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PART V, SECOND REVISION, CHAPTER 3: INTRODUCTION TO THE CLASS PTEROBRANCHIA LANKESTER, 1877

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Class PTEROBRANCHIA Lankester, 1877

[Pterobranchia LANKESTER, 1877, p. 448]

Fixed, sedentary to planktic organisms with communal or colonial zooids divided into three regions: preoral lobe (cephalic shield), collar, and trunk; collar extends to form one or more pairs of arms, each bearing double row of ciliated tentacles; trunk elongated posteriorly to form a zooidal stalk that extends to pectocaulus as interconnection between zooids in colonial forms; soft gymnocaulus connects developing buds and permanent terminal zooid in *Rhabdopleura;* external organic (?collagen, keratin, or chitin) housing or domicile (tubarium) composed of series of tubes built from sequential addition of rings or half-rings of organic material (fusellum) in most taxa. *Cambrian (Series 2,* Stage 3–4, *Olenellus* Zone)–*Recent:* worldwide in marine environments.

The Pterobranchia can be differentiated into two main groups: the pseudocolonial Cephalodiscida and the entirely colonial Graptolithina. The Cephalodiscida include organisms with separate individuals, but clonal, asexually produced zooids are connected to their mother individuals when immature (Fig. 1.1). After reaching maturity, they may separate from their mother zooid and lead an independent life in their communal housing constructions. There is no apparent difference between sexually and clonally produced mature zooids in the Cephalodiscida.

The truly colonial Graptolithina start their colonies from a sexually produced mother zooid, the sicular zooid, comparable to the ancestrula of the Bryozoa. All subsequently produced clonal zooids are interconnected for life through the stolon system (Fig. 1.2). Apart from extinct benthic and planktic graptolites, which constitute the largest group of taxa, the Graptolithina also includes the small group of extant, benthic rhabdopleurids (MITCHELL & others, 2013), found nearly unchanged since the early Ordovician (e.g., ANDRES, 1980; MIERZEJEWSKI, 1986).

The Pterobranchia show a number of special developments and features that set them apart from the rest of the phylum Hemichordata—namely, small-sized, individual zooids with a specialized anatomy, a complex cycle of sexual and asexual reproduction, and most importantly, from a fossil point of view, the secretion of a special housing structure, the tubarium (Fig. 1.2). In short, the Pterobranchia can be described as tube-building, communal to colonial, marine organisms with a benthic to planktic lifestyle and a complex sexual and asexual cycle of reproduction.

EVOLUTIONARY ORIGINS

Latest interpretations (e.g., CANNON & others, 2014; NANGLU, CARON, & CAMERON, 2015; SIMAKOV & others, 2015) indicate monophyly of the Pterobranchia relative to the Enteropneusta (Fig. 2). Information on the early evolution of the Pterobranchia is scarce

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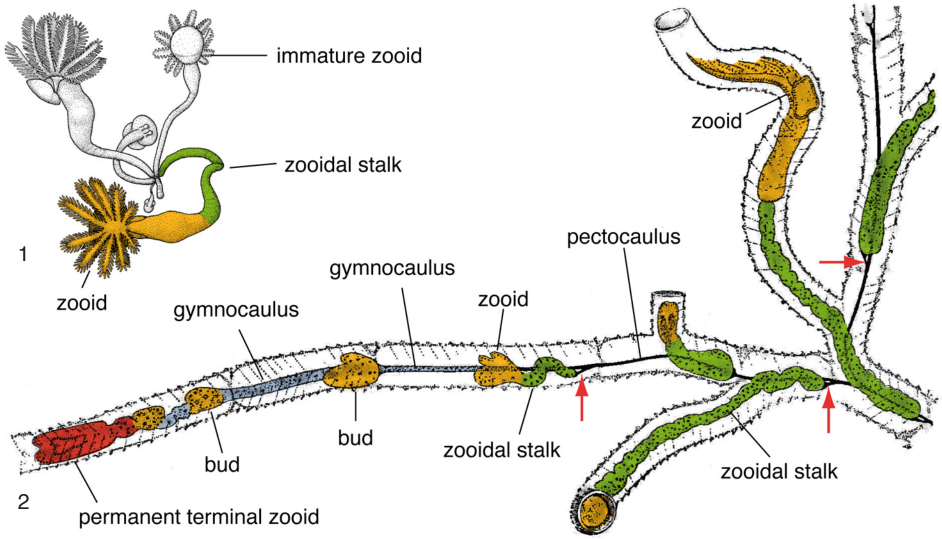

FIG. 1. Pterobranch organization. *1, Cephalodiscus gracilis* M'INTOSH, 1882, zooid with juveniles (adapted from Lester, 1985, fig. 2); *2, Rhabdopleura normani* ALLMAN, 1869, part of tubarium with permanent terminal zooid, showing terminology of the stolon system (adapted from Ridewood, 1907, fig. 7). *Red arrows* point to the short zooidal stolons of the *Rhabdopleura* zooids.

and can only be estimated from the record of a few early to middle Cambrian fossil tubarium fragments. The cladistic analysis of benthic graptolites (MITCHELL & others, 2013) shows a poor resolution of most groups, but the Cephalodiscida can easily be differentiated by their non-colonial development. The invariably colonial Graptolithina show the highest amount of evolutionary diversification with the planktic Graptoloidea as the geologically most important group. The Enteropneusta differ from the Pterobranchia by the position of the anus at the end of their elongated body; the Pterobranchia have a U-shaped gut with the anus positioned directly below the collar.

If these interpretations are correct, the evolution of the pterobranchs may be based upon the miniaturization of the individuals, associated with a simplification of their body construction and loss of complex internal organs, and eventually, the exploration of a colonial lifestyle with the generation of numerous asexually produced members or zooids. The evolution of these characteristics and the origin of the secretion of the typical pterobranch tubarium is not clear. Many of the features of fossil zooids can only be estimated from the characters of extant taxa, as the actual organisms are almost completely unknown from the fossil record.

The miniaturization of the pterobranch zooids can be simply understood by comparing the related enteropneusts, worm-like organisms of up to 2 m in length, with the generally small pterobranch zooids (~0.6–10 mm). However, miniature enteropneusts, measuring less than 1 mm long, have also been discovered (WORSAAE & others, 2012). Cephalodiscid zooids can reach lengths of several mm and, thus, are larger than the 0.6–2 mm long rhabdopleurid zooids. The size of the zooids of the extinct taxa of the Graptolithina is more difficult to estimate (e.g., SUDBURY, 1991; RIGBY & SUDBURY, 1995), but considering the small tubes and apertural openings in most taxa, they would not have been larger than the zooids of a modern *Rhabdopleura*.

The construction of the pterobranch tubarium can be quite complex, and details are discussed in various Treatise (Part V, Second Revision) chapters on the taxonomy

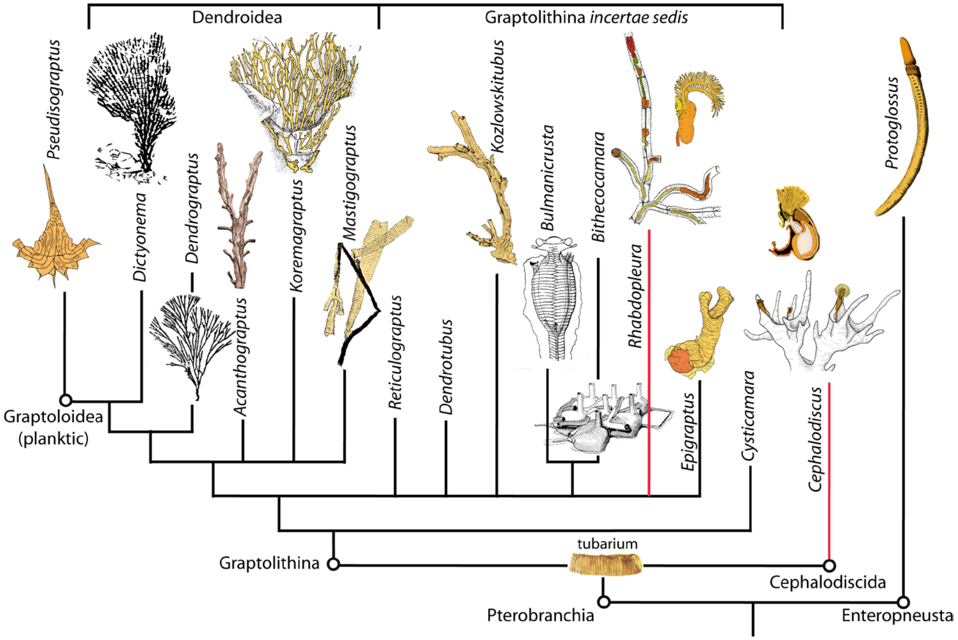

FIG. 2. Relationships of the main groups of the Graptolithina. Diagram based in part on Maletz (2014a). *Red lines* in diagram indicate extant members.

of the individual groups. The general features of both fossil and extant Pterobranchia are described in Chapter 4 on tubarium morphology (see MALETZ, LENZ, & BATES, 2016). The evolutionary origin of the peculiar housing system of the Pterobranchia is unclear. One possibility, based on the tube-dwelling habitat of the Cambrian acorn worms *Spartobranchus* and *Oesia,* may be that tubes are a hemichodate plesiomorphy. If this is true, these tubes were then elaborated upon in the Pterobranchia and lost on the branch to the extant worms (CARON, CONWAY MORRIS, & CAMERON, 2013; NANGLU & others, 2016).

Modern Enteropneusta produce mucus-lined burrows from glands on the proboscis (NØRREVANG, 1965; NANGLU, CARON, & CAMERON, 2015). The composition of this mucus and its possible relationship to the secretionary material of the tubaria in the Pterobranchia may be important to study in the future, especially since NANGLU, CARON, AND CAMERON (2015) suggested that the burrows of *Spartobranchus* from the Cambrian Burgess Shale were unlikely to be based on the secretion of mucus alone, as these fragile burrows would then have easily been destroyed. The tubes of *Oesia,* previously described as the alga *Margaretia,* were fibrous, but unlike pterobranch tubes, were permeated with holes (NANGLU & others, 2016).

In the Enteropneusta, the proboscis is completely covered with the mucus secreted from its glandular cells, while in the Pterobranchia, the glandular secretion is limited to a special area on the proboscis, the cephalic shield (DILLY, 1986, 1988). In *Rhabdopleura,* secretion of the dome of the colony occurs by secretory cells of the ventral epidermis of the larva, and this site probably becomes the ventral surface of the cephalic shield in the later ontogeny of the zooid (LESTER, 1988a, 1988b). There is no information on mucus production in modern pterobranchs. Interestingly, non-fusellar tissue occurs in some rhabdopleurids (e.g., KULICKI, 1971; MIERZEJEWSKI, 1986; MIERZEJEWSKI & KULICKI, 2003) and may be indicative of early development of tubarium secretion.

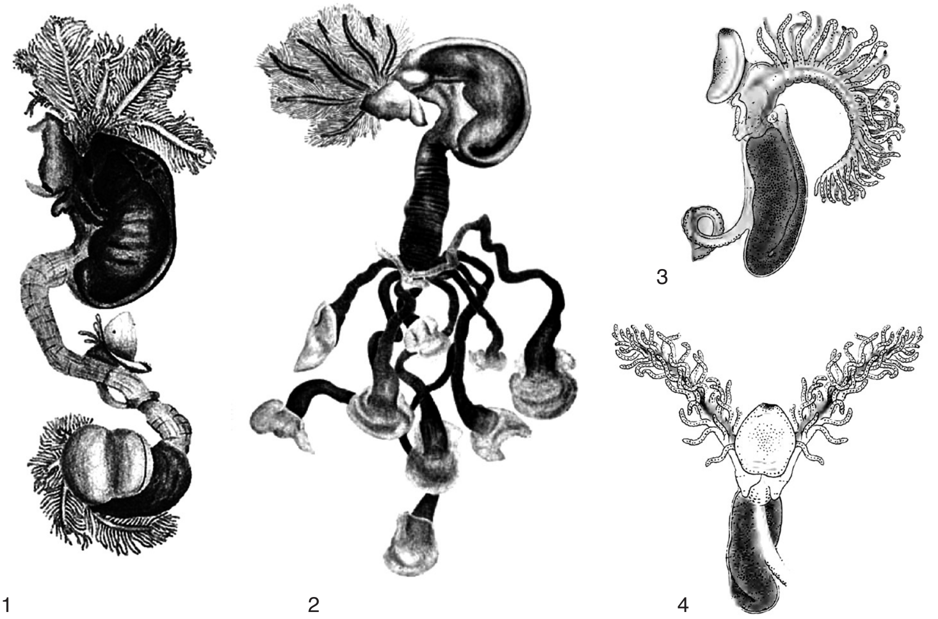

Fig. 3. Pterobranch zooids. *1, Cephalodiscus* (*Acoelothecia*) *kempi* John, 1931, mature zooid with two buds in different stages of development (John, 1931, pl. 35,*2*); *2, Cephalodiscus* (*Cephalodiscus*) *fumosus* John, 1931, mature zooid with at least nine budding individuals (John, 1931, pl. 35,*3*); *3–4, Rhabdopleura normani* Allman, 1869, lateral (*3*) and ventral (*4*) view of zooids (adapted from Sars, 1874, pl. 1,*1–2*).

PTEROBRANCH ZOOIDS

The zooidal anatomy of the Pterobranchia is known from the few extant taxa and has been described in detail. Pterobranch zooids (Fig. 3–4) are divided into three parts: the cephalic shield or proboscis (protosome), the collar bearing the arms (mesosome), and the trunk (metasome). A slender, flexible zooidal stalk is found at the end of the trunk and connects the individual zooids of the colonies to the stolon system, or pectocaulus, in the Graptolithina (Fig. 1.2), and to a common, motile, ciliated disc in most Cephalodiscida (Fig. 1.1). The zooidal anatomy of the Cephalodiscida (*Cephalodiscus, Atubaria*) and Graptolithina (*Rhabdopleura*) differs in a number of modifications of the body, such as the number and development of the arms, gonads, and the presence or absence of gill pores. Other differences can be seen in the size of the zooids and their interconnections.

Masterman (1897, 1898a, 1898b, 1900, 1903), Harmer (1905), Anderson (1907), Schepotieff (1907b, 1908), John (1932), Dilly, Welsch, and Rehkämper (1986a, 1986b, 1986c) and Welsch, Dilly, and Rehkämper (1987) described the anatomy of the zooids of *Cephalodiscus* in some detail. Horst (1939) and Hyman (1959) provided an overview of the knowledge. Stach, Gruhl, and Kaul-Strehlow (2012) described the central nervous system. The mature zooids of *Cephalodiscus* (Fig. 3.1–3.2) are about 2–14 mm long and bear four to nine pairs of tentaculated arms on the dorsal side of the collar. The cephalic shield is flexible and possesses a characteristic red pigment line parallel to the posterior edge. The arms form two curved rows on the dorsal side of the collar, while the ventral side bears the mouth of the zooid. The arms are extensions of the collar coeloms and have about 25–50 paired tentacles. A terminal glandular or tentacular knob is present in some species of *Cephalodiscus*. The trunk consists of a wide, saclike, anterior part which culmimates in a slender stalk used for attachment. The U-shaped gut and the gonads are

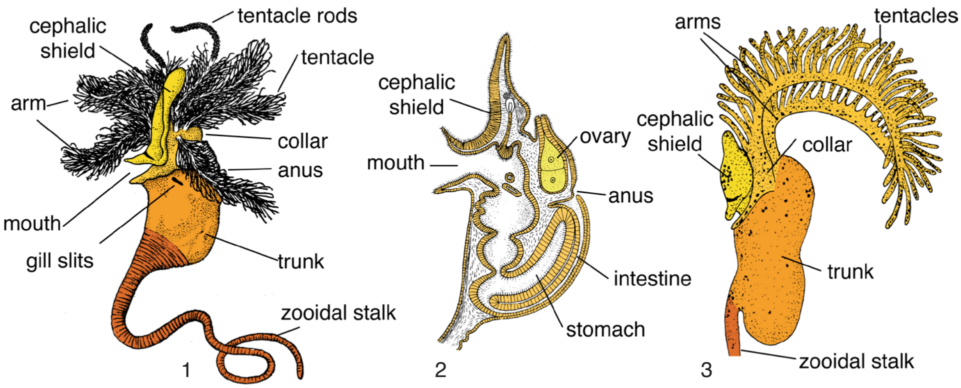

FIG. 4. Zooidal anatomy. *1–2, Atubaria heterolopha* SATO, 1936; *1,* single zooid (adapted from Komai, 1949, fig. 1); *2,* sagittal section of the body of a female zooid (adapted from Komai, 1949, fig. 2); *3, Rhabdopleura normani* ALLMAN, 1869, single zooid with part of zooidal stalk (adapted from Hyman, 1959, fig. 67C).

found in the trunk (Fig. 4.2). A single pair of gill pores can be found behind the posterior border of the collar. The zooidal stalk is hollow and has a ciliated adhesive disc at the end, with which the zooid attaches itself to the tubarium. This is also where the asexually produced buds appear (Fig. 3.1–3.2). The zooids of *Cephalodiscus* grow attached to the adhesive disc until they mature (Fig. 3.2), and then they may separate and live free. After maturation, they are also able to produce new zooids by asexual budding.

The zooids of *Atubaria* (Fig. 4.1) are similar to those of *Cephalodiscus* but differ in the development of the arms. The antero-internal arm pair bears a long, tentacular rod distally, covered with granules like the clubs on the arms of certain *Cephalodiscus* species. Another difference is the lack of an adhesive disc at the end of the stalk. All known zooids of *Atubaria* are female (SATO, 1936). Nothing is known on the lifestyle and reproduction of this taxon. According to SATO (1936), the two different zooidal forms can be identified as immature and mature specimens, suggesting that the juveniles separate at an early stage from their mother zooid or do not represent clonally reproduced individuals.

Details of the zooidal anatomy of *Rhabdopleura* (Figs. 3.3–3.4) are provided by LANKESTER (1884), SCHEPOTIEFF (1904, 1906, 1907a, 1909), LESTER (1988a, 1988b), and MAYER and BARTHOLOMAEUS (2003). The mature zooids of *Rhabdopleura* are about 1 mm or less in length. They are organized similarly to *Cephalodiscus* and are differentiated into cephalic shield, collar, and trunk regions (Fig. 4.3). The cephalic shield is oval and has a central glandular region for the secretion of the tubarium. The red pigment strip is sometimes present as in *Cephalodiscus*. The collar of *Rhabdopleura* bears a single pair of arms with paired tentacles, and the mouth is on the shorter ventral side.

The zooids of a *Rhabdopleura* colony are interconnected for life through the stolon system or pectocaulus (Fig. 1). A single zooid, the sicular zooid, is the founder of the colony and is the only sexually produced zooid. All subsequent zooids develop asexually on the advancing stolon of the colony. Thus, contrary to the situation in *Cephalodiscus,* each zooid of *Rhabdopleura* is only able to produce a single further zooid through asexual budding.

HYMAN (1959) provided an overview on the internal anatomy of the pterobranchs, but details are not discussed here, as the zooidal anatomy is not known from the fossil record and unlikely to be gained from fossil specimens. The zooids are either male, female, or neuter, but hermaphroditic ones also exist. The most important difference in the anatomy between enteropneusts and pterobranchs can be seen easily in the form of the gut. The small pterobranch zooids have a U-shaped gut and the anus is found below the collar on the dorsal side of the body, opposite to the mouth (Fig. 4.2).

The sexes are separate in *Cephalodiscus* but impossible to differentiate externally. Male and female zooids may occupy a single tubarium, but tubaria may also include a single sex. Hermaphroditic zooids, in which one gonad is female and the other is male, are not uncommon. HARMER (1905) described *Cephalodiscus sibogae* with neuter and male zooids, but no females. The neuter zooids appear to normally have four pairs of tentaculate arms and lack gonads, while the males have two arms without tentacles, a vestigial digestive tract, and a trunk filled with two large testes.

The stolon system (Fig. 1) is a defining feature of the colonial Graptolithina and connects the individual zooids. The Cephalodiscida do not possess an equivalent of the soft stolon or gymnocaulus, nor do they have the black stolon or pectocaulus (SCHEPOTIEFF, 1906) of the Graptolithina. Instead, buds develop from a common point or ciliated disc (Fig. 1.1). Cephalodiscid zooids attach to this point by a flexible, extendable zooidal stalk. In *Rhabdopleura,* the zooidal stalk connects the stolon to a gymnocaulus or pectocaulus. These can bifurcate and have the potential to differentiate and form asexual zooid buds. The stolon develops from the gymnocaulus of the advancing terminal zooid in *Rhabdopleura*.

LANKESTER (1884) described and illustrated the stolon system of *Rhabdopleura normani* in some detail and differentiated the gymnocaulus and pectocaulus. The gymnocaulus, or soft stolon, is the flexible connection of the zooid to the black stolon or pectocaulus, a hard and inflexible structure. A short zooidal stolon as the direct connection between the zooidal stalk and the main stolon can usually be observed; the zooidal stalk is not a continuation of the main stolon (red arrows in Fig. 1.2). According to LANKESTER (1884), the pectocaulus develops from the gymnocaulus through the formation of a sclerotized cuticle around the gymnocaulus, which he termed the caulotheca or stalk-pipe. LANKESTER (1884, p. 634) differentiated between the axial stalk and the contractile stalk of the zooid, but remarked that both are "essentially the same thing." The zooidal stalks differ considerably from the gymnocaulus behind the permanent terminal zooid of the Rhabdopleura colony, as they are unable to produce new buds for zooidal growth (Fig. 1.2). Therefore, the zooidal stalk is separated here from the gymnocaulus.

URBANEK and DILLY (2000, p. 201) described the stolon of *Rhabdopleura* as a thread of soft tissue produced by the terminal zooid through an extension of its stalk. The gymnocaulus produces a chain of buds behind the terminal zooid, thus forming the colonial organism. According to URBANEK and DILLY (2000), the stolonal threads show distinct diaphragm complexes from which the zooids develop. The origin and construction of these diaphragm complexes are unclear, but a comparison can be made to the dormant buds. These are encased completely into a thickened, pigmented wall or capsule. The diaphragm complexes are similarly constructed but show an open end. Thus, the diaphragm complex may represent a protective shell for the developing buds (see STEBBING, 1970a, p. 210; URBANEK & DILLY, 2000, p. 216). The walls of the stolon, the dormant buds, and the diaphragm complexes are constructed from crassal fabric (URBANEK & TOWE, 1974), thus, they may be secreted similarly from the surface of the organism and in this respect differ from the tubarium secretion. Contracted specimens of *Rhabdopleura compacta* can be seen with the coiled gymnocaulus within the diaphragm complex (URBANEK & DILLY, 2000, p. 216), clearly indicating that the zooids are moving in and out of their tubes.

The development of the stolon is more complex in dendroid graptolites with diad and triad budding, but details are only known from a few taxa (e.g., Bulman, 1944; Kozłowski, 1948, 1963; Bates & Urbanek, 2002; Saunders & others, 2009). Saunders and others (2009) described the development in *Desmograptus micronematodes* (Spencer, 1884) and presented evidence of a development similar to the diaphragm complex of *Rhabdopleura* in the dendroid graptolites. Due to the durability of the stolon system, it may be preserved in many sediments, as can be seen from numerous fragments previously identified as hydroid remains (e.g., Kozłowski, 1959; Mierejewski, 1986; Maletz, 2014a; Muscente, Allmon, & Xiao, 2015). Studies of the fossil record of early planktic graptolites rarely mention the presence of a stolon system (e.g., Hutt, 1974; Legrand, 1974; Cooper & others, 1998), even though it is clear from the tubarium construction that it must have been present. Very likely, the stolon was not strongly sclerotized and, thus, was not preserved in the fossil record.

ONTOGENY AND ASTOGENY

All extant Pterobranchia from which we know any details, may have a life cycle with a double mode of reproduction—sexual reproduction resulting in a single zooid (the sicular zooid), and asexual budding that forms all subsequent zooids in the pterobranch colony (Fig. 5). The ontogeny of the zooids combines with the budding mechanism to form the astogeny of the colony or pseudo-colony. There is no information available on the ontogeny and life cycle in *Atubaria*, even though mature and immature specimens were found. These are all separate individuals, and a clonal origin has not been verified. The evolutionary origin of this asexual, clonal development in the Pterobranchia is not unique in the deuterostomes, but can be compared to that of the colonial tunicates. Pterobranchs are unique among animals in that the colonies may be male, female, or contain zooids of both sexes.

Details of the breeding and fertilization are incompletely known for the pseudo-colonial *Cephalodiscus*. It is not known if fertilization is internal and embryos are released from the zooid, or if fertilization is external. The embryos develop in the tubarium. Within a short time, they metamorphose into a ciliated larva (Andersson, 1907, fig. 23; Hyman, 1959, fig. 63D) and hatch from the fertilization membrane. Schiaparelli, Cattaneo-Vietti, and Mierejewski(2004) described a protective larval cocoon in *Cephalodiscus densus*. The larva may swim freely for a short time before it settles. At metamorphosis, probably during the free-swimming period (John, 1932, p. 201), it attains the typical zooidal shape with the stalk and the arms in a rudimentary state. When the juvenile *Cephalodiscus* finds a suitable place to establish a new colony, it settles, develops the arms and stalk, and begins to secrete its tubarium. Further development and astogenetic growth of the *Cephalodiscus* pseudo-colony is by asexual budding. This asexual budding of new zooids occurs near the base of the stalk. Dilly (1985) referred to this site as a sucker, but in *Cephalodiscus gracilis* it is a ciliated and motile pad. This common point or pad is the location of cell division and differentiation resulting in new zooidal buds (Fig. 1.1, Fig. 3.2). Dilly (2014) interpreted these *Cephalodiscus* buds as representing a colonial organism and counted up to an estimated fourteen individuals, as he was unable to definitively observe individual zooids. When mature, the zooids can detach themselves from the colony, produce new zooids through asexual budding, and secrete a new pseudo-colonial tubarium.

Lester (1988a, 1988b) described in some detail the life cycle of *Rhabdopleura normani* (Fig. 5), especially the ontogenetic development of the sicular zooid (called ancestrula in Lester, 1988a) from the early larval stage onwards. The uniflagellated spermatozoans are elongated, filiform (Lester, 1988a), and are probably released into the seawater. The fertilization site is not known, but may occur within the tubarium, where the eggs are kept in special brood chambers by the female zooids. The females of *Rhabdopleura normani* secrete the initial part of their individual tube,

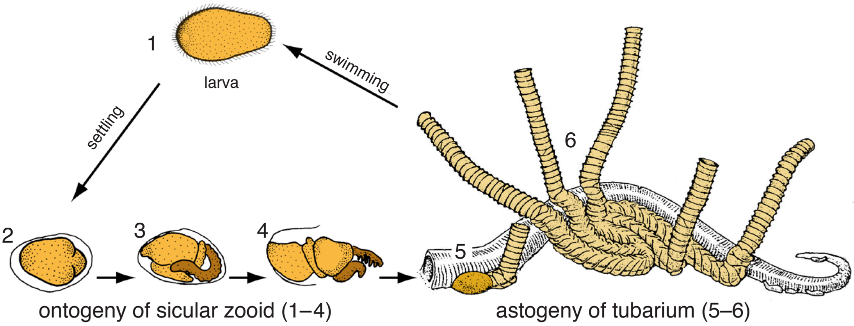

FIG. 5. The ontogeny and astogeny of *Rhabdopleura compacta* (adapted from Maletz, 2015, fig. 5). *Rhabdopleura* colony is attached to a tube of *Serpula vermicularis* (adapted from Stebbing, 1970b, fig. 3).

which is coiled at least 360° (LANKESTER, 1884; LESTER, 1988a). This structure is used as a brood chamber in which the embryos hatch. The fertilized egg develops into a ciliated larva and escapes from its parential tube by squeezing itself past the female zooid and the younger embryos and then swims for up to 24 hours before settling (Fig. 5.1). After finding a suitable place to establish a new colony, the larva secretes the prosicular dome and metamorphoses into a mature zooid (Fig. 5.2–5.4).

The mature sicular zooid attaches with its stalk on one side of the dome and produces a hole in the other side of the dome, through which it emerges to secrete the first tube. The first asexually budded zooid develops from the base of the stalk of this founding sicular zooid (LESTER, 1988a), but further development has not been observed in *Rhabdopleura normani.* A similar development can be seen in *Rhabdopleura compacta.* STEBBING (1970a) described the early astogenetic development of the colony of *Rhabdopleura compacta,* and stated that the sicular zooid secretes only a few segments of a creeping tube with the typical dorsal zigzag suture before forming an erect tube with fusellar full rings and the typical collar structures. At this stage, the zooid is fully developed and starts to bud off the asexually produced zooid from the base of the gymnocaulus. This second zooid secretes a septum, separating part of the dome. After this, it breaks down the wall of the dome and secretes its own tube. Further development is not described; thus, it is unclear from what point the next bud originates and which zooid will form the permanent terminal bud.

The sexes are separate in *Rhabdopleura normani* (LESTER, 1988a), but both may be found in a single colony together with neuter individuals as in *Rhabdopleura compacta* (STEBBING, 1970a). Often, several sicular zooids are associated and together form intermingling colonies. Thus, it may be difficult to identify and separate individual colonies of *Rhabdopleura.* Zooids that reproduce sexually are apparently often morphologically different from other zooids. They generally show reduced arms and tentacles, but also reduced inner organs, suggesting that they do not feed themselves (STEBBING, 1970a).

The life cycle of the extinct graptolite taxa (Fig. 6) is expected to be similar to that of the extant *Rhabdopleura,* as all taxa are truly colonial, evidenced by the presence of the common canal connecting the individual thecal tubes (BARRANDE, 1850; MALETZ, 2015). Historically, graptolites have been considered extinct and no modern relatives have been recognized, even though the graptolites were identified as the group most closely related to the extant *Rhabdopleura.* Therefore, the mystery of the soft-body anatomy of the graptolite zooids remained unresolved, especially since no remains of fossil graptolite zooids showing anatomical details have been discovered. The secretion of the graptolite tubarium has been

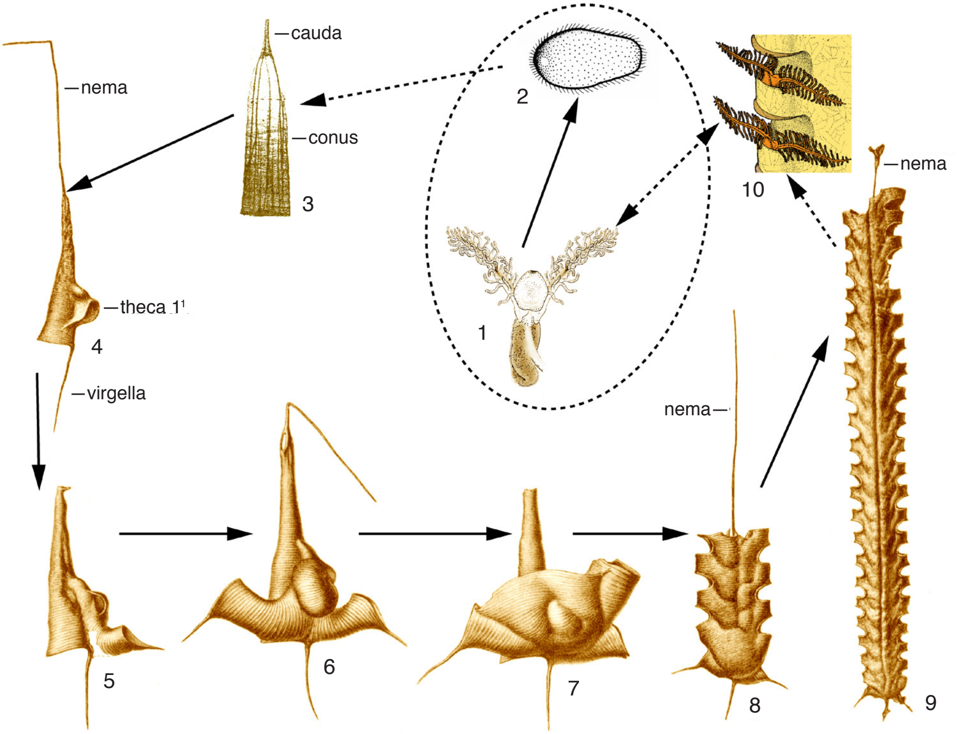

FIG. 6. Ontogeny (*1–3*) and astogeny (*4–10*) of the Graptolithina, based on the astogenetic series of tubaria of *Pseudamplexograptus distichus* (EICHWALD, 1840) (Maletz, 2015, fig. 6).

difficult to explain, but problems have also arisen from a lack of information on the secretion of the tubaria in the extant pterobranchs *Rhabdopleura* and *Cephalodiscus*. KIRK (1972), among others (e.g., BULMAN, 1970; RICKARDS, 1975; URBANEK, 1976), preferred the explanation that secretion of the graptolite tubarium occurs underneath a peridermal membrane. After a detailed investigation of the construction of the tubaria from fuselli and cortical tissues, CROWTHER and RICKARDS (1977), CROWTHER (1978), and ANDRES (1977, 1980) suggested a pterobranch-like zooid was responsible for the construction. BULMAN (1955, 1970) based his reconstruction of graptolite zooids on a rhabdopleurid type of zooid, and this analog has been used frequently (see ERDTMANN, 1982; SUDBURY, 1991; UNDERWOOD, 1993; RIGBY & SUDBURY, 1995). Since the recognition of the extant genus *Rhabdopleura* as a living graptolite (MITCHELL & others, 2013), the debate has reached consensus that graptolite zooids are bilaterally symmetrical, small organisms, probably with a single pair of arms comparable to those of *Rhabdopleura*. Still, a certain variability should be considered likely for the anatomy of the zooids, though it cannot be proven from the fossil record.

LIFESTYLE

A number of researchers have observed and described the lifestyle and development of the extant Pterobranchia since the earlier appearance of works by SARS (1874), SCHEPOTIEFF (1906), BURDON-JONES(1954), and GILMOUR (1979), among others. The zooids of all pterobranchs are able to crawl out of their inhabited tubes and roam on the surface of the tubarium. While the zooids of the unattached *Cephalodiscus* can glide freely inside and outside the tubaria, the zooids of *Rhabdopleura* are more restricted by their attachment to the stolon. However, the stolons can be stretched to allow considerable movement of the zooids. The zooids of *Rhabdopleura* can retract quickly into the tubes when disturbed, but the subsequent extension is by slow, ciliary gliding. The zooids of *Cephalodiscus* and *Rhabdopleura* secrete external cortical bandages during the zooidal movements outside of the tubaria. The presence of external cortical bandages in extinct graptolite taxa indicates that this was also the case in these organisms.

Very little is known on the ecology of the various pterobranch species, even though living zooids have been observed a number of times (e.g., Andersson, 1907; Gilchrist, 1915; Rigby, 1993). Colonies of *Cephalodiscus* have been found at depths ranging from intertidal to ~650 m, attached to various substrates, from remains of other organisms to rock surfaces. Species can be found from tropical to Arctic and Antarctic regions, but according to the sparse record (see Hyman, 1959, p. 177), such discoveries of cephalodiscids may be merely accidental and not indicative of their real biogeographical distribution. The zooids filter feed from the tips of their tubaria (Lester, 1985), but their dietary needs are unknown.

Rhabdopleura has been found at depths ranging from shore facies to 550 m deep (Dilly & Ryland, 1985), but appear to be most common at depths between 100–300 m from tropical to Arctic and Antarctic regions. The taxon appears to be worldwide in distribution, but has rarely been found due to its small size and, therefore, may easily be overlooked. For example, only in relatively recent times, have rhabdopleurids been discovered in the Mediterranean Sea (Laubier, 1964, 1966). Specimens are usually attached to rocks, corals (*Lophelia*), or other living or dead remains of organisms, but they can also hide under empty shells, as is often the case with *Rhabdopleura compacta* (Stebbing, 1970b).

THE FOSSIL RECORD

The fossil record of the Pterobranchia relies completely on the presence of the sclerotized tubaria, as the tiny zooids are not preservable (Maletz, 2014b; Maletz & Steiner, 2015). It is known from observing modern pterobranchs that the zooids are unrecognizable after only a few days of decay (Briggs & others, 1995). The poor fossil record of putative pterobranch zooids shows some lumps of diagenetic minerals in the regions where zooids may be expected (e.g. Bjerreskov, 1978; Rickards & Stait, 1984; Loydell, Orr, & Kearns, 2004), but no definite details of the animals' anatomy. However, Durman and Sennikov (1993, fig. 3,*2*) and Sennikov (2015) described the remains of possible zooids from a middle Cambrian (Drumian) rhabdopleurid (*Sphenoecium obuti* Durman & Sennikov, 1993) as including an indication of arms and tentacles. The photos of the zooids in Sennikov (2015) and the interpretative drawings indicate some features, but are not entirely convincing. Zalasiewicz and others (2013, p. 143) described the "polymorphic organization in a planktonic graptoloid," based on a strongly tectonized, single tubarium of *Dicranograptus* sp. No evidence of zooidal development was found, and the interpretation of the specimen as most likely representing a stolon-like system is conjectural.

Few early fossil taxa have been compared to the Pterobranchia (Fig. 7). Among these is the genus *Herpetogaste*r Caron, Conway Morris, & Shu, 2010, based on a number of well-preserved specimens from the middle Cambrian Burgess Shale of British Columbia (Caron, Conway Morris, & Shu, 2010). The suggested relationship of these specimens to the Pterobranchia was supported by the presence of a muscular stalk with an attachment disc and the presence of paired dendritic oral tentacles (Fig. 7.1). However, the presence of the tentacles on the anterior of the head, its dendritic construction, the size of the organism, and the attachment site of the stalk in the middle of the segmented body makes a relationship unlikely and suggests an independent evolution of this stalked organism.

Hou and others (2011) described *Galeaplumosus abilus* Hou, & others, 2011,

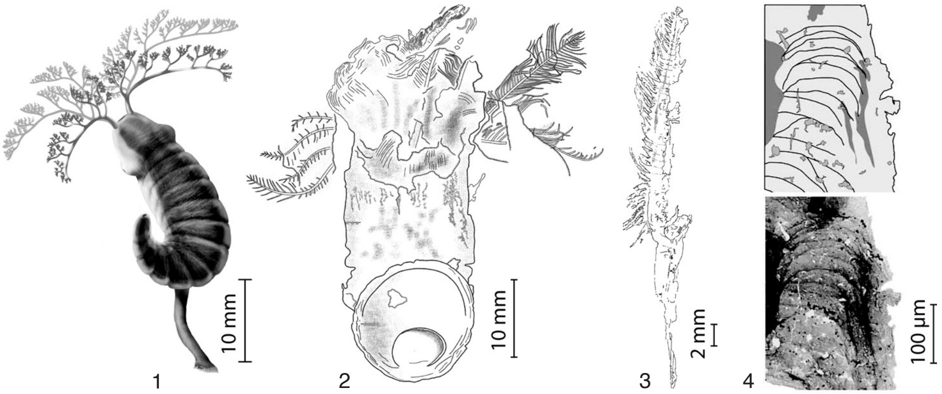

FIG. 7. Putative early pterobranchs. *1, Herpetogaster collinsi*, reconstruction (Caron, Conway Morris, & Shu, 2010); *2, Xianguangia* CHEN & ERDTMANN, 1991 (illustration drawn and used with permission by Ou, 2015); *3, Galeaplumosus abilus*, holotype (Hou & others, 2011, fig. 2a); *4,* pterobranch fusellum (Harvey & others, 2012, fig. 4).

from the lower Cambrian of China, as the oldest, best-preserved, and largest pterobranch of the fossil record, based on a single specimen (Fig. 7.3). The specimen consists of arms (probably paired) with rows of paired tentacles, part of a body, and possible indications of a tube with a banding interpreted as fusellar. This specimen is highly fragmentary and a pterobranch relationship cannot be substantiated. OU QIANG (China University of Geosciences, personal communication, 2015) suggested that the fragment may represent a single arm of the possible stem-group cnidarian *Xianguangia* CHEN & ERDTMANN, 1991 (Fig. 7.2).

The specimens of *Ectocystis communis* NITECKI and SCHRAM, 1976, from nodules in the Carboniferous Mazon Creek biota of Illinois, are large (several cm long) and possibly represent colonial organisms. Apart from the general outline, details of the anatomy of this organism are not available. The outline vaguely resembles large pterobranch zooids. The arms are not differentiated into tentacles as in pterobranchs, and other characters cannot be compared with the known pterobranch anatomy. Thus, there is no compelling evidence to identify *Ectocystis* as a pterobranch.

HARVEY and others (2012) provided the oldest evidence of true Pterobranchia from a few fragments of fusellar wall material found in the middle Cambrian Kaili Formation of China (Fig. 7.4), but it is unclear whether this fragmentary material can be referred to the Cephalodiscida or the Graptolithina. Early definite pterobranchs include *Sphenoecium mesocambricus* (ÖPIK, 1933) from the middle Cambrian of Sweden and Norway (ÖPIK, 1933; BENGSTON & URBANEK, 1986; MALETZ & STEINER, 2015). A number of specimens from the Wheeler Shale of Utah, USA, have been referred to *Sphenoecium wheelerensis* MALETZ & STEINER, 2015. A poorly illustrated specimen of *Dalyia annularoides* RESSER & HOWELL, 1938, from the Kinzers Formation of Pennsylvania may represent the genus *Sphenoecium,* and, thus, this specimen from the lower Cambrian *Olenellus* Zone would be the oldest recorded pterobranch fossil.

RICKARDS and DURMAN (2006) and MALETZ and STEINER (2015) discussed middle to upper Cambrian Graptolithina and provided a general analysis of the evolutionary relationships of the early taxa. Very little is known on the evolution of upper Cambrian pterobranch taxa until the sudden appearance of planktic graptolites close to the base of the Ordovician system. After the extinction of the planktic graptolites in the Lower Devonian (Emsian), the fossil record of the Graptolithina is very poor. Only a few specimens of rhabdopleurids and cephalodiscids have been found from

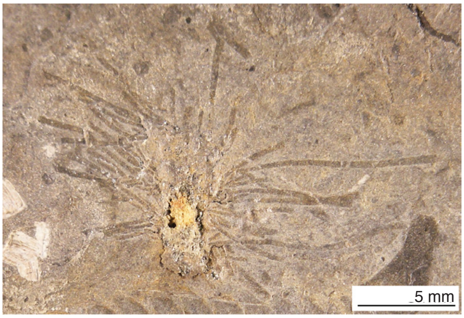

FIG. 8. *Yuknessia* (p. 12).

the Lower Ordovician to the Eocene (e.g., RICKARDS, CHAPMAN, & TEMPLE, 1984; MIERZEJEWSKI, 1986).

PTEROBRANCHIA *incertae sedis*

MALETZ and STEINER (2015) included the genus *Yuknessia* WALCOTT, 1919 as *incertae sedis* in the Pterobranchia, as they were not able to recognize details supporting an inclusion in the Cephalodiscida or Graptolithina, even though they provided definite evidence of fusellar construction (see also LODUCA & others, 2015).

Yuknessia. WALCOTT, 1919, p. 235 [**Y. simplex;* M]. Organisms with long, slender thecal tubes formed from organic material and bearing evidence of fusellar construction; thecal tubes may widen towards the aperture; circular attachment structures at base of tubes; no interconnection between individual tubes recognizable. *Cambrian (Series 3,* Stage 5, *Bathyuriscus/Elrathina–Ptychagnostus punctuosus* Zones): Canada, USA.——FIG. 8. **Y. simplex* WALCOTT, 1919, USNM 35406, holotype (Maletz & Steiner, 2015, fig. 15).

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