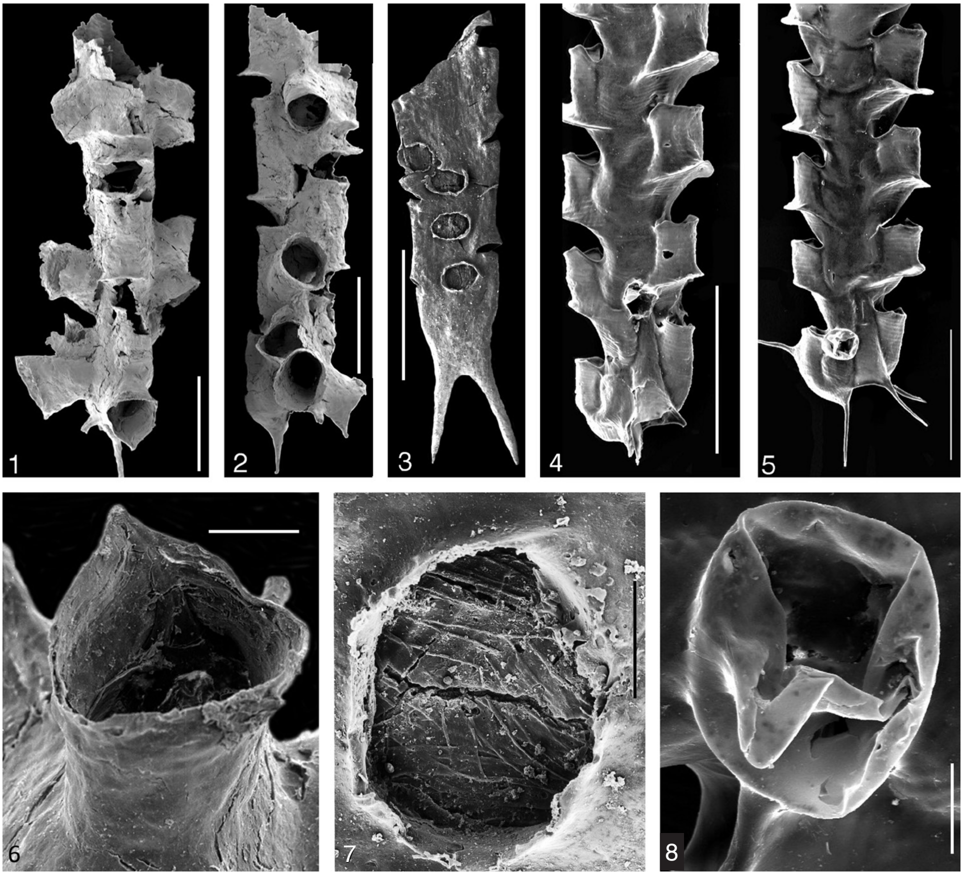

FIG. 4. Possible parasitic developments on Graptoloidea. *1–2, Geniculograptus typicalis* (HALL, 1865) specimen in different views (new, photos provided by David Loydell); *3, Diplacanthograptus spiniferus* (RUEDEMANN, 1912) (Bates, 1994, pl. 1); *4–5, Anticostia lata* (ELLES & WOOD, 1906), from type block of *Climacograptus inuiti* COX, 1933 (new); *6,* detail of *1; 7,* detail of *3; 8,* detail of *5*; scale bars, 1 mm in *1–5,* 0.1 mm in *6–8*.

LIFE HISTORY STRATEGIES

Graptolite colonies grew by the distal addition of new thecae. Controls on colony size in benthic graptolites are not clear, since most taxa are found only as fragmented remains and their original growth pattern and size cannot be reliably determined. Diverse benthic graptolite faunas indicate that colonies were able to reach dimensions of more than 50 cm in diameter containing thousands of zooids (BOUČEK, 1957; BULL, 1987). Modern *Rhabdopleura* colonies, on the other hand, are relatively small but still may contain dozens of zooids (see LANKESTER, 1884, pl. 37). Growth and final size appears to be restricted mainly by their ecology.

In multiramous planktic graptolites, colonies grew by the distal addition of thecae simultaneously to all stipes in the colony; their maximum size appears to be unconstrained by their colony design, with some colonies reaching a meter in diameter (see PRITCHARD, 1892). Some Silurian monograptids also reached a considerable length (LOYDELL & LOVERIDGE, 2001). In a few axonophoran species, maximum length appears to have been constrained by the development of an appendix (as in the Retiolitidae) or by the presence of distal vanes (nematularia) at the extremity of the nema, which usually were not overgrown by the developing stipes (e.g., *Archiclimacograptus decoratus*). In many graptolites, there were no obvious constraints on stipe development, yet colonies never exceeded a few cm in length or, in extreme cases (e.g., *Brevigraptus*, *Corynoides*, *Peiragraptus*), a few thecae in total.

Rigby and Dilly (1993) estimated the life span of individual graptolite colonies. They used the rate of fusellar ring accretion in *Rhabdopleura* to calculate that a graptoloid zooid takes an average of 6.6 days to secrete a theca. According to these estimations, the life span of a 3 cm long biserial graptoloid was 1.6–2.4 years, and a 75 cm long *Monograptus flemmingii* approximately 13 years. Damage and repair and possible re-colonization of tubes by successive generations of zooids (Rigby, 1994) may even increase this estimate.

Population structure and dynamics of graptoloids in bedding-plane assemblages have been investigated by Rigby (1993), and in chemically isolated material from limestone nodules by Underwood (1998). The survivorship analyses by Rigby indicate increasing mortality rates with age, but analyses by Underwood indicate constant to decreasing mortality rates with age. Clearly, further such studies are needed before reliable conclusions can be drawn about their ecological implications.

Synrhabdosomes are monospecific assemblages of radially arrayed tubaria attached by the distal extremities of their nemata and are found in various groups of graptolites, from the Dichograptina to biserial and uniserial axonophorans. They have been interpreted as: 1) reproductive adaptations (e.g., Ruedemann, 1895; Kozłowski, 1949; Zalasiewicz, 1984; Underwood, 1993; Ge & Chen, 1995); 2) as chance entanglements (Rigby, 1993; Goldman & Mitchell, 1994); and 3) as adaptations for a variety of other purposes (Kirk, 1969; Gutiérrez-Marco & Lenz, 1998). Synrhabdosomes are rare and found only in a few species; they were clearly not obligate associations that formed part of the life history and ecology of most graptoloids (Maletz, 2014).

SPECIES ASSOCIATIONS AND LOCAL POPULATIONS

Within most graptolitic black shale formations, occasional bedding planes are crowded with colonies, sometimes dominantly of one species. Sometimes all tubaria are at about the same stage of astogenetic growth, suggesting mass mortality (Fig. 5). On the other hand, recurring species associations are common. On some layers, juveniles are associated with mature specimens of the same species, while on others either only juveniles or only mature specimens are found (Moors, 1968; Pannell, Clarkson, & Zalasiewicz, 2006). Recurring species associations and monospecific assemblages suggest some segregation of species within water masses.

Multiple species on single bedding planes are common. Highly diverse bedding plane assemblages are less common but not rare in black shale settings (Fig. 6). Although time averaging probably enhanced this diversity, a range of species is likely to have lived in the overlying waters. A diverse Middle Ordovician fauna preserved within a volcanic ash fall was interpreted by Mitchell, Brussa, and Astini (1998) as an instantaneous "catastrophic kill" of the entire suite of depth-stratified populations that lived in the overlying water column. Current evidence, therefore, suggests that many graptolite species lived in swarms, spatially differentiated from neighboring swarms (Cooper & others, 2012). These same species and others, however, are also found in low abundance at widely scattered localities, so swarming was not obligatory. However, quantitative evidence is sparse, and the effects of current sorting and transport need to be allowed for, particularly in turbidites (Moors, 1970).

PATTERNS OF FACIES OCCURRENCE

Graptolite tubaria are made of an organic scleroproteic material that can be destroyed

FIG. 5. A monospecific death assemblage of *Isograptus victoriae maximus* (counterparts) from the Dapingian (Castlemainian), Middle Ordovician, Aorangi Mine, New Zealand (Cooper & others, 2012, fig. 7).

FIG. 6. A diverse bedding plane assemblage from the Dapingian (Yapeenian), Middle Ordovician, Aorangi Mine, New Zealand (Cooper & others, 2012, fig. 9).

under oxic conditions. Thus, they are best preserved in organic-rich sediments in the typical graptolitic black shales (see RUEDEMANN, 1911), where the decay of organic material is hindered by the anoxic conditions under which the sediments are formed.

Graptolites are found in a wide range of marine sediments, from shales of various colors to silt- and sandstones, carbonates, and cherts (Fig. 7). They are most common, however, in fine-grained clastics in black or dark shales, where the flattened remains can

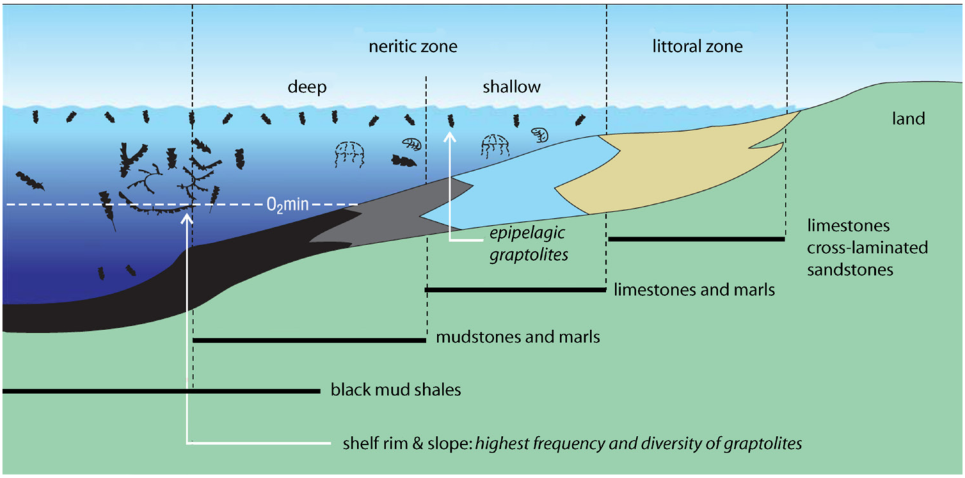

Fig. 7. Schematic distribution of the lithofacies and graptolite biofacies (adapted from Podhalańska, 2013, fig. 3).

be found on numerous bedding surfaces. This sedimentary facies is characteristic of the outer shelf to deep-water regions or basinal regions of the oceans, but graptolites can be found in most sediments representing inner cratonic to deep, marine-basin settings. They are associated with various fossil groups, but in shale sequences are commonly the only fossil group present; rarely, groups such as conodonts, scolecodonts and phosphatic brachiopods are found on the same bedding planes. However, organic-walled microfossils (acritarchs, chitinozoans) may be common in these sediments.

In turbidite successions, graptolites are mainly found in the fine-grained E horizon of the Bouma sequence or in intercalated, pelagic black shales (Hills & Thomas, 1954; Moors, 1969, 1970; Cooper, 1979). More rarely, they are preserved in the A or C horizon as transported fragments (Finney & Berry, 1997; Cooper & others, 2012). Alignment of tubaria on the bedding plane is common and indicates bottom currents and possible transportation (e.g., Ruedemann, 1897; Moors, 1968).

GRAPTOLOID BIOFACIES AND BIOTOPES

The abundance and diversity of graptoloids in sedimentary rocks bordering the Ordovician continents (Fortey & Cocks, 1986; Chen, Zhang, & Mitchell, 2001; Finney & Berry, 2003) suggest that a favorable life zone existed in the region of the outer shelf and slope. Finney and Berry (1997) interpreted the favorable habitat to be associated with upwelling zones providing nutrients and enhancing bioproductivity.

Although graptoloids are found in sedimentary rocks representing depositional environments ranging from inner shelf and craton to the open ocean, many workers have recognized the preferred association of some species with a particular depth facies or offshore facies belt. Both lateral partitioning and depth partitioning of the graptoloid biotope have been proposed and many models have been put forward (Fig. 8). Many researchers have recognized a depth zonation of graptoloids in the water column (Ross, 1961; Berry, 1962, 1974; Berry & Boucot, 1972; Erdtmann, 1976, 1984; Kaljo, 1978; Kirk, 1978; Mu & others, 1979, 1986; Cisne & Chandlee, 1982; Bates & Kirk, 1984; Lenz & Chen, 1985; Chen, 1990; Cooper, Fortey, & Lindholm, 1991; Lenz & others, 1993; Goldman, Bergström, & Mitchell, 1995; Goldman, Mitchell, & Joy, 1999; Chen, Zhang, & Mitchell, 2001; Cooper & Sadler, 2010), and most models incorporate a depth

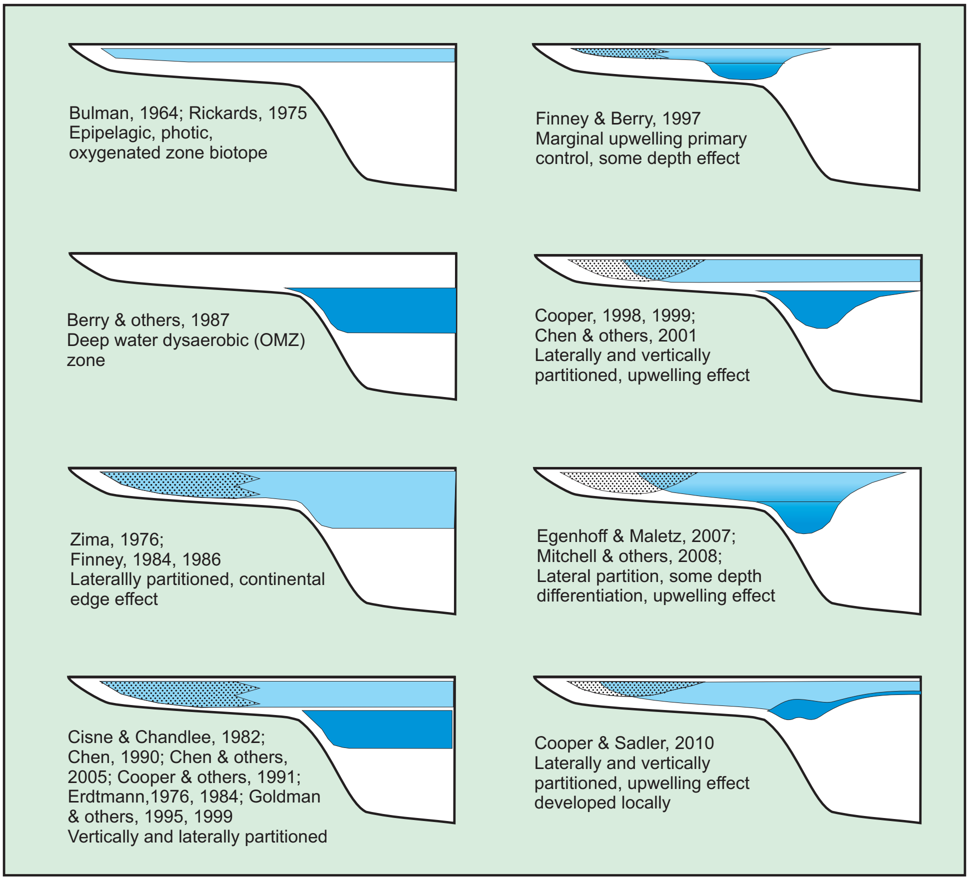

FIG. 8. Some previous models of the graptoloid habitat (Cooper & others, 2012, fig. 18).

component. Some models propose lateral partitioning as the dominant differentiating mechanism of species groups (see below).

Although quantitative data are sparse and the biofacies preference of most species is unknown, a consensus model employing both lateral and vertical partitioning was formed (CHEN, 1990; CHEN & others, 2005; COOPER, FORTEY, & LINDHOLM, 1991; COOPER & others, 2012). This model was based mainly on species of the Early to Middle Ordovician age, the time period in which most ecological analysis has been done. Three species groups were recognized: 1) taxa restricted to the deep-water facies; 2) taxa present in both the neritic and deep-water facies; and 3) taxa found only in the neritic facies. Group 1 species were inferred to have lived in a deep water biotope and group 2 species in a shallow, epipelagic biotope (Fig. 8, Fig. 9); these two groups were thus separated primarily by depth zonation, which, in modern oceans, is caused by such factors as vertical gradients in water temperature, chemistry, aeration, light intensity, and nutrient supply. The distinctness of the two groups is confirmed by their species extinction probabilities; extinction risk is significantly higher for group 1 species than for group 2 species (COOPER & SADLER, 2010; see also BOYLE & others, 2014). Group 3 species, which are restricted to inner- and mid-shelf waters (neritic biotope), were constrained by lateral partitioning of the water mass, perhaps comparable with the modern continental

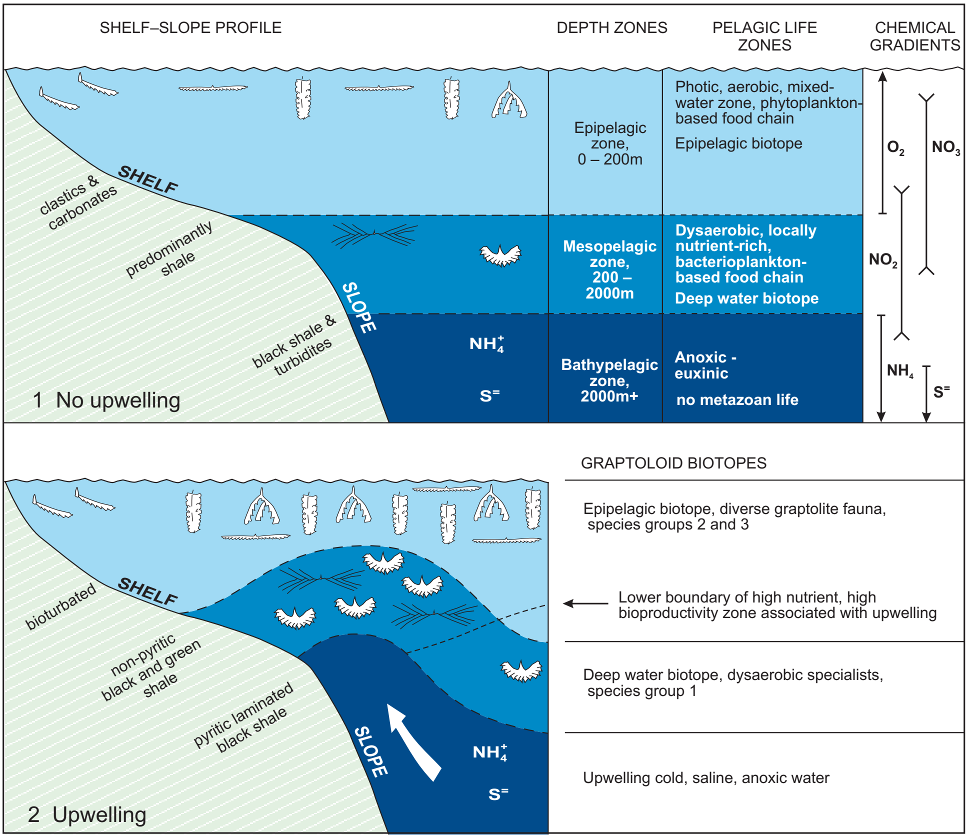

FIG. 9. *1,* Inferred graptoloid life zones in a density-stratified ocean with no upwelling. Epipelagic and deep water graptoloid biotopes are indicated, neritic (inshore) biotope not shown; *2,* in marginal upwelling zone, tongues of dense, oxygen-depleted but nutrient-rich water are brought up into the epipelagic zone (the nutrient pump) generating a nutrient-rich, high-bioproductivity environment (adapted from Cooper & others, 2012, fig. 19 and references cited therein).

edge effect. Groups 1 and 2 contained many pandemic species, whereas group 3 species were largely endemic in their distribution. The model was applied to Late Ordovician graptoloid species (GOLDMAN & others, 2013) and, more loosely, to Silurian species (BERRY & BOUCOT, 1972; MU & others, 1986; LENZ & others, 1993; BOUCOT & CHEN, 2009).

In an alternative approach, lateral partitioning is assumed to be the dominant discriminating mechanism (ZIMA, 1976; FINNEY, 1984, 1986). The model proposed by EGENHOFF and MALETZ (2007) and MALETZ and others (2011) does not recognize a discrete habitat for group 2 species or the distinction between species groups 1 and 2.

In modern oceans, the epipelagic life zone extends from the water surface to a depth of ~200 m, where the light level is only at about 1% of that at the surface. Nearly 90% of all marine life exists in this zone, and it is where nearly all primary productivity takes place, mainly by the phytoplankton. This is the obvious biotope of group 2 and group 3 species and was likely to be the zone in which most planktic (and benthic) graptolites thrived. In the mesopelagic zone, below 200 m depth to ~2000 m, the ocean waters are depleted of oxygen and there is no light. Bacterioplankton are the basis of the food web, and bioproductivity is generally lower than in the epipelagic zone, although locally, highly productive subzones are present (BRINTON, 1979; LONGHURST & HARRISON, 1989). In marginal upwelling areas, nutrient-rich waters enrich the epipelagic zone and greatly increase bioproductivity; this in turn enhances the development of a high-nutrient dysaerobic zone at depths where specialized mesopelagic-zone species thrive (LONGHURST, 1967; JUDKINS, 1980; LONGHURST & HARRISON, 1989; BRASIER, 1995). This deep-water biotope is thought to be the analog of the group 1 species habitat (BERRY, WILDE, & QUINBY-HUNT, 1987, 1989; COOPER & others, 2012), and ancient upwelling zones to be the sites of abundant and diverse graptolite assemblages (FINNEY & BERRY, 1997).

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