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PART V, SECOND REVISION, CHAPTER 14: ORDER CEPHALODISCIDA: INTRODUCTION AND SYSTEMATIC DESCRIPTIONS

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Order CEPHALODISCIDA Fowler, 1892

[CEPHALODISCIDA FOWLER, 1892, p. 297] [= Cephalodiscoidea BEKLEMISHEV, 1951]

Fixed, sedentary marine organisms with communal zooids divided into three regions, preoral lobe (cephalic shield), collar, and trunk; collar extends to form several pairs of arms, each bearing double row of ciliated tentacles; trunk elongated posteriorly to form stalk with sucker at base from which new zooids are generated asexually; external proteinaceous housing or domicile (the tubarium) composed of series of tubes built from sequential addition of full rings or half rings of organic material in most taxa; tubaria with separate zooidal tubes to communal dwellings; housing construction lacking in one genus. *Cambrian (Series 3, Stage 5)–Holocene* (extant): worldwide in marine environments.

INTRODUCTION

The Cephalodiscida are a group of pseudocolonial, benthic organisms, often living in large communities, known largely from extant members. The 18 described extant species belong to a single genus, *Cephalodiscus,* which is divided into four subgenera: *C. (Orthoecus), C. (Idiothecia), C. (Cephalodiscus),* and *C. (Acoelothecia).* Species found in waters of the Antarctic are: *C. (C.) hodgsoni* RIDEWOOD, 1907 (=*C. (C.) aequatus* ANDERSSON, 1907); *C. (C.) inaequatus* ANDERSSON, 1907; *C. (I.) nigrescens* HARMER, 1905; *C. (O.) densus* ANDERSON, 1907; and *C. (O.) solidus* ANDERSSON, 1907. *C. (C.) dodecalophus* M'INTOSH, 1887 is found in subantarctic waters. Species found in temperate regions include: *C. (I.) levinseni* HARMER, 1905; *C. (I.) evansii* RIDEWOOD, 1918; *C. (O.) australiensis* JOHNSTON & MUIRHEAD, 1951; and *C. (I.) gilchristi* (RIDEWOOD, 1906). Those in tropical regions include: *C. (C.) gracilis* HARMER, 1905; *C. (C.) sibogae* HARMER, 1905; *C. (C.) indicus* SCHEPOTIEFF, 1909; and *C. (C.) graptolitoides* DILLY, 1993. Most species were described from fixed specimens acquired at great depths during expeditions of the late 19th and early 20th centuries and have not been studied since. Most recent observations of living colonies were of a shallow water population of *C. (C.) gracilis* from Bermuda.

Zooid morphology is fairly homogenous across species (MALETZ & CAMERON, 2016). Individual zooids are small (1–10 mm) and exhibit the tripartite body plan characteristic of the phylum Hemichordata. The anterior body region (prosome) consists of a ciliated cephalic shield used for locomotion and secretion of the tubarium. The mesosome, or collar region, extends into two to nine pairs of arms (depending on species and developmental stage) used in filter feeding. Ciliated tentacles on each arm capture food particles, and cilia on the arms transport it towards the mouth. The trunk contains the U-shaped digestive tract and extends into an extensible stalk. The stalk ends in an adhesive disk, from which asexually budded individuals originate. Unlike rhabdopleurid

Maletz, Jörg, & Paul Gonzalez. 2017. Part V, Second Revision, Chapter 14: Order Cephalodiscida: Introduction and systematic descriptions. Treatise Online 100:1–8, 4 fig.

pterobranchs, cephalodiscids possess gill slits, a defining feature of Deuterostomia. In enteropneust hemichordates and filter-feeding chordates, the pharynx is perforated with tens to hundreds of gill slits used in pumping water. In cephalodiscids, only one pair of gill slits is present. This reduction may be associated with the evolution of external filter feeding with arms and tentacles in the pterobranch lineage.

Cephalodiscid communities appear to originate from a single, sexually produced founder zooid, comparable to the sicular zooid of the Graptolithina (MALETZ & CAMERON, 2016). Subsequently formed members of the pseudocolony are produced asexually through budding from the base of the stalk. Mature zooids may separate from the stalk of the mother zooid and lead an independent life but stay in the community. Thus, in many tubaria, a number of interconnected zooids (up to 20 in some species) at various stages of development can be found attached to the base of the stalk of the mother individual, and entirely separate individuals may be rare (see LESTER, 1985; DILLY, 2014). Mature zooids formed through asexual budding appear to be able to reproduce asexually. This method of asexual reproduction differs from rhabdopleurid pterobranchs, in which asexually budded individuals remain connected by a stolon system. In this regard, cephalodiscids represent an intermediate strategy between solitary enteropneusts and fully colonial rhabdopleurid pterobranchs.

TUBARIUM CONSTRUCTION

The Cephalodiscida secrete a housing construction, the tubarium, from fuselli and cortical material (with the possible exception of *Atubaria* SATO, 1936, in which zooids appear to be living as naked individuals on corals). Contrasting with their highly conserved zooidal morphology, the tubaria of the Cephalodiscida are very diverse and form the basis of their taxonomy. Because the tubarium is the only feature that can be compared with graptolites, observations on tube building and behavior in extant cephalodiscids may provide insights into the morphology and behavior of extinct species.

The tubaria can be encrusting, compact, or even branched, dendroid in shape, and replicating many shapes, as seen in colonial Graptolithina. In many taxa, the individual dwelling tubes of the zooids are completely separate, forming pseudocolonies where large masses of tubes are connected by or enclosed in extrathecal (cortical?) material. However, in some taxa, a communal dwelling of interconnected tubes or other three-dimensional constructions is formed for the protection of the zooids. Apertural openings may be smooth and straight or bear a variety of elaborations, from robust rutelli to strong apertural spines.

There are three major types of tubarium organization in *Cephalodiscus:* 1) In *Cephalodiscus (Orthoecus),* the tubarium is composed of discrete, nearly straight and parallel-sided tubes (Fig. 1.5). The individual tubes originate from a basal surface, a hardground or rock surface, and create a meadow. Tubes are built of somewhat annular growth increments resembling the fuselli of graptolites and are cemented together by secondary deposits that contain large amounts of embedded foreign material (sand, debris). 2) In *Cephalodiscus (Idiothecia),* the individual tubes are partly enclosed in a thick development of cortical tissue and form erect structures, often with branching stipes. These tubes are closed at the base and have straight to rutellate openings oriented in every direction (Fig. 1.1). Observations in *C. (Idiothecia) nigrescens* show that more than one adult and its buds may share a single tube (DILLY, 2014). 3) In the subgenus *C. (Cephalodiscus),* discrete cylindrical tubes are lacking, and the tubarium consists of an interconnected network of irregularly shaped cavities. The openings in the communal tubaria (often termed ostia) are either simple or adorned with single or multiple spines (Figs 1.2–1.3, 1.6) on which zooids perch to feed (LESTER, 1985). Addition of material between preexisting

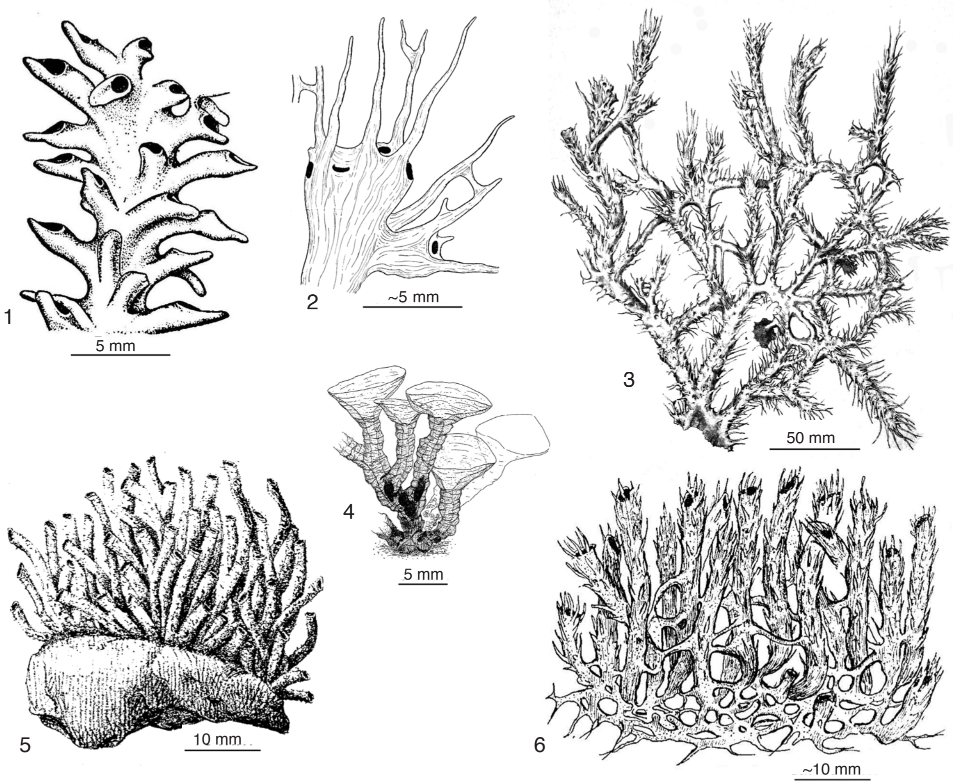


FIG. 1. Tubarium shape in the Cephalodiscidae. *1, Cephalodiscus (Idiothecia) levinseni* HARMER, 1905 (Kozłowski, 1949, fig. 9c); *2, Cephalodiscus (Cephalodiscus) hodgsoni* RIDEWOOD, 1907, fragment showing apertures with multiple spines (John, 1931, fig. 1); *3, Cephalodiscus (Cephalodiscus) dodecalophus* M'INTOSH, 1887 (M'Intosh, 1887, pl. 1); *4, Cephalodiscus (Cephalodiscus) calciformis* EMIG, 1977 (Emig, 1977, fig. 1); *5, Cephalodiscus (Orthoecus) rarus* ANDERSSON, 1907 (Andersson, 1907, pl. 2, *6*); *6, Cephalodiscus (Cephalodiscus)* sp. (Dawydoff, 1948, fig. 82).

spines is common, and spines are often embedded into the walls of the tubarium. Most species form erect branching tubaria, with lateral connections resembling the dissepiments and anastomosis of the Graptolithina. Encrusting forms are also found (for example, *Cephalodiscus graptolitoides*). Thecal apertures of the *Cephalodiscus (Cephalodiscus) calciformis* EMIG, 1977 have a very unusual shape, a wide, funnel-shaped structure not found in any other pterobranch (Fig. 1.4). The tubes of the tubarium are interconnected and inhabited by the zooids and their attached asexually developing buds. These zooids are comparable to those in other species of *Cephalodiscus (Cephalodiscus),* but little detail is known about their development and interconnection. In the monospecific subgenus *Acoelothecia*, the tubarium is dissolved into a complex mesh of spines and bars in which the zooids roam freely.

The phylogeny of the extant subgenera of *Cephalodiscus* is unresolved, and as a result, the relationships of the constructional features of their tubaria are unknown. The complete individual tubes of *Cephalodiscus (Idiothecia)* RIDEWOOD, 1906 and *Cephalodiscus (Orthoecus)* ANDERSSON, 1907 may represent the plesiomorphic mode of tubarium construction, as their features are shared with those of the closely related Graptolithina.

In many aspects, the tubarium construction of the Cephalodiscidae shows features also apparent in the construction of the tubaria of the Graptolithina. Erect tubaria show branching and lateral connection of "stipes," even though the zooids do not work in a colony but are separate as individuals. Gonzalez and Cameron (2012) investigated the ultrastructure of *Cephalodiscus* tubaria in the subgenera *Cephalodiscus*, *Idiothecia,* and *Orthoecus* and noted a continuum in thickness and development of fusellar-like and cortical-like layers but were unable to recognize clearly differentiated cortical bandages. The investigation indicated that fibril type and arrangement may be evolving independently from larger scale features of the pterobranch tubaria. The interpretation of cortical material in *Cephalodiscus* (see Kozłowski, 1967; Dilly, 1993) may be misleading, as the material is not differentiated into the distinct bandages of the Graptolithina (see, for instance, Crowther & Rickards, 1977; Crowther, 1978, p. 474). Thus, the evolutionary origin of the cortical bandages might not be traced back to the cephalodiscids.

THE FOSSIL RECORD

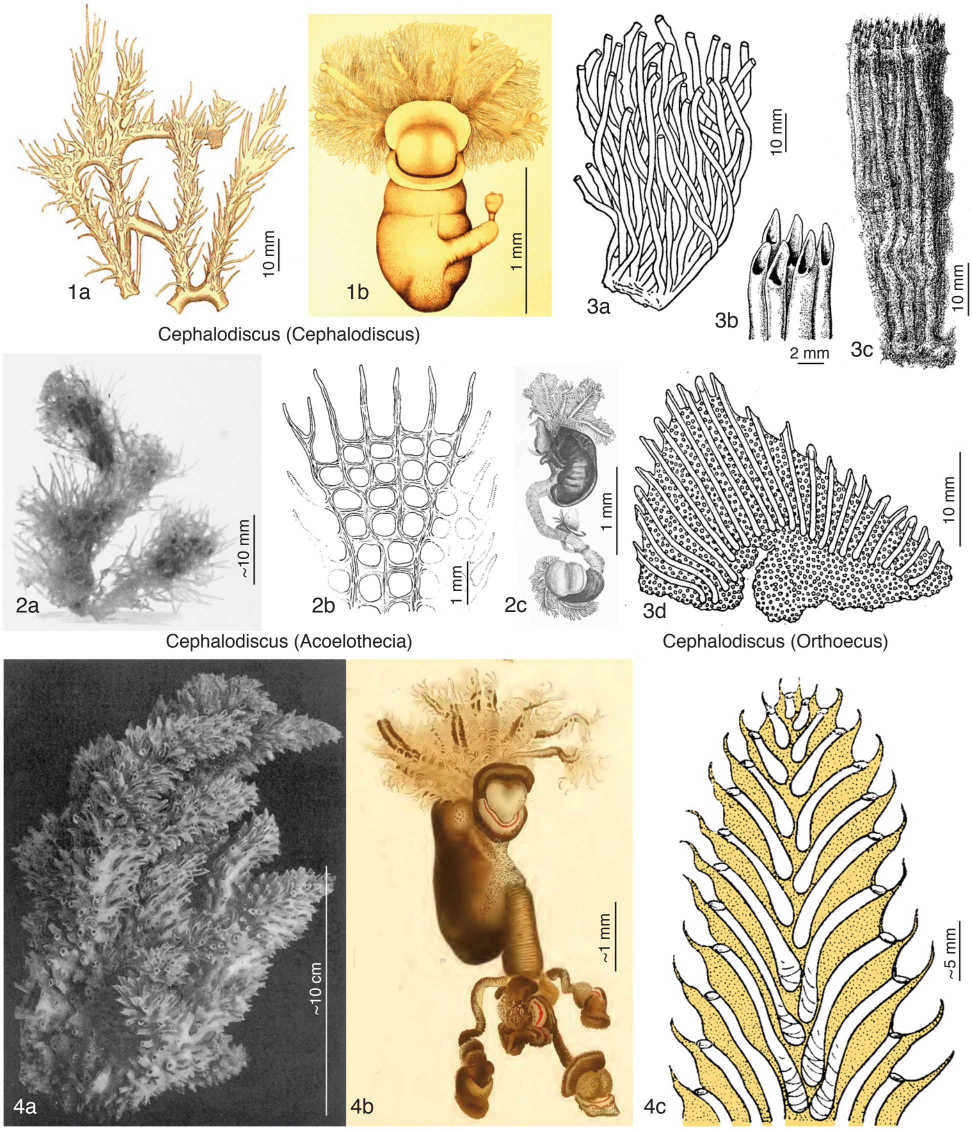
The Cephalodiscida are mainly known from modern, extant taxa, but a few possible fossil cephalodiscid taxa have been described. These are preserved only in the form of their tubaria, and their zooids are absent from the fossil record. As a result, differentiating fossil cephalodiscids from closely related Graptolithina can be difficult as interconnected housing constructions are present in both taxa. The oldest possible cephalodiscid taxon may be a fragment found in the Kaili Formation of China (Harvey & others, 2012), but the poor preservation precludes the identification as a cephalodiscid or graptolitid (Maletz, 2014).

Rickards and Durman (2006) referred the upper Cambrian genus *Aellograptus* Obut, 1964 and its type species *A. savitskyi* Obut, 1964 to *Cephalodiscus,* thus synonymyzing *Aellograptus* with *Cephalodiscus*. The genus is here kept as a separate cephalodiscid genus, as details of the tubarium construction are not available. The size difference from *Cephalodiscus levinseni* tubaria quoted by Rickards and Durman (2006) may be regarded as a species-specific character. Other potential cephalodiscid genera are the Ordovician taxa *Eocephalodiscus* Kozłowski, 1949, *Melanostrophus* Öpik, 1930, and *Pterobranchites* Kozłowski, 1967. Of these, only *Eocephalodiscus* has unanimously been referred to the cephalodiscids, and to its own family Eocephalodiscidae (see Kozłowski, 1949). The affinity of the genus *Melanostrophus* has been the focus of a long debate. The genus was known from very fragmentary and poor material, in which Eisenack (1937) first recognized fusellar construction. Zessin and Puttkamer (1994) discussed new material of *Melanostrophus* and erected the family Melanostrophidae for this taxon. Mierzejewski and Urbanek (2004) referred to *Melanostrophus* as a "*Cephalodiscus*-like taxon" based on their investigation of isolated fragments. *Pterobranchites* is known from small fragments and its tubarium construction is unknown. Similarities to the encrusting *Cephalodiscus graptolitoides* may be seen. Schweigert and Dietl (2013) described *Cephalodiscus? nusplingensis* as a possible cephalodiscid pterobranch from the Upper Jurassic Nusplingen lithographic limestone of Germany but were unable to verify the presence of fusellar construction.

Family CEPHALODISCIDAE
Harmer, 1905

[Family Cephalodiscidae Harmer, 1905, p. 5] [incl. Eocephalodiscidae Kozłowski, 1949, p. 194; Melanostrophidae Zessin & Puttkamer, 1994 p. 564; Atubaridae, *nomen dubium;* herein]

Fixed, sedentary marine organisms with communal zooids divided into three regions, the preoral lobe (cephalic shield), collar, and trunk; collar extends to form several pairs of arms, each bearing double row of ciliated tentacles; trunk elongated posteriorly to form stalk with sucker at base, from which new zooids are generated asexually; external proteinaceous housing or domicile (the tubarium) composed of series of tubes built from sequential addition of full rings or half rings of organic material in most taxa; tubaria with separate zooidal tubes to communal dwellings, lacking in one genus.



Cephalodiscus (Cephalodiscus)

Cephalodiscus (Acoelothecia)

Cephalodiscus (Orthoecus)

Cephalodiscus (Idiothecia)

FIG. 2. Extant Cephalodiscidae (p. 6–7).

Cambrian (Series 3, ?Stage 5)–Holocene: worldwide in marine environments.

The Cephalodiscida include a single family, the Cephalodiscidae HARMER, 1905. A differentiation of the Eocephalodiscidae KOZŁOWSKI, 1949 for fossil members appears unnecessary, as is the introduction of the Melanostrophidae ZESSIN and PUTTKAMER, 1994, based on the taxon *Melanostrophus*, recently recognized as a possible cephalodiscid pterobranch (MIERZEJEWSKI & URBANEK, 2004). The later authors rejected the genus *Stolonofolliculus* ZESSIN & PUTTKAMER, 1994 with its type *Melanostrophus signum* ÖPIK, 1930 and, thus, the Stolonofolliculidae ZESSIN and PUTTKAMER, 1994 as a *nomen dubium* (MIERZEJEWSKI & URBANEK, 2004, p. 521–522). The name Atubaridae has been used in Encyclopedia of Life and Catalogue of Life (online at eol.org), but appears to be a

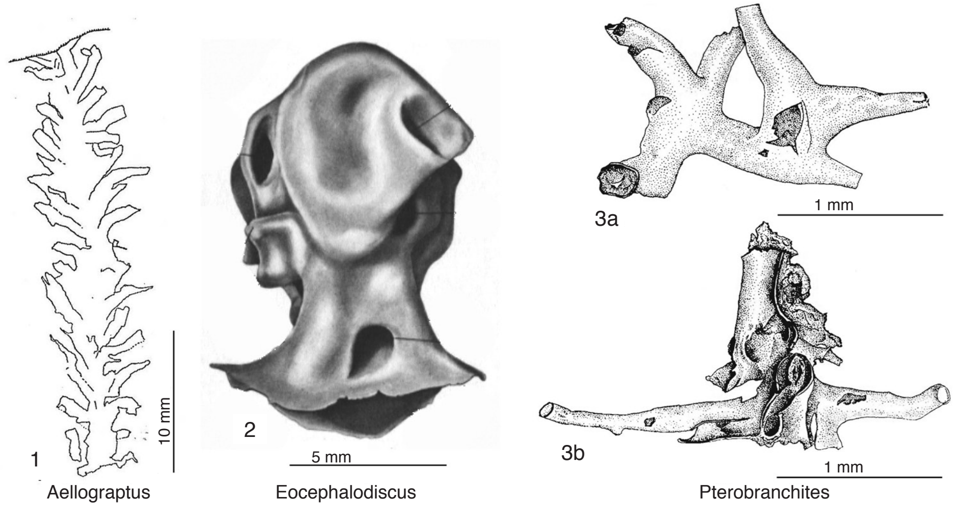


FIG. 3. Fossil Cephalodiscidae (p. 7).

nomen dubium, as a published diagnosis and description is not available.

A number of subgenera have been erected in the genus *Cephalodiscus* based on the tubarium construction but not on the anatomy of the zooids. If known from the fossil record only, these subgenera would certainly have been treated as separate genera.

Cephalodiscus M‘Intosh, 1882, p. 348 [**C. dodecalophus;* OD]. Tubarium composed of series of tubes secreted from the sequential addition of full rings or half rings of organic material in most taxa; tubarium with separate zooidal tubes to communal dwellings and may be reduced to a meshwork of bars; tubarium shape varies from encrusting to erect and branching; with or without spines at apertures. *Cambrian (Series 3, ?Stage 5)–Holocene:* worldwide in marine environments.

C. (**Cephalodiscus**) M‘Intosh, 1882, p. 348 [**C. dodecalophus;* OD] [=*Demiothecia* Ridewood, 1906, p. 191 (type species never selected)] [non *Cephalodiscus* Berlese, 1918, p. 12; =*Capitodiscus* Vitzthum, 1931, p. 144; Arachnida]. Encrusting to erect branched tubarium with communal cavity open to all zooids; apertures with single or multiple long spines. *Cenozoic (Eocene)–Holocene* (extant): worldwide.——Fig. 2,*1a–b*. **C. (C.) dodecalophus* (type specimen not designated by M‘Intosh, 1882); *a,* fragment of tubarium showing branches and bridges, long apertural spines common; *b,* zooid with attached bud (M‘Intosh, 1887, pl. 2).

C. (**Acoelothecia**) John, 1931, p. 241 [**C. (A.) kempi;* M]. Tubarium consists of meshwork of spines and bars; no true communal cavity present; spaces between meshwork irregular and occupied by zooids and their buds. *Holocene* (extant): Antarctic Ocean (Ross Sea, Victoria Land, McMurdo Sound, Ross Island, Cape Royds).——Fig. 2,*2a–c*. *C. (A.) kempi* (type specimen not designated by John, 1931); *a,* part of tubarium (John, 1931, pl. 34,*2*); *b*, small piece showing spines and bars (John, 1931, fig. 4); *c,* zooid with buds (John, 1931, pl. 35,*2*).

C. (**Idiothecia**) Ridewood, 1906, p. 191 [**C. nigrescens* Lankester, 1905, p. 400; SD Bulman, 1970, p. 17)]. Tubaria with individual tubes for each mature zooid; tubarium erect, with complex stipes or without branching; apertures with blunt lips or rutelli; individual tubes enclosed in masses of spongy material forming bulk of tubarium; in longer tubes lower part may be closed off; zooids lack end swellings or refractive beads on arms (John, 1931, p. 233–235). *Holocene* (extant): worldwide.——Fig. 2,*4a–c*. *C. (I.) nigrescens; a,* holotype, tubarium (Lankester, 1905, pl. 8); *b,* zooid with several buds (Ridewood, 1907, pl. 3,*8*); *c,* section through tubarium (Dawydoff, 1948, fig. 83; Ridewood, 1907, pl. 4,*10*).

C. (**Orthoecus**) Andersson, 1907, p. 11 [**C. solidus;* SD Bulman, 1970, p. 17)]. Encrusting tubaria with individual tubes for each mature zooid; basal parts of tubes may be connected by extratubarial spongy material; individual tubes laterally connected to each other or distally free and isolated; apertures simple, straight, or with short rutellum. *Holocene* (extant): worldwide.——Fig. 2,*3a*. *C. (O.) densus* Andersson, 1907, small tubarium; see Ridewood, 1918, p. 40 for synonymy of *C. rarus* (Kozłowski, 1949, fig. 9A).——Fig. 2,*3b–d*. **C. (O.) solidus;* thecal apertures *(b)* and fragment *(c)* of tubarium

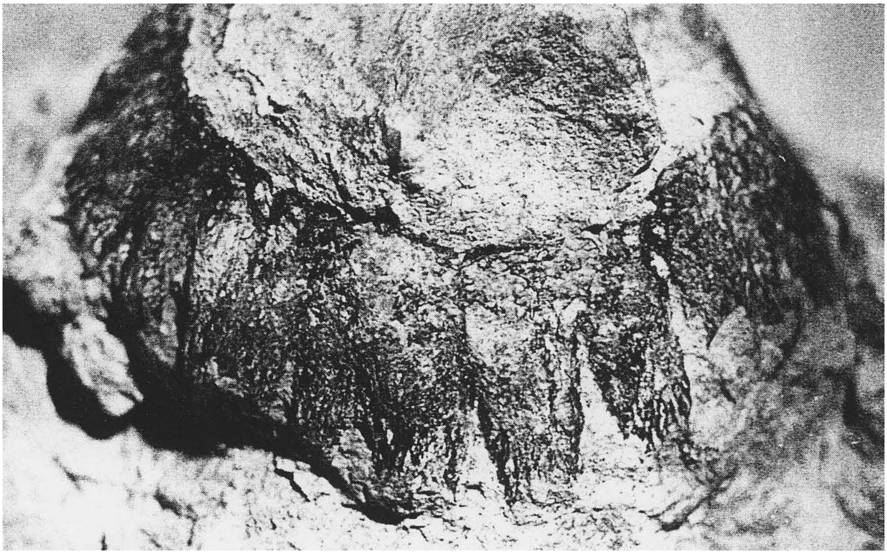


FIG. 4. Fossil Cephalodiscidae (p. 7).

(Kozłowski, 1949, fig. 9); *d*, specimen showing sand grains in the tissue surrounding the zooidal tubes (Ridewood, 1918, fig. 2).

Atubaria SATO, 1936, p. 105 [**A. heterolopha;* OD]. Cephalodiscid zooids without known tubarium. *Holocene* (extant): Asia (Japan, Dyogasima, Sagami-Bay, east side of Honshu). Illustration in MALETZ and CAMERON (2016, fig. 4).

Aellograptus OBUT, 1964, p. 306 [**A. savitskyi;* M]. Elongate, unbranched, or sparsely divided tubarium with numerous short, projecting, cylindrical thecae. *Cambrian (Furongian, Paibian):* Russia (Siberia), Australia (Tasmania).——FIG. 3.*1*. **A. savitskyi,* paratype, SM A79058, Siberia (Rickards & Durman, 2006, fig. 23B).

Eocephalodiscus KOZŁOWSKI, 1949, p. 195 [**E. polonicus;* OD]. Compact tubarium with isolated chambers for zooids; chambers with large round openings; no apertural elaborations. *Lower Ordovician (Tremadocian):* Poland.——FIG. 3,*2*. **E. polonicus,* holotype (Kozłowski, 1949, pl. 33,*1b*).

Melanostrophus ÖPIK, 1930, p. 10 [**M. fokini;* OD]. Skeleton composed of long, slender, circular, subcircular, or subpolygonal erect zooidal tubes, rarely branched; zooidal tube wall made of thin fusellar layer and very thick outer and inner cortical deposits; tubes fused by their walls to form a cuplike colony. *Middle Ordovician (Upper Darriwilian)–Upper Ordovician (Sandbian,* Kukruse Stage): Estonia, Germany (glacial boulder).——FIG. 4. **M. fokini,* scale unknown (Zessin & Puttkamer, 1994, fig. 2).

Pterobranchites KOZŁOWSKI, 1967, p. 123 [**P. antiquus;* OD]. Tubarium of irregularly aggregated tubes and elongated vesicles; no apertural elaborations. *Lower Ordovician (Tremadocian):* Poland (glacial boulder).——FIG. 3,*3a–b*. **P. antiquus,* syntypes, two fragments of a single colony (Kozłowski, 1967, fig. 11).

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