A New Species of *Pachycerianthus,* with a Discussion of the Genus and an Appended Glossary[1]

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ABSTRACT: A new species of *Pachycerianthus* from southern California is described and the status of the genus is discussed. A glossary of the terms used in the taxonomy of the order is appended.

The order Ceriantharia consists of long, solitary, anemone-like Anthozoa, without a pedal disc or external skeleton, with numerous single tentacles in two crowns, coupled mesenteries, and a single siphonoglyph. Earlier authors related these anemones to the Actiniaria, but they are recognized by recent authors, such as Wells and Hill (1956), as being most closely related to the Antipatharia or "black corals."

Previous knowledge of the taxonomy and morphology of the Californian Ceriantharia is meagre. McMurrich (1893:202–203) described a species, *Cerianthus vas,* from one poorly preserved specimen that had been collected at Isla de Cedros, Baja California, Mexico. The whereabouts of this specimen is unknown and the information given is insufficient to allow identification of the species or to place it in any recent genus or family. Torrey and Kleeberger (1909) described three species: *Cerianthus aestuari, C. benedeni,* and *C. johnsoni,* basing their descriptions on animals collected from Mission Bay, San Diego Bay, and San Pedro Harbor, California, respectively. The description of the latter species was based on two specimens. Although these descriptions were incomplete, enough morphological data were given so that McMurrich (1910:11) placed *Cerianthus benedeni* in the genus *Botruanthus,* which he erected for it. He placed the other two species in the genus *Pachycerianthus* Roule. Carlgren (1951:433–436) described *Pachycerianthus insignis* from a single incomplete specimen, and redescribed *Botruanthus benedeni* from four specimens, all taken from the Gulf of California.

Child (1908) reported on regeneration in *Pachycerianthus aestuari.* Other authors have referred to forms collected in California, but have not identified them. When specimens were obtained by divers near Los Angeles it was found that they belonged to previously undescribed species. One of these species is described here with a discussion of the genus *Pachycerianthus* in which it is placed.

As indicated by Torelli (1960:373), the terminology used for the various anatomical structures in the Ceriantharia is greatly confused in the literature. A glossary of terms used in the taxonomy of this group is therefore appended, and the terminology used throughout this work has been standardized for uniformity.

Material and Methods

The sea anemones on which the anatomical descriptions are based were collected by Dr. Rimond Fay and Mr. Philip Bernard of the Pacific Bio-marine Supply Company between July, 1958 and August, 1960 and were maintained in the sea water tanks of the Department of Zoology, University of California at Los Angeles. On removal from the tanks, the animals were anaesthetized for 2–8 hours in equal parts of sea water and a solution of 0.36M $MgCl_2.6H_2O$. They were fixed for approximately 15 minutes in 10% neutral formalin (with an excess of $MgCO_3$), overnight in picro-formol solution (one part concentrated formalin: 3 parts saturated picric acid), and stored in 70% ethanol. In each case the solutions were pipetted into the coelenteron.

Preliminary identification of nematocyst types was done on fresh material. The nematocyst

[1] Much of the data presented in this paper was included in a dissertation submitted to the University of California, Los Angeles, in partial fulfillment of the requirements for the Ph.D. degree. Manuscript received February 3, 1964.

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measurements given in this section were obtained from portions of five of the paratypes of the species sectioned and stained with Heidenhain's iron hematoxylin and eosin, Mallory's triple stain, and acid haemalum and light green. Ten nematocysts of each type were measured in each portion of each animal examined.

RESULTS AND DISCUSSION

Family CERIANTHIDAE

DIAGNOSIS: Ceriantharia without acontioids or cnidorages.

Genus *Pachycerianthus* Roule, 1904.

DIAGNOSIS: Cerianthidae with the second couple of protomesenteries short and sterile. Arrangement of metamesenteries in each quartette M,B,m,b (1,3,2,4) more or less distinct.

DISCUSSION

Torelli (1961:25–27) claims that the genus *Pachycerianthus* proposed by Roule (1904*a*: 792–793) is invalid since it is not clearly distinguished from the genus *Cerianthus*. Her opinion is partly based on an incorrect interpretation of the terms in the literature. It is therefore first necessary to trace briefly the history of some of the terms used to describe the mesenterial filaments and their appendages.

Haime (1854:374) noted the presence of "cordons pelotonnes" along the edge of some of the mesenteries of *Cerianthus membranaceus*. Von Heider (1879:216–217) and Hertwig and Hertwig (1879:578–580) described the "Mesenterial-filamente" of the same species in more detail. The mesenteries of this species have numerous branching appendages, the "Mesenterialfaden," which are not homologous to the acontia of the Actiniaria (as von Heider thought), since they possess ascending and descending limbs of the mesenterial filament separated by a portion of endoderm. Van Beneden (1897:27–37) further investigated the structure of the "filaments mésentériques," or "craspedes" of Gosse (1860:xxiii) in specimens of several adult and larval species. He found "fils mésentérique" with a structure similar to Hertwig and Hertwig's "Mesenterialfaden" and also, in several larval species, much longer and rounder appendages near the posterior end of the mesentery which he believed to be true "acontie." McMurrich (1910:19) used the term "craspedoneme" to distinguish Hertwig and Hertwig's "Mesenterialfaden" from these "acontia."

Carlgren (1912*a*:68–72; 1912*b*:383–385), re-investigating the same species examined by van Beneden, showed that true acontia were not present even there but rather structures homologous with the craspedonemes were present in which the endoderm was reduced so as to be surrounded by the two limbs of the filament. Bourne (1919:60–61) also noted differences between the "acontia" of Ceriantharia and those of the Actiniaria. In some portions of the collected works of van Beneden published posthumously in 1923, the term "acontie" is used. However, in another portion he, in agreement with the above authors, also states that the Ceriantharian structures are not homologous with those of the Actiniaria. Carlgren suggested the term "mucocraspedoneme" for the structures found in the Ceriantharia, but in later papers adopted the term "acontioid" introduced by Pax (1914:394).

With this background, no purpose was served by Torelli's statement (1960:376–379) that acontia are not present in Ceriantharia, especially since her opinion was based on an investigation of two species for which previous authors had not even claimed the presence of acontioids, i.e., *Cerianthus membranaceus* and *Pachycerianthus dohrni* (the *Cerianthus viridis* of her paper).

We may now consider the description of *Pachycerianthus*. Roule (1904*a*: 792–793; 1904*b*:708–710) described *Pachycerianthus benedeni* and designated it the type of the genus. The description is poor but includes the following characters of possible generic significance:

1. Mesenteries are short; only the ventral mesenteries (S_3 in the terminology proposed by van Beneden) reach the aboral extremity and border a narrow band which continues the sulcus and contains the vestiges of the D and S_1 mesenteries.

2. The mesenteries on either side of the S_3 diminish in length toward the dorsal region but do not show a distinct quatro-septal dispo-

sition; the irregular diminution gives them, rather, a biseptal arrangement.

3. All the mesenteries, except those which occupy exactly the dorsal region, possess some "craspedes" in the zone placed immediately below the enterostome. Some mesenteries have "fils mésentériques" on their "craspedes," and alternating ones do not carry them. The mesenteries deprived of "fils mésentériques" are fertil and possess "aconties" on a rather large part of their inferior extremity; their series begins with the S_3 and continues with the uneven numbered mesenteries S_5, S_7, S_9, etc.

As Torelli (1961:25–27) pointed out, this description is extremely incomplete, and hence it is very difficult to place the genus in the modern classification of the order. Some of her comments (1960:374–375; 1961:25) about the lack of clarity can be discounted, however, since she has translated incorrectly the term "fils mésentériques" in the third item above as mesenterial filaments. As noted earlier the term was used by van Beneden (1897:33) and other French authors to refer rather to the "Mesenterialfaden" or craspedonemes. Correctly translated, the third passage states that some mesenteries have craspedonemes on their "craspedes" or mesenterial filaments and alternate mesenteries have "aconties" on them.

It is the interpretation of the term "aconties" in the third passage above that is most problematical. McMurrich (1910:10–14, 22–24), in his classification of the order, placed the genus in a family characterized by the presence in the larva of "acontia" or, as they were later called, acontioids, but included adult species both with and without acontioids. Carlgren (1912*a*:37–48) believed that the structures must be ordinary craspedonemes since acontioids in all the better known species are single, rather than scattered over a large part of the lower end of the mesentery. He placed the genus in the family Cerianthidae characterized by the lack of both acontioids and cnidorages. Although Carlgren is probably correct, the question can only be resolved definitely by reference to the type specimen; unfortunately the location of this material is at present unknown. In the meantime we may assume, as Torelli (1961:26) also does, although for the wrong reason, that these appendages are ordinary craspedonemes. *Pachycerianthus* is therefore retained in the Cerianthidae.

Without re-examination of the original material, Carlgren (1912*a*:40–48) defined the genus *Pachycerianthus* as "Cerianthidae whose second couple of protocnemes are short, sterile, and provided with an extremely well-developed region of the cnido-glandular tract. Arrangement of the metacnemes (=deuterocnemes McMurrich) in each quartette M,B,m,b (1,3,2,4) more or less distinct." He originally included eight species in the genus and later (1924*a*: 182–186; 1940:15; and 1951:435–436) added three more. All of these species (even *P. benedeni,* if we are considering the first quartette) have M,B,m,b metamesenterial arrangement. All except *P. benedeni* are known to have short, sterile second protomesenteries, and it is probable that in that species they are also sterile since very small mesenteries are rarely fertile. However, Carlgren has placed in the genus several species (including *P. benedeni*) in which the extent of the cnido-glandular tract is unknown, and also others, such as *P. maua,* in which it is very short. In addition, as Torelli (1960:375–376) has indicated, the distinctness of the histological demarcation by Carlgren (1912*a*:59–67) of the mononeme into the cnido-glandular tract and the craspedion is questionable. (The mononeme is the aboral monofilar portion of the mesenterial filament.) It seems desirable therefore that this character be eliminated as a differential one not only in this but in all genera of cerianthids.

The 10 species (other than *P. benedeni*) placed in the genus by Carlgren comprise a distinct taxonomic entity with the remaining characters with which Carlgren defined *Pachycerianthus* and with no acontioids. *C. bicyclus* Torelli, 1961 and *P. torreyi* n.sp. of the present work may also be added. This group is separated from the genera *Cerianthus, Cerianthe-opsis,* and *Ceriantheomorphe* by the possession of short, sterile second protomesenteries, and from *Ceriantheopsis* by the MBmb arrangement of the metamesenteries in *Pachycerianthus.* Torelli (1961:27) does not believe that the properties of the second protomesenteries

are important enough to serve as generic characters or to distinguish *Pachycerianthus* from *Cerianthus*. These mesenteries, however, are the first couple of mesenteries to develop and could therefore be expected to be the most stable in the grown animal. McMurrich (1910: 23–24) considered the form of these mesenteries to be characteristic, even at the familial level.

In summary, it should be stated that an intensive search must be made for the type specimen of *P. benedeni*. It is not in the collections of the Musée Océanographique de Monaco, the Musée de Bruxelles, the British Museum (Natural History), or the Museum National d'Histoire Naturelle, Paris, the most likely repositories. If it cannot be found, it will be necessary to declare the species a *nomen dubium*. Since the other twelve species presently included in the genus appear to constitute a taxonomic entity, the declaration of the *nomen dubium* would necessitate selection of a new type species and generic name for the taxon. In the meantime, *Pachycerianthus* is retained in the Cerianthidae and includes the following species: *P. aestuarii* (Torrey and Kleeberger, 1909); *P. benedeni* Roule, 1904; *P. bicyclus* (Torelli, 1961) n. comb.; *P. dohrni* (van Beneden, 1923); *P. fimbriatus* McMurrich, 1910; *P. insignis* Carlgren, 1951; *P. johnsoni* (Torrey and Kleeberger, 1909); *P. maua* (Carlgren, 1900); *P. monostichus* McMurrich, 1910; *P. multiplicatus* Carlgren, 1912; *P. plicatus* Carlgren, 1924; *P. solitarius* (Rapp, 1829); and *P. torreyi* n. sp.

Pachycerianthus bicyclus is distinguished from all other members of the genus by having two cycles of marginal tentacles but three or four cycles of labial tentacles, and lacking craspedonemes but possessing aboral appendices on the second protomesenteries and first order metamesenteries. Torelli (1961:24–25) states that the specimens from which *P. bicyclus* was described may not have reached full growth, so that the species may prove to be an immature stage of another. Since *P. solitarius* from the same area differs only in the number of cycles of marginal tentacles, these species will probably prove to be synonymous.

Pachycerianthus torreyi n. sp.

DIAGNOSIS: Siphonoglyph running length of actinopharynx. Directive mesenteries extending well beyond siphonoglyph. Second protomesenteries between once and twice length of directives. Metamesenteries having definite MBmb arrangement. M_1 definitely longer than any other mesentery. M_3 longer than M_2. m_2 and m_3 shorter than m_1. B_1 shorter than P_3. M_1 with trineme almost to end of mesentery, craspedonemes scattered over most of its length, very short or no mononeme.

LOCALITIES: Latigo Cove; and just inside breakwater, Los Angeles Harbor (type locality), California.

HABITAT: 12–18 meter depth; in mud, or mixed gravel and mud, bottom.

HOLOTYPE and PARATYPES: To be deposited in USNM.

DESCRIPTION (based on 10 adult specimens):

Coloration of live animals. Column red-brown, darkest just below oral disc and toward aboral pore, with narrow buff ring immediately around aboral pore. Marginal tentacles buff (shading to bright pink towards tips in one specimen). Oral tentacles darker, with purplish tinge.

Coloration of animals fixed in picro-formol. Red pigments of live animals faded, leaving column light yellow-brown, tentacles yellowish buff.

Length in anaesthetic. 13–31 cm (type 18.5 cm).

Tentacles. Marginal arrangement 2(dt)431.4231.4231... Labial arrangement 2(dt)313.4232.4312... or 3(dt)413.4232.4312... (type). In each crown division into third and fourth cycles indistinct in some specimens. Directive labial tentacle present. Marginal tentacle number approximately 90–125 (type approximately 100).

Siphonoglyph. Running length of actinopharynx. Attached mesenteries 10 (type) or 12. Hyposulcus indistinct, less than one-tenth length of siphonoglyph. Hemisulcus distinct, flat orally, continued down directive mesentery as a filament without ciliated tracts.

Protomesenteries. Directive mesenteries shorter or longer (type) than siphonoglyph. Second protomesenteries sterile, less than twice length of directive mesenteries, with aboral lobe varying greatly in length (long in type), trineme running to near tip of aboral lobe, usually (type) with several craspedonemes at aboral end of trineme, convoluted mononeme running around tip of lobe. Third protomesenteries sterile, approximately same length (type) or shorter than P_2, longer than P_1, trineme much shorten than in P_2 with a number of craspedonemes at aboral end, mononeme relatively long and highly convoluted along border of broad section of mesentery.

Metamesenteries. Definite MBmb arrangement (Fig. 1). Reproductive organs in macrosepta only. M_1 mesenteries at least five-sixths length of column, never reaching aboral pore; remaining mesenteries less than two-thirds length of M_1 in most specimens (longest mesentery approximately seven-eights of M_1 in one specimen). Macrosepta generally decreasing in length toward multiplication chamber; M_3 longer than M_2, m_2 and m_3 shorter than m_1, m_3 longer or shorter (type) than m_2. M_1 with trineme almost to aboral end of mesentery, craspedonemes scattered over most of its length, sometimes with an aboral lobe of mesentery or bunch of craspedonemes at aboral end of trineme, short mononeme (type) or none, reproductive region to above level of craspedonemes, hermaphroditic. Macroseptum m_1 with long trineme terminating much farther from aboral end than in M_1, trineme with scattered craspedonemes and sometimes with an aboral bunch, mononeme well developed, convoluted or straight (slightly convoluted in type). Extent and form of trinemes and mononemes of other macrosepta variable. B_1 shorter than P_3, with short trineme with bunch of craspedonemes at aboral end, highly convoluted mononeme along broad section of mesentery. Other B and b with structure similar to B_1 although bunch of craspedonemes of trineme may be reduced or absent.

Nematocysts (based on five adult specimens). Of column, atrichs 29.6–83.2 × 5.0–29.6 μ very common, microbasic b-mastigophores 18.5–43.2 × 3.2–8.0 μ scarce, holotrichs 42.2–67.6 × 10.0–16.2 μ rare. Of marginal tentacles, atrichs 24.0–36.8 × 4.0–7.2 μ scarce, microbasic b-mastigophores 20.0–49.6 × 3.0–9.0 μ common, spirocysts 7.6–43.2 × 1.2–5.6 μ numerous. Of labial tentacles, atrichs 24.0–33.6 × 3.6–6.4 μ scarce, microbasic b-mastigophores 19.2–45.2 × 2.0–8.4 μ common, spirocysts 13.2–33.6 × 1.2–5.2 μ numerous. Of actinopharynx, atrichs 24.8–40.8 × 3.6–6.4 μ scarce, microbasic b-mastigophores 20.8–44.4 × 2.8–7.6 μ common, spirocysts 11.2–26.8 × 1.6–4.4 μ very rare. Of ciliated tract of macroseptum,

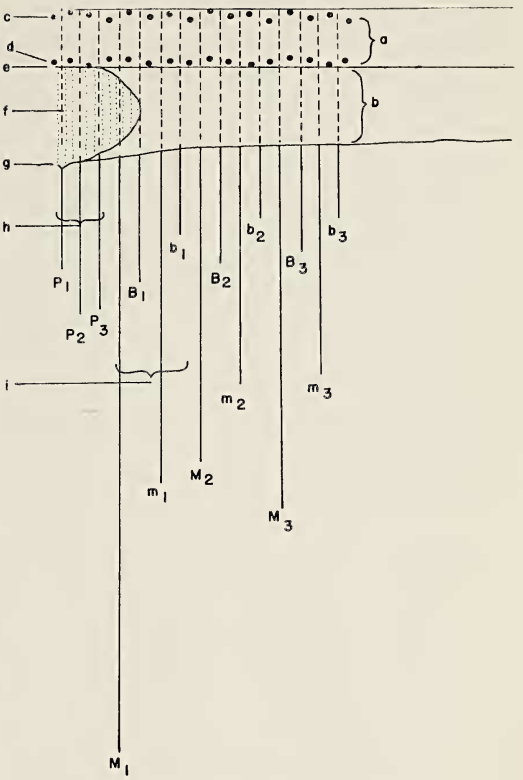

FIG. 1. Diagram of the internal arrangement of *Pachycerianthus torreyi*. View of half the animal cut longitudinally and pinned flat. Approximately ½ × vertically, 5½ × horizontally. *a*, Oral disc; *b*, actinopharynx; *c*, marginal tentacle bases; *d*, labial tentacle bases; *e*, mouth; *f*, siphonoglyph; *g*, hemisulcus; *h*, protomesenteries; *i*, first quartette of metamesenteries; P_1, directive mesentery; P_2, second protomesentery; P_3, third protomesentery; M_1, M_2, M_3, first order metamesenteries; m_1, m_2, m_3, second order metamesenteries; B_1, B_2, B_3, third order metamesenteries; b_1, b_2, b_3, fourth order metamesenteries.

atrichs 21.2–32.8 × 2.4–4.4 μ rare or absent, microbasic b-mastigophores 18.4–50.8 × 2.8–9.2 μ scarce, spirocysts 14.4–26.8 × 1.8–5.2 μ common. Of peloton of microseptum, microbasic b-mastigophores 18.4–30.0 × 4.4–7.6 μ very common.

Pachycerianthus torreyi is clearly distinguished from the two species described by Torrey and Kleeberger (1909) from southern California. The present species and *P. aestuari* differ in that the latter possesses a siphonoglyph which does not reach the lips of the actinopharynx and has four mesenteries commonly reaching the terminal pore. Other characters of *P. aestuari* which may differentiate it from *P. torreyi* are a tentacle number which never exceeds 34, a single cycle of marginal tentacles, and a very broad siphonoglyph.

Pachycerianthus johnsoni differs from *P. torreyi* in that the directive mesenteries do not extend beyond the siphonoglyph, as is the case in the present species. Other characters of *P. johnsoni* with possible diagnostic value are that gonads are frequently borne on the third order mesenteries, that the siphonoglyph is narrow, and that the B_1 may be longer than the P_3. Among approximately one hundred cerianthid specimens taken and examined from deeper water in Los Angeles Harbor, the type locality for *P. johnsoni,* no specimens of this species were found. It is probable that it is a shallow water species and that the mud-flat habitat where the two specimens were collected has been eliminated by harbor installations.

The clarity with which the present species can be distinguished from the other species included in the genus depends, in good part, on the detail in which they have been described. We have seen that the type species, *P. benedeni,* was very poorly described, but it is possible to distinguish it since there is a regular diminution in the length of the metamesenteries, i.e. M_3 is shorter than M_2. *Pachycerianthus insignis,* based on a single incomplete specimen from the Gulf of California, has several metamesenteries almost reaching the aboral pore, and a P_2 that is more than twice the length of P_1.

Pachycerianthus torreyi is most similar to *P. plicatus,* an Indonesian species, differing only in the relative lengths of the M_2 and M_3 mesenteries. *Pachycerianthus fimbriatus,* from the same area as *P. plicatus,* differs in the same character and possibly in the arrangement of the labial tentacles. *Pachycerianthus bicyclus* and *P. solitarius* differ from *P. torreyi* in the absence of craspedonemes of the trineme and in that several M mesenteries nearly reach the aboral pore. The latter character may also be used to distinguish *P. monostichus, P. dohrni,* and *P. multiplicatus* from the present species. *Pachycerianthus maua* differs by having the M_3 mesentery shorter than the M_2, and also by possessing an unusual type of aboral craspedoneme.

The name, *torreyi,* is in honor of Dr. H. B. Torrey, one of the earliest workers on cerianthárian taxonomy in California.

GLOSSARY

As Torelli (1960:373) has pointed out, the terminology applied to the Cerianthária has become exceedingly complicated through the multiplication of terms. In the following glossary the full definition of a structure has been placed with the presently accepted term and other terms have been referred to this definition. English nomenclature or anglicised terms are used. Terms have been added from other languages where these are not direct translations. The application of certain terms to related groups of animals has been given when they are likely to cause confusion.

1 (metamesentery) (Carlgren, 1912*b*:368)—longest metamesentery in each quartette, i.e. metamesentery of the first order.

1 (tentacle) (Carlgren, 1900:25–26; McMurrich, 1910:17–18)—tentacle of innermost cycle of a crown.

1 subscript (metamesentery) (Carlgren, 1924*a*: 169–170)—belonging to first metamesenterial quartette (*q. v.*).

1 subscript (protomesentery) (Carlgren, 1912*a*: 12)—belonging to first protomesenterial couple.

1 superscript (Beneden, 1923:24–25)—closest structure to siphonoglyph in metasome (*q. v.*).

1d superscript (Beneden, 1897:10–11)—first structure to right with reference to directive plane at the siphonoglyph.

1g superscript (Beneden, 1897:10–11)—first structure to left with reference to directive plane at siphonoglyph.

a superscript (Beneden, 1923:23)—belonging to second somatomere of the prosome (*q.v.*).

Acontioid (Pax, 1914:394)—long threadlike, simple or slightly branched craspedoneme, rounded in cross section, with many mucous cells and reduced endoderm, at or near aboral end of mesenterial filament.

Acontium (Gosse, 1858:125; 1860:xxiii–xxv, 5; Hertwig and Hertwig, 1879:562–565; Torelli, 1960:376–379) — thin threadlike structure of Actiniaria containing numerous nematocysts, attached at one end to a mesentery, usually below the filament.

Acontium (Beneden, 1897:30–33; Bourne, 1919:60–61; Carlgren, 1912*a*:42, 68–72)—acontioid (*q.v.*).

Acontium (Heider, 1879:217)—craspedoneme (*q.v.*).

Acromere (Beneden, 1923:22)—"segment" of body, including the directive chamber, directive mesenteries and directive tentacles (by analogy to *Amphioxus*).

Actinocoel (Bourne, 1919:35)—intermesenterial chamber (*q.v.*).

Actinopharynx (Beneden, 1897:13–14)—tube leading from mouth into coelenteron, lined by longitudinally ridged, invaginated, ectoderm which is supported by mesogloea.

Actinostome (Beneden, 1897:9–10, 13–14)—mouth (*q.v.*).

Animal length—external distance from base of marginal tentacles to aboral pore.

Armature (Weill, 1930:147; 1934:21–22)—spines on tube of nematocyst.

Atrich (Weill, 1930:146; 1934:37, 50–52, 624–626)—nematocyst with isodiametric, unarmed, tube open at tip.

Axenteron (Beneden, 1897:20)—central portion of coelenteron undivided by mesenteries.

Axial body (Moebius, 1866:387; Weill, 1934: 22–24)—straight basal section of nematocyst tube within the capsule.

b (McMurrich, 1910:14–15)—shorter brachyneme, i.e. microseptum, of a metamesenterial quartette.

B (McMurrich, 1910:14–15)—longer brachyneme, i.e. microseptum, of a metamesenterial quartette.

Biseptum (Beneden, 1897:23)—two longest or two shortest mesenteries of a metamesenterial quartette.

b-mastigophore (Carlgren, 1940:3–4)—mastigophore with shaft tapering gradually to terminal tube.

Botrucnid (Beneden, 1897:32; Carlgren, 1912*a*: 72–74)—stalked bunch of cnidorages (*q.v.*).

Brachyneme (McMurrich, 1910:14)—microseptum (*q.v.*).

Buccal cone (Beneden, 1897:9)—raised portion of oral disc immediately surrounding mouth of some larval forms.

Buccal disc (Vogt, 1888:29)—oral disc (*q.v.*).

Buccal tentacle (Vogt, 1888:9–10)—labial tentacle (*q.v.*).

Capsule (Weill, 1934:21, 27–30)—hollow case of nematocyst.

Cerinula (Beneden, 1897:147; 1923:19)—larval stage with at least three couples of mesenteries.

Ciliated tract (Hertwig and Hertwig, 1879: 557)—continuation of ciliated ectoderm and mesogloea from a furrow of the actinopharynx along one side of a mesenterial filament.

Ciliated tract region (Carlgren, 1912*a*:59–60)—trineme (*q.v.*).

Cloison (Fisher, 1887:383; Faurot, 1895:50)—mesentery (*q.v.*).

Cloison prequatroseptale (Beneden, 1897:24)—protomesentery (*q.v.*).

Cloison primitive (Beneden, 1897:23)—one of second couple of protomesenteries.

Cloison quatroseptale (Beneden, 1897:24)—metamesentery (*q.v.*).

Cnida (Gosse, 1858:125; 1860:xxii, xxix–xxxiv, 269; Weill, 1934:330)—nematocyst *sensu* Haime (*q.v.*).

Cnida cochleata (Gosse, 1858:126–127; 1860: xxxiii–xxxiv; Bedot, 1896:534; Weill, 1930: 149)—spirocyst (*q.v.*).

Cnida glomifera (Gosse, 1858:126; 1860:xxxii–xxxiii; Weill, 1934:89–90) — nematocyst with nearly oval capsule containing long, isodiametric, loosely coiled tube (not in present use).

Cnidoglandular tract (Hertwig and Hertwig, 1879:557; Carlgren, 1949:8)—continuation

of ciliated ectoderm from a ridge of the actinopharynx along the length of a mesenterial filament.

Cnidoglandular tract (Carlgren, 1912*a*:59–66)—plectocraspedon (*q. v.*).

Cnidom (Weill, 1926:1245; 1934:351)—nematocyst complement of coelenterate at any given moment of its existence.

Cnidoneme (Beneden, 1923:154)—acontioid (*q. v.*).

Cnidorage (Beneden, 1897:32; Carlgren, 1912*a*: 72–73)—rounded projection of mesentery containing numerous nematocysts.

Coelenteron (Beneden, 1897:14)—main cavity of the animal.

Column (Gosse, 1860:2, 268; Beneden, 1897: 9)—body cylinder below oral disc and tentacles.

Column length—internal distance from aboral end of actinopharynx to aboral pole.

Commissural plane (Faurot, 1895:50, 59)—directive plane.

Continuous mesentery (Heider, 1879:216–217; McMurrich, 1890:137)—mesentery reaching the aboral pore, especially applicable to a second protomesentery.

Cordon pelotonné (Haime, 1854:374)—mesenterial filament (*q. v.*).

Couple of mesenteries (Faurot, 1895:103; Beneden, 1897:20–21; Carlgren, 1906:66)—two corresponding mesenteries on opposite sides of directive plane.

Craspedum (Gosse, 1858:125; 1860:xxiii–xxiv, 5; Bourne, 1919:54–55; Torelli, 1960:374)—mesenterial filament (*q. v.*).

Craspedion (Carlgren, 1912*a*:60–68; Torelli, 1960:375–376)—telocraspedon (*q. v.*).

Craspedoneme (McMurrich, 1910:19–22)—threadlike or flattened, sometimes branched, process of the mesogloea and entoderm of mesentery over which pass ascending and descending limbs of mesenterial filament.

Crown of tentacles (Haime, 1854:350, 363; Faurot, 1895:218, 236–240)—all cycles of tentacles grouped around mouth or all cycles near edge of oral disc.

Cycle of mesenteries (Carlgren, 1912*a*:51)—order of mesenteries (*q. v.*).

Cycle of tentacles (Haime, 1854:365–367; Heider, 1879:213; Faurot, 1891:70–71)—ring of tentacles all equidistant from mouth or from margin of oral disc.

d superscript (Beneden, 1897:10–11)—droit, i.e. right with reference to the directive plane at the siphonoglyph.

d superscript (Beneden, 1923:23)—directive.

D (Beneden, 1897:20)—cloison directrice, i.e. directive mesentery (*q. v.*).

Deuterocneme (McMurrich, 1910:6–10)—metamesentery (*q. v.*)

Directive chamber (Carlgren, 1900:27; 1906: 66)—Intermesenterial chamber between two directive mesenteries.

Directive mesentery (Hertwig and Hertwig, 1879:538, 572)—one of couple of mesenteries closest to directive plane at siphonoglyph.

Directive plane (Carlgren, 1906:66)—plane symetrically bisecting the animal, running through siphonoglyph and point diametrically opposite as seen in cross-section.

Directive tentacle (Carlgren, 1900:25, 1906: 66)—tentacle opening into directive chamber.

dm. (Carlgren, 1924*a*:169)—directive mesentery (*q. v.*).

Dorsal—opposite to ventral (*q. v.*).

dt. (Carlgren, 1924*a*:169)—directive tentacle (*q. v.*).

Ecthoraeum (Gosse, 1858:126; 1860:xxxi–xxxv, 269)—tube of nematocyst (*q. v.*).

Enteroid (Lacaze-Duthiers, 1873:302; Faurot, 1895:50–51, 234–235)—mesenterial filament (*q. v.*).

Enterostome (Beneden, 1897:14)—opening from cavity of actinopharynx into coelenteron.

Filamentchen region (Carlgren, 1912*b*:365)—telocraspedon (*q. v.*).

Filamentseptum (Heider, 1879:216; Carlgren, 1912*a*:51)—sterile mesentery (not in present use) (cf. Genitalseptum).

Fils mésentériques (Beneden, 1897:33)—craspedoneme (*q. v.*).

g superscript (Beneden, 1897:10–11)—gauche, i.e. left with reference to directive plane at siphonoglyph.

Genitalseptum (Heider, 1879:216; Hertwig and Hertwig, 1879:580–581)—fertile mesentery not reaching to aboral pore (cf. Filamentseptum).

Grenzstreifen (Carlgren, 1924*b*:347)—mesenteret (*q.v.*).

Hampe (Faurot, 1895:50)—main portion of mesentery excluding mesenterial filament.

Hampe (Weill, 1934:26)—shaft of nematocyst (*q.v.*).

Hemisulcus (Beneden, 1897:37–38; Carlgren, 1912*a*:50, 63)—continuation of half hyposulcus along edge of a directive mesentery.

Holotrich (Weill, 1930:145; 1934:37–38, 49–50, 64, 624–626; Cuttress, 1955:134–137)—basophilic nematocyst with an isodiametric, open-ended, tube armed along its entire length.

Hoplotelic terminal tube (Weill, 1930:147; 1934:38)—terminal tube bearing spines.

Hyposulcus (Beneden, 1897:15, 37–38; Carlgren, 1912*a*:50, 63)—grooved structure connecting the directive mesenteries, continuation of the siphonoglyph below the border of the actinopharynx.

Intermesenterial chamber (Faurot, 1895:228)—portion of coelenteron between two adjacent mesenteries.

Isorhize (Weill, 1930:145; 1934:37, 49, 624)—nematocyst with isodiametric tube open at tip.

l (Beneden, 1923:23)—loge de multipication, i.e. multiplication chamber.

L (Beneden, 1897:10)—loge, i.e. intermesenterial chamber, other than directive chamber.

L (Beneden, 1923:23)—loge directrice, i.e. directive chamber.

L with superscript (Beneden, 1923:23)—loge other than directive chamber.

Labial tentacle (Haime, 1854:368–369)—tentacle of one of cycles surrounding mouth (cf. marginal tentacle).

Lame (Haime, 1854:371, 374)—mesentery (*q.v.*).

Loge (Haime, 1854:371)—intermesenterial chamber (*q.v.*).

m (McMurrich, 1910:14–15)—shorter macrocneme, i.e. macroseptum, of metamesenterial quartette.

m (Beneden, 1897:113)—multipication chamber (*q.v.*).

M (McMurrich, 1910:14–15)—longer macrocneme, i.e. macroseptum, of metamesenterial quartette.

M (Beneden, 1897:10)—loge directrice, i.e. directive chamber (*q.v.*).

Macrobasic mastigophore (Weill, 1934:38, 64–68; Cuttress, 1955:133–134)—mastigophore in which shaft is more than three times capsule length.

Macrobimesenterium (Carlgren, 1912*a*:51)—macrobiseptum (*q.v.*).

Macrobiseptum (Beneden, 1897:23–24)—two longest mesenteries of a metamesenterial quartette.

Macrocneme (Stephenson, 1920:456)—mesentery of Actiniaria attached to actinopharynx with strong retractors, gonads, and filaments.

Macrocneme (McMurrich, 1910:14) macroseptum of Ceriantharia (*q.v.*).

Macroseptum (Faurot, 1891:68–69; 1895:233–234; Torelli, 1960:374)—one of two longest metamesenteries in a quartette.

Marginal tentacle (Haime, 1854:363–368)—tentacle of one of cycles near edge of oral disc (cf. labial tentacle).

Mastigophore (Weill, 1930:146; 1934:38, 58)—nematocyst with well-defined isodiametric shaft and terminal tube with open tip.

Median plane (Beneden, 1897:12)—directive plane (*q.v.*).

Median streak (Carlgren, 1912*a*:60–67)—spirocyst-glandular tract (*q.v.*).

Median streak (McMurrich, 1910:20–21)—central tract of trineme.

Median tentacle (Beneden, 1897:10)—directive tentacle (*q.v.*).

Mesenterial length—distance from aboral end of actinopharynx to aboral end of mesentery.

Mesenterialfaden (Hertwig and Hertwig, 1879: 579–580)—craspedoneme (*q.v.*).

Mesenterial filament (Frey and Leuckart, 1847: 12–18; Hertwig and Hertwig, 1879:556)—thickened rim running along free border of mesentery from end of actinopharynx aborally.

Mesenteret (Beneden, 1897:27; Carlgren, 1931: 8)—projection of mesentery bearing the peloton.

Mesentery (Frey and Leuckart, 1847:11; Lacaze-Duthiers, 1873:301–302; Bourne, 1900: 8–9)—longitudinal extension into coelenteron from body wall, attached to actino-

pharynx and bearing thickened filament upon its free inner edge below actinopharynx.

Mesogloea (Bourne, 1887:303, 311–320; Torelli, 1952:154–156)—supporting layer between ectoderm and endoderm.

Metacneme (Duerden, 1900:47, 1902:388–397)—metamesentery (*q.v.*).

Metamesentery (Carlgren, 1912*a*:50–51, 59; 1912*b*:361)—any mesentery other than protomesenteries.

Metasome (Beneden, 1923:21–22)—central portion of body excluding prosome and telomere (*q.v.*). (by analogy to *Amphioxus*).

Microbasic mastigophore (Weill, 1934:38, 58–64, 624–626)—mastigophore in which shaft is at most three times capsule length.

Microbimesenterium (Carlgren, 1912*a*:51)—microbiseptum (*q.v.*).

Microbiseptum (Beneden, 1897:23–24)—two shorter mesenteries of metamesenterial quartette.

Microseptum (Faurot, 1891:68–69; 1895:233–234; Torelli, 1960:374)—one of two shortest metamesenteries in quartette.

Mononeme (Beneden, 1923:79–80)—aboral monofilar region of mesenterial filament.

Mouth (Rapp, 1829:654; Haime, 1854:350, 372)—opening from exterior to cavity of actinopharynx.

Mucocraspedoneme (Carlgren, 1912*a*:71)—acontioid (*q.v.*).

Multipication chamber (Vogt, 1888:24)—intermesenterial chamber opposite directive chamber, in which new mesenterial couples are formed.

Mundscheibe (Hertwig and Hertwig, 1879:471; Heider, 1879:212)—oral disc (*q.v.*).

Nematocyst (Haime, 1854:354–357, 365; Bedot, 1886:51–52; Cuttress, 1955:124–126)—capsule containing an expellable coiled tube.

Nematocyst (Bedot, 1889:607–608; 1896:535–536; Weill, 1934:330)—nematocyst *sensu* Haime excluding spirocysts.

Odd tentacle (Agassiz, 1863:527; Fischer, 1889:24)—directive tentacle (*q.v.*).

Oesophagus (Haacke, 1879:276, 293; Jourdan, 1879:103, 108–109)—actinopharynx (*q.v.*).

Oral disc (Faurot, 1895:47–48, 218)—disc at one end of animal bearing mouth and tentacles.

Order of mesenteries (Carlgren, 1912*b*:375–376, 386; Torelli, 1960:374)—all metamesenteries of same relative lengths in their respective quartettes.

Orthocraspedon (Bourne, 1919:55–57)—trineme (*q.v.*).

p. superscript (Beneden, 1923:23)—belonging to third somatomere of prosome (*q.v.*).

P (Carlgren, 1912:8)—protomesentery (*q.v.*).

Peloton (Faurot, 1895:235–236; Beneden, 1897:27, 46; 1923:51–52, 79)—highly convoluted section of mononeme.

Penicillus (Stephenson, 1929:178–179; Weill, 1934:91–92)—nematocyst containing short, stout, armed tube (not in present use).

Peristome (Vogt, 1888:29)—portion of oral disc between tentacle crowns.

Plectocraspedon (Bourne, 1919:55–57)—portion of mononeme indistinctly delimited by abundance of large, thick-walled nematocysts and large coarsely-granular gland cells, usually anterior to telocraspedon.

p-mastigophore (Carlgren, 1940:3–4; Cuttress, 1955:129–131, 133–134; Hand, 1961:189–190, 193)—mastigophore in which abrupt reduction of shaft to terminal tube allows funnel-shaped invagination of axial body.

Protocneme (Duerden, 1900:47; McMurrich, 1910:6–10)—protomesentery (*q.v.*).

Protomesentery (Carlgren, 1912*a*:50–51, 59, 1912*b*:361)—one of mesenteries arising in first embryological stage (presently considered to be one of the first three mesenteries on either side of directive plane at siphonoglyph).

Prosome (Beneden, 1923:21)—anterior portion of body including three cycles of protomesenteries and associated tentacles, intermesenterial chambers adjoining and portions of columnar wall, peristome and actinopharynx (by analogy to *Amphioxus*).

Quartette of metamesenteries (Faurot, 1891:67–68; 1892:238; 1895:231–234)—any group of four mesenteries in a series as counted from protomesenteries, each group showing similar pattern of relative mesenterial lengths.

Quatromere (Beneden, 1924:43)—four successive somatomeres (*q. v.*).

S. (Beneden, 1897:20)—cloison, i.e. mesentery, other than directive mesenteries.

S with superscript (Beneden, 1923:25)—sarcoseptum, i.e. mesentery.

Sarcoseptum (Haacke, 1879:277, 293)—mesentery (*q. v.*).

Sarcosepte antipathoide (Beneden, 1923:18)—protomesentery (*q. v.*).

Sarcosepte cerianthoide (Beneden, 1923:19)—metamesentery (*q. v.*).

Schlundrinne (Hertwig and Hertwig, 1879: 513, 572)—siphonoglyph (*q. v.*).

Septum (Gosse, 1860:xiii–xiv, 5, 268)—mesentery (*q. v.*).

Shaft (Carlgren, 1940:3)—thickened basal part of tube, of some nematocysts.

Siphonoglyph (Hickson, 1883:693–694; McMurrich, 1890:131, 136)—smooth ciliated groove of actinopharynx.

Somatomere (Beneden, 1923:21–22)—"segment" of body including a couple of mesenteries, the intermesenterial chambers 'anterior' to them, and the associated tentacles and adjoining portions of columnar wall, peristome and actinopharynx (by analogy to *Amphioxus*).

Spiral cnida (Gosse, 1858:126–127; 1860: xxxiii–xxxiv; Weill, 1934:326)—spirocyst (*q. v.*).

Spirocyst (Bedot, 1889:607–608; 1896:534–536; Weill, 1934:325–342, 624; Cuttress, 1955:124–126, 136)—capsule containing an acidophilic, very regularly spiralled, tube of uniform diameter which irregularly everts (cf. Holotrich).

Spirocyst-glandular tract (Carlgren, 1912*a*:60–67)—telocraspedon and histologically similar medial tract of trineme.

Spirula (Stephenson, 1929:179; Weill, 1934: 91–92)—nematocyst containing long slender tube with enlarged or armed basal portion (not in present use).

Stomatodaeum (McMurrich, 1890:136)—actinopharynx (*q. v.*).

Stomodaeum (Bourne, 1900:7, 51)—actinopharynx (*q. v.*).

Sulculus (Haddon, 1889:300)—siphonoglyph other than the sulcus of Actiniaria (*q. v.*).

Sulculus (Carlgren, 1912*a*:55–56)—siphonoglyph of Ceriantharia if considered homologous to sulculus of Actiniaria (*q. v.*).

Sulcus (Haddon, 1889:300)—ventral siphonoglyph of Actinaria, i.e. that one homologous to single siphonoglyph of *Peachia.*

Sulcus (Kingsley, 1904:347–351; Torelli, 1960: 383) siphonoglyph of Ceriantharia if considered homologous to sulcus of Actiniaria (*q. v.*).

t (Beneden, 1897:10–11)—labial tentacle other than directive tentacle.

t (Beneden, 1923:23)—labial directive tentacle (*q. v.*).

t with superscript (Beneden, 1923:23)—labial tentacle other than directive tentacle.

T (Beneden, 1897:10–11)—marginal tentacle other than directive tentacle.

T (Beneden, 1923:23)—median marginal tentacle, i.e. marginal directive tentacle.

T. with superscript (Beneden, 1923:23)—marginal tentacle other than directive tentacle.

T.M. (Beneden, 1897:10–11)—median marginal tentacle, i.e. marginal directive tentacle.

Telocneme (McMurrich, 1910:11–13)—continuous mesentery (*q. v.*).

Telocraspedon (Bourne, 1919:55–57)—portion of mononeme indistinctly delimited by abundance of spirocysts and eosinophilous mucus gland cells, usually posterior to plectocraspedon.

Telomere (Beneden, 1923:22)—"segment" of body including multipication chamber (by analogy to *Amphioxus*).

Terminal tube (Weill, 1934:26, 37)—thin distal part of tube, in some nematocysts.

Thread (Gosse, 1858:126; 1860:xxix–xxxiv)—tube of nematocyst (*q. v.*).

Thread (Carlgren, 1940:3)—terminal tube of nematocyst or entire tube of thickened basal portion is absent.

Trineme (Beneden, 1923:79–80)—adoral trifilar region of mesenterial filament.

Tube (Weill, 1934:21–22, 36–38)—eversible hollow structure coiled within capsule of nematocyst.

Ventral (Kolliker, 1870–1872)—end of directive plane on which single siphonoglyph of pennatulids is placed (by convention).

Ventral (Beneden, 1897:12)—aboral portion of column of Ceriantharia (by analogy with the orientation of *Amphioxus*).

Ventral (Haacke, 1879:294; Carlgren, 1893: 242–246; 1912*a*:54–58)—end of directive plane opposite single siphonoglyph of Ceriantharia if siphonoglyph is not considered homologous to that of the pennatulids.

Ventral (Hertwig and Hertwig, 1879:572; Faurot, 1895:62, 228, 250; McMurrich, 1910:9; Torelli, 1960:383)—end of directive plane on which single siphonoglyph of the Ceriantharia is placed if it is considered homologous to siphonoglyph of pennatulids.

ACKNOWLEDGMENTS

I would like to acknowledge the guidance of Dr. B. C. Abbott throughout this work. Collection and preliminary identification were made at the Department of Zoology, University of California, Los Angeles. The taxonomy and histology were completed at the Department of Zoology, University of British Columbia. I am most grateful for the facilities and aid given me at the University of British Columbia, especially by Dr. W. Hoar and Dr. N. Band. The technical assistance of Mrs. J. Eales and Mrs. J. McDonald is appreciated. I am indebted to Dr. C. Hand for reading the manuscript.

Most of the animals used were collected under a University of California, Los Angeles, Patent Fund Grant to the author. Necessary supplies and equipment were purchased under a United States Public Health Service Grant No. H-4019 to Dr. B. C. Abbott and a Sigma Xi Grant-in-aid to the author.

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