

A Fifth Morphological Polyp in Pennatulacean Octocorals, with a Review of Polyp Polymorphism in the Genera *Pennatula* and *Pteroeides* (Anthozoa: Pennatulidae)

Gary C. Williams^{1,*}, Bert W. Hoeksema², and Leen P. van Ofwegen²

¹Department of Invertebrate Zoology and Geology, California Academy of Sciences, 55 Music Concourse Drive, San Francisco, CA 94118, USA

²Netherlands Centre for Biodiversity Naturalis, Darwinweg 2, Leiden 2333 CR, the Netherlands

(Accepted May 30, 2012)

Gary C. Williams, Bert W. Hoeksema, and Leen P. van Ofwegen (2012) A fifth morphological polyp in pennatulacean octocorals, with a review of polyp polymorphism in the genera *Pennatula* and *Pteroeides* (Anthozoa: Pennatulidae). *Zoological Studies* **51**(7): 1006-1017. Four types of polyps that differ in morphology and function were previously described in pennatulacean octocorals: oozooids, autozooids, siphonozooids, and mesozooids. Here we describe a 5th type of polyp, the acrozooid, found in members of 2 species of the genus Pteroeides from tropical western Pacific coral reef regions. The polyps appear in clusters of up to 14 in number on the ventral side and distal terminus of the rachis, and are characteristically urn-shaped, with 8 triangularly shaped tentacles. The polyp walls contain smooth, elongated rod-like sclerites, which are similar to those found in the coenenchyme of parent colonies. We postulate that these polyps represent maturing asexual budding structures. http://zoolstud.sinica.edu.tw/Journals/51.7/1006.pdf

Key words: Sea pens, Acrozooids, Asexual budding, Zooids, Western tropical Pacific.

he pennatulaceans represent an order of colonial octocorallian anthozoans commonly referred to as sea pens. They are a highly specialized group of cnidarians in that virtually all of the estimated 200 valid species have muscular basal peduncles for anchorage in soft substrata such as sand, mud, or abyssal ooze. Because of this unique feature, sea pens are able to exploit extensive regions of the soft sea floor. They are distributed worldwide throughout much of the marine realm from the intertidal to over 6200 m in depth (Williams 1995, Williams and Cairns 2011). The global diversity, general biology, and history of discovery regarding pennatulaceans were recently reviewed by Williams (2011).

Adult pennatulacean colonies are composed of several types of polyps (often called "zooids" in the older literature), four of which were previously described. Hickson (1916: 3) stated, "The zooids of the Pennatulid colony are of three or 4 kinds The three kinds that are found in the colonies of all species are called, the oozooid, the autozooids, and the siphonozooids. In the colonies of some species a fourth kind of zooid is found which I propose to call the mesozooid". In addition, Bayer et al. (1983) provided definitions for each kind of polyp.

The oozooid, also known as the primary polyp, forms the combined peduncle and rachis of mature colonies. The oozooid gives rise to the secondary polyps of the rachis (i.e., all other types of polyps) by lateral budding of the body wall. These include autozooids, which are found in all pennatulaceans, and are often the largest and more conspicuous of the secondary polyps, with 8 pinnate tentacles surrounding the mouth. Autozooids function in

^{*}To whom correspondence and reprint requests should be addressed. E-mail:gwilliams@calacademy.org

capturing and digesting food, and providing for the nourishment and protection of gametes. All pennatulaceans also bear siphonozooids, which are smaller than autozooids and often appear as circular raised protuberances on the rachis or polyp leaves. Tentacles of siphonozooids are highly reduced or absent. Siphonozooids produce inhalant currents of water which distend the canals and inflate the peduncle and rachis. Finally, mesozooids are often intermediate in size between autozooids and siphonozooids, with highly reduced or no tentacles. They have an exhalant function, expelling water from the canals and hence promoting deflation of the peduncle and rachis. According to Hickson (1916: 11), "Zooidstreifen der Rachis" of Niedermeyer (1911: 6, 7) and possibly "Scheitelzooiden" of Jungersen (1888: 638) are synonymous with mesozooids. The portrayal of siphonozooids by Brafield (1969: 318, fig. 1C) matches the description of mesozooids by Hickson (1916: 11; pl. 9, figs. 66, 67). Mesozooids were reported from perhaps 4 species of Pennatula and possibly the genus Renilla (Jungersen 1888, Hickson 1916, Williams 1990), and several species of Pteroeides (Kükenthal 1909, Brafield 1969, Niedermeyer 1911 1912).

Here we describe a newly identified type of polyp, which we call the "acrozooid", from specimens of 2 unidentified species of pennatulaceans in the genus Pteroeides. Acrozooids are morphologically distinct from all other known polyp types in pennatulaceans, in that they are found only at the bases of the distal-most polyp leaves, they do not extend into the interior of the colony, and all of their features are consistent with those of primary polyps such as tentacles, the pharynx, gastric cavity, mesenterial filaments, longitudinal musculature, and sclerites (Fig. 2C). Although the functions of acrozooids are not known at present, we speculate that these polyps function as asexual budding structures based on morphological features and their regional placement on parent colonies, along with previous observations regarding other octocorals.

MATERIALS AND METHODS

A specimen of *Pteroeides* sp. 1 (RMNH Coel. 40122) was collected by A. Fortuin on 1 Dec. 1990 from ~10-20 m in depth near Amahusu, Ambon I., Moluccas, Indonesia (3°43'44"S, 128°08'23"E) at station 31 of the Rumphius Biohistorical Expedition of the Nationaal Natuurhistorisch Museum, Leiden,

the Netherlands. A specimen of *Pteroeides* sp. 2 (CAS 185934) was collected by G.C. Williams on 15 May 2011 from ~18 m in depth from Sepok Point, Maricaban Island, Batangas Province, Luzon, the Philippines (13.68800°S, 120.82700°E), at station HEP 69 of the Hearst Philippines Expedition of the California Academy of Sciences, San Francisco, CA, USA.

Underwater photographs were taken of the specimen of *Pteroeides* sp. 2, which was collected by scuba *in situ* (Fig. 3A-D). Other specimens were also photographed *in situ*, but were not collected. The 2 specimens that were collected were fixed and preserved in 70%-95% ethanol. Sclerites were isolated and prepared for microscopic examination according to the methods of Williams and Mattison (2006). Scanning electron micrographs were made of sclerites from the acrozooids of *Pteroeides* sp. 1, using a LEO 1450 VP scanning electron microscope (Carl Zeiss, Oberkochen, Germany) at the California Academy of Sciences (Fig. 6).

RESULTS

Two pennatulacean specimens in 2 unidentified species (both in the genus *Pteroeides*) are currently known to possess the polyps described in this paper, and are not considered identifiable at present due to the necessity of a thorough taxonomic revision of the genus.

The acrozooid - a 5th kind of pennatulacean polyp (Figs. 1-6)

Description

A range of 6-14 acrozooids is present on the proximal portions of several polyp leaves adjacent to the point of attachment of the leaf with the rachis, at the distal-most ventral portion of the colony (Figs. 1A, 2A, 3, 4; Gosliner et al. 1966: 93). Each acrozooid is globular or urn-shaped, and ca. 2 mm wide by 2-4 mm long (Fig. 11). An individual acrozooid does not have a basal stalk, and is directly attached to the base of a polyp leaf (Fig. 11), adjacent to the ventral surface of the rachis of the parent colony (Figs. 2A, B, 3A-G). The distal end of each acrozooid has 8 triangular tentacles, which are joined only at their bases (Fig. 3D, F, G). The free, tapering portions of the 8 appendages are not tightly adjacent and therefore provide an

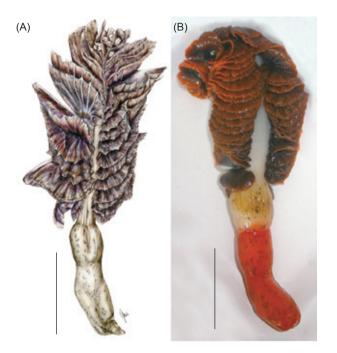


Fig. 1. (A) *Pteroeides* sp. 1 (RMNH Coel. 40122), ventral side of an entire wet-preserved colony showing acrozooids on the distal-most polyp leaves of the colony. Illustration by Jessica Machnicki, California Academy of Sciences. Scale bar = 45 mm. (B) *Pteroeides* sp. 2 (CAS 185934), ventral side of entire living colony; acrozooids are hidden by distal-most polyp leaves. Scale bar = 60 mm.

opening to the polyp interior (Fig. 3D, F, G). The color of the acrozooids, both in life and ethanolpreserved, is a milky or somewhat translucent white, with a pure-white border marking the edges of the tentacles and mesenteries of the interior (Fig. 3; Gosliner et al. 1996: 93).

A longitudinal section of an acrozooid was made to reveal the internal structures (Fig. 2C). The proximal base of the acrozooid is attached to a polyp leaf near its point of insertion to the rachis. The gastric cavity of the acrozooid does not extend into the interior of the polyp leaf or any other region of the parent pennatulacean colony. A small pharynx (\leq 1.0 mm long) is subtended by mesenterial filaments, which appear to be attached to the proximal-most portion of the polyp. Several bands of longitudinal musculature run along the wall of the gastric cavity.

Each acrozooid possesses relatively numerous, smooth, rod- or spindle-like calcareous sclerites, 0.31-3.90 mm long. These are not 3-flanged, nor ornamented with tubercles (Figs. 5, 6). The sclerite shape ranges from elongate to needle-like: a few are ovoid and more robust. Most of the sclerites have smoothly rounded ends, although a few have more-acute tips or have irregularly shaped to slightly bifurcated tips (Fig.

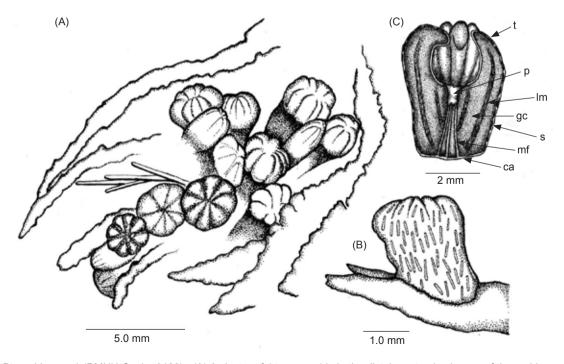


Fig. 2. *Pteroeides* sp. 1 (RMNH Coel. 40122). (A) A cluster of 14 acrozooids in the distal-most polyp leaves of the rachis; scale bar = 5.0 mm. (B) A single acrozooid showing placement of polyp wall sclerites; scale bar = 0.1 mm. (C) Longitudinal section of an acrozooid showing the internal anatomy. ca, contact area with polyp leaf; gc, gastric cavity; lm, longitudinal musculature; mf, mesenterial filament; p, pharynx; s, sclerite; t, tentacle. Scale bar = 2.0 mm.

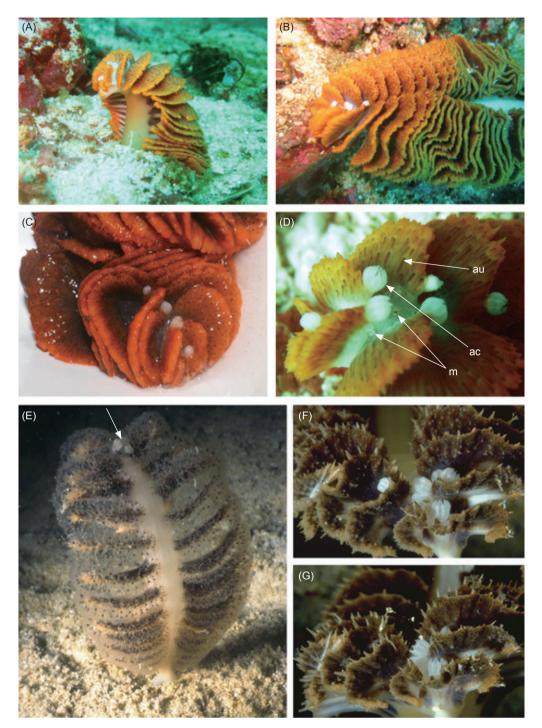


Fig. 3. *Pteroeides* sp. 2 (CAS 185934), photographs of the living colony. (A) Underwater photograph showing exposed distal portion of rachis, with rest of colony buried in the sandy substratum; maximum height of the portion shown is ca. 65 mm. (B) Underwater photograph of distal portion of ventral side of rachis with acrozooids; length of the portion shown is ca. 80 mm. (C) Distal extremity of rachis showing acrozooids surrounded by terminal polyp leaves; acrozooids ca. 2.0-2.5 mm wide. (D) Detail of underwater photograph of distal portion of ventral side of rachis showing placement of acrozooids; maximum width of acrozooids ca. 2.5 mm. ac, acrozooid; au, autozooid; m, mesozooids. (E) Underwater photograph of ventral side of a colony of *Pteroeides* sp. with numerous fully extended autozooids on the polyp leaves, and a few acrozooids near the distal extremity of the rachis (arrow); South Sulawesi, Indonesia; scale not given. (F) Underwater photograph of the distal portion of a colony of *Pteroeides* sp., showing a group of acrozooids with relatively closed tentacles. Minute white spots on the polyp leaves are autozooids with retracted tentacles; Ambon, Indonesia; scale not given. (G) Same as in F, but acrozooids with more-open and extended tentacles; Ambon, Indonesia; scale not given. A-D by G.C. Williams; E-G by B.W. Hoeksema.

6). Sclerites are more or less longitudinally placed throughout most of the structure of the polyp walls (Fig. 2B).

We introduce the term "acrozooid" (from the Greek, *akron*, for extremity, summit, highest point),

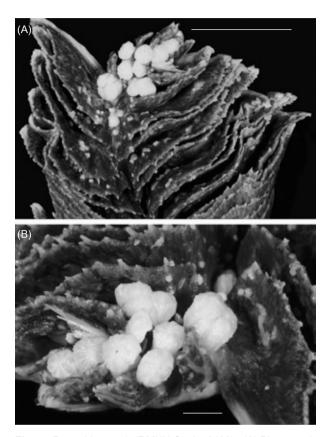


Fig. 4. *Pteroeides* sp. 1. (RMNH Coel. 40122). (A) Photograph of the distal part of the rachis showing polyp leaves and a cluster of acrozooids. Scale bar = 15 mm. (B) Photographic detail of the cluster of acrozooids. Sscale bar = 2 mm.

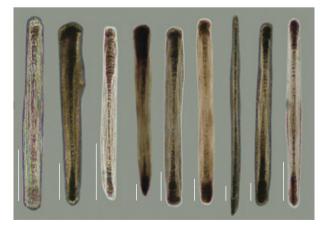


Fig. 5. *Pteroeides* sp. 1 (RMNH Coel. 40121), compound microscopic images of acrozooid sclerites. Scale bars = 0.1 mm.

since this kind of polyp has thus far been found only on the apexes of the rachis (distal terminus of the ventral side) on 2 *Pteroeides* specimens.

Comparison of acrozooids with autozooids

Autozooids and acrozooids are both relatively large and conspicuous polyps and are therefore compared as follows. Acrozooids are clearly distinguishable from all other types of pennatulacean secondary polyps by comparative morphology. Acrozooids are not structurally linked to other polyps but are rather self-contained. They emanate directly from the distal rachis of the parent colony in Pteroeides sp. The gastric cavities of acrozooids are not elongated and tubular as in autozooids. Acrozooids are independent from one another, and consequently are not contained in a common coenenchyme with other zooids as in autozooids (Fig. 9). In contrast to autozooids, acrozooids are relatively short and hemispherical to ovoid (Fig. 4). Acrozooids are directly attached to the rachis of the parent colony only at their bases or proximal extremities (Fig. 2B, C). In addition, they are independent from

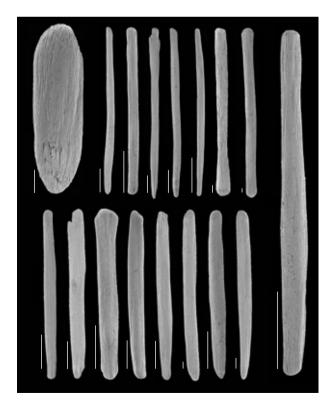


Fig. 6. *Pteroeides* sp. 1 (RMNH Coel. 40122), scanning electron micrographs of acrozooid sclerites. Scale bars = 0.1 mm.

adjacent polyps and do not possess lateral canals (solenia), which emanate from the polyp walls that join them to other zooids. Acrozooids have short, deltoid tentacles with smooth margins (Fig. 3D).

Autozooids, on the other hand, are the feeding polyps of the octocoral colony, and with the exception of acrozooids, are the largest and most conspicuous of the secondary polyps (Williams 1990: 34). They have 8 conspicuous, pinnate

tentacles surrounding the mouth of each polyp (Fig. 9). Functions include the capture and digestion of food, and providing for the nourishment and protection of gametes. In the genus *Pteroeides*, autozooids are restricted to polyp leaves of the parent colony and do not emanate directly from the rachis (Figs. 3D, 7B). Autozooids are structurally linked to adjacent autozooids by a network of solenia (small lateral canals). They have long

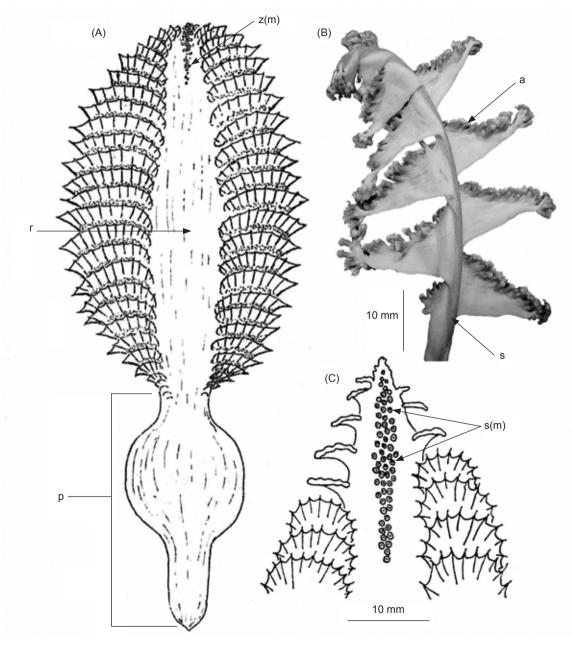


Fig. 7. Pennatulacean polyps. (A) *Pteroeides spinosum*, adapted from Niedermeyer (1911, 104); z(m), *Zooidstreifen der Rhachis* of Niedermeyer (1911), mesozooid of Hickson (1916); r, rachis; p, peduncle; scale not given. (B) *Pennatula* sp. (JSLII 3666), distal portion of rachis, a, autozooid, s, siphonozooid. (C) Apex of the rachis of *Pteroeides spinosum*. Adapted from Brafield (1969: 318). s(m), siphonozooids of Brafield (1969), mesozooid of Hickson (1916). Scale bars for B and C = 10 mm.

gastric cavities that are imbedded in the common and massive tissues in the polypary of the colony, along with other autozooids (Fig. 9).

DISCUSSION

Approximately 30 species of *Pteroeides* have been described or reported from the coral triangle region (Hoeksema 2007) by Herklots 1858, Bleeker 1859, von Kölliker 1869-1872, Broch 1910, and Kükenthal 1915. Regarding our knowledge of the past literature pertaining to *Pteroeides*, we do not know of any mention, study, or description of polyps resembling acrozooids in any of the descriptions of the 25 species that are regarded as valid (Williams 2011). However, inadequate or

Fig. 8. *Pteroeides spinosum* (CAS 182523). (A) Dorsal side of colony. (B) Ventral side of colony. (C) Enlargement of distal portion of rachis shown in B. Scale bars: A and B = 45 mm; C = 5 mm. a, autozooid; m, mesozooid; n, needle-like sclerites; pl, polyp leaf; r, rachis.

poorly figured original descriptions in the literature mean that the validities of these species are not ascertainable at present. A taxonomic revision of the genus is clearly necessary.

Prior to the collection of specimens, the polyps here named acrozooids were known only from a single underwater photograph of an unidentified species of *Pteroeides* from Manado, Indonesia (photograph by M. Severns, in Gosliner et al. 1996: 93, # 307), and labeled as a stauromedusan cf. *Lipkea* sp. The subsequent collection of specimens allowed for the recognition of sclerites in the polyp walls of the polyps and their consequent determination as octocoral polyps.

Aside from photographic evidence, collected material of acrozooids is presently known only from 2 unidentified specimens of the genus Pteroeides. A subsequent search for additional specimens with acrozooids was unsuccessful, nor has any new relevant knowledge regarding these polyps been acquired to date. A survey of specimens in the marine invertebrate collections of the California Academy of Sciences (San Francisco, CA, USA) and the Naturalis Nationaal Natuurhistorisch Museum (Leiden, the Netherlands) revealed no pennatulacean specimens with acrozooids, nor has the phenomenon to our knowledge previously been reported by other institutions with marine invertebrate collections, or by other researchers or divers.

Polyp polymorphism in the Pennatulacea

The 5 kinds of polyps differ morphologically, and also have demarcated functions. Although oozooids, autozooids, and siphonozooids are found in all pennatulacean taxa and serve to help define this group of octocorals, other kinds of polyps are known only from a few species in 2 or 3 genera. Mesozooids were reported from perhaps 4 species of *Pennatula* and possibly the genus *Renilla* (Jungersen 1888, Hickson 1916, Williams 1990), and several species of *Pteroeides* (Kükenthal 1909, Niedermeyer 1911 1912, Brafield 1969). Acrozooids are presently known only from 2 unidentified species of the genus *Pteroeides* (Table 1).

A review is given here of the comparative morphologies and functions of the 3 kinds of secondary pennatulacean polyps that differ from acrozooids and autozooids.

1) Oozooid (Figs. 7A, 8A, B). Otherwise known as a primary polyp, an oozooid forms the

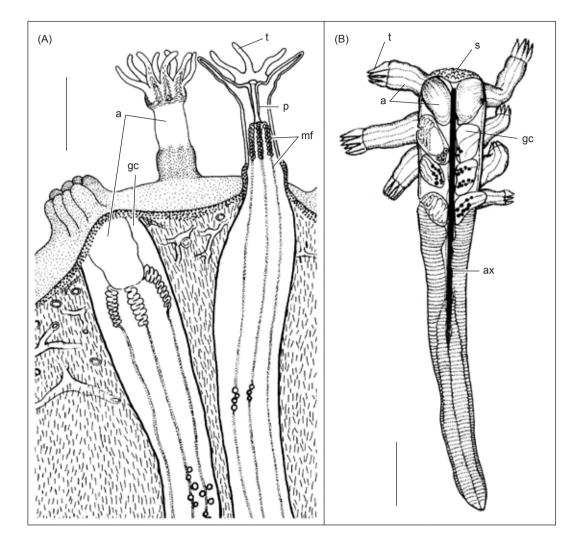


Fig. 9. Autozooid morphology in octocorals. (A) The soft coral *Eleutherobia variabile*. Scale bar = 2 mm. Adapted from Williams (1986: 254). (B) The pennatulacean *Cavernularia dedeckeri*. Scale bar = 10 mm. Adapted from Williams (1989: 300). a, autozooid; ax, central axis; gc, gastric cavity; mf, mesenterial filament; p, pharynx; s, siphonozooid; t, tentacle.

Table 1.	Polyp	polymorphism	in pennatulacean	octocorals
----------	-------	--------------	------------------	------------

Polyp	Synonyms	Таха	Part of colony	Function	Reference
Oozooid	primary, axial, initial, or principal polyp	All	entire colonial length	forms peduncle and rachis of adult colony	Hickson (1916: 7)
Autozooid		All	rachis, polyp leaves	food capture and digestion	Hickson (1916: 11)
Siphonozooid		All	rachis, polyp leaves	inhalant currents	Hickson (1916: 11)
Mesozooid	Rhachidiozooid, Scheitelzooid (?), Exhalant zooid	Pennatula, Pteroeides	rachis, polyp leaves	exhalant currents	Hickson (1916: 11)
Acrozooid		Pteroeides	distal, ventral region of rachis	asexual budding (P)	Williams and Ofwegen (present paper)

P, postulated.

combined peduncle and rachis of mature colonies. The oozooid gives rise by lateral budding of the body wall to secondary polyps of the rachis, i.e., autozooids, siphonozooids, mesozooids, and presumably acrozooids. Bayer et al. (1983: 9) defined the oozooid as, "the persistent and modified primary polyp of Pennatulacea." Williams (1990: 34) provided a description of an oozooid.

2) Siphonozooid (Fig. 7B). Siphonozooids are smaller than autozooids and often appear as circular raised protuberances on the rachis or polyp leaves. The tentacles are highly reduced or absent. Sclerites are absent from the vast majority of taxa. Siphonozooids may differ in appearance depending on the particular taxon. For example, the sea pen *Funiculina quadrangularis* has relatively tall to cylindrical siphonozooids, while in most other species, siphonozooids are represented by hemispherical mound-like protuberances. Siphonozooids produce inhalant currents of water which distend the canals and inflate the peduncle and rachis. Bayer et al. (1983: 11) defined a siphonozooid as "a polyp with strongly developed siphonoglyph and reduced tentacles or none, commonly with reduced mesenterial filaments; usually much smaller than autozooids." Williams (1990: 34) also described a siphonozooid.

3) Mesozooid (Figs. 7A, C, 8C). Mesozooids are often intermediate in size between autozooids and siphonozooids, with highly reduced or no

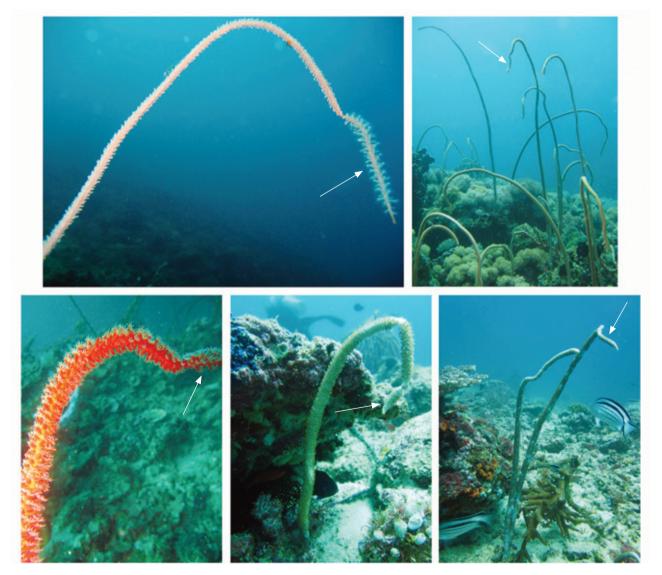


Fig. 10. Gorgonian sea whips, *Junceella fragilis*, showing apical asexual buds in varying stages of development (arrows); underwater photographs taken in southwestern Luzon, the Philippines, at 10-20 m in depth, between Apr. 2008 and May 2010; scale not given.

tentacles. As in siphonozooids, sclerites are absent from most if not all mesozooids. They have an exhalent function, expelling water from the canals and hence promoting deflation of the peduncle and rachis. According to Hickson (1916: 11), "Zooidstreifen der Rachis" of Niedermeyer (1911: 6-7) and possibly "Scheitelzooiden" of Jungersen (1888: 638) are synonymous with mesozooids. The portraval of siphonozooids by Brafield (1969: 318, fig. 1C) matches the description of mesozooids by Hickson (1916: 11; pl. 9 figs. 66, 67). In figure 3D, several polyps, presumably mesozooids, can clearly be seen on the rachis between polyp leaves with welldeveloped acrozooids. Bayer et al. (1983: 9) and Williams (1990: 34) described a mesozooid as a polyp that is structurally intermediate between an autozooid and a siphonozooid.

Inferences regarding the function of acrozooids

In lieu of direct experimental evidence or observations at present regarding the function of acrozooids, we inferred that they are asexual buds (incipient primary polyps), which presumably arise by budding, in contrast to oozooids, which arise from fertilized eggs. It was further postulated that these blastozooids may separate from the parent colony, subsequently settling on suitable substrata, and begin a new colony as primary polyps. Hence, these acrozooids may become the primary polyps of new colonies. It is here presumed that they are genetic clones of the parent colony from which they emanate.

We investigated 3 possible alternative explanations and provide our opinions regarding the probable invalidity of each explanation: (1) Acrozooids are unusually large inhalant or exhalant zooids. Zooids that create water currents in the interior of the pennatulacean colony do so by possessing a well-developed siphonoglyph. Bayer et al. (1983: 11) defined a siphonoglyph as "the strongly ciliated groove extending down one side of the pharynx; = sulcus." Inhalant and exhalant zooids (siphonozooids and mesozooids) have strongly developed siphonoglyphs, whereas they are absent in acrozooids. (2) Acrozooids are odd zooids formed at a site where the original polyp was damaged. Skeletal anomalies or other growth deformations have been recorded in corals (Goldberg et al. 1984, Sutherland et al. 2004). The idea of some other polyp type going wild, after predation, is not new. Benayahu (1998) reported on tissue and polyp re-growth after predation of the soft coral Sinularia nanolobata. The result is much smaller lobes than normal, as one would expect. Similarly, the soft coral Funginus heimi (Tixier-Durivault 1970) is presumed to actually be a species in the genus Heteroxenia after predation, resulting in smaller polyps (Fabricius and

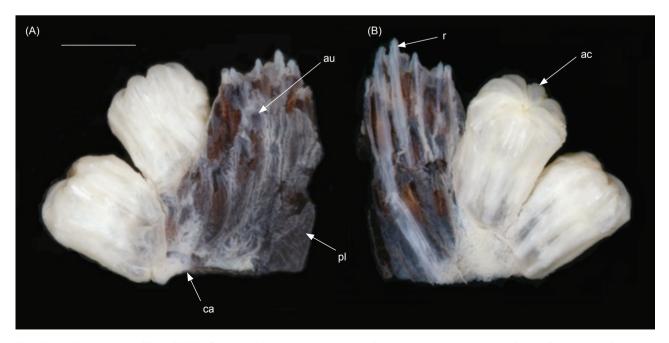


Fig. 11. A distal polyp leaf from RMNH Coel. 40122 showing placement of 2 acrozooids. (A) Upper surface. (B) Lower surface. ac, acrozooid; au, autozooid; ca, contact area of polyp leaf with rachis; pl, polyp leaf; r, ray (needle-like sclerite). Scale bar = 2.0 mm.

Alderslade 2001: 142), not larger ones as is the case with acrozooids on Pteroeides spp. Evidence of predation or other inhibitory cause or damaging agent was not detected in either of the 2 colonies of Pteroeides that harbor acrozooids. Additionally, acrozooids emanate from the basal portion of polyp leaves, and are not associated with the calcified internal axis or other skeletal elements, hence the view that these polyps result from skeletal anomalies is ruled out. (3) Acrozooids are polyps of some completely different octocoral, growing on the pennatulacean. Since acrozooids possess pennatulacean sclerites, they are here determined to be a kind of pennatulacean polyp. Sclerites of acrozooids (Figs. 5, 6) are structurally identical to those of the Pteroeides colonies upon which they are attached (elongate rods and needle-like spindles). To our knowledge, another sea pen or other octocoral growing on a living sea pen colony has never been observed, nor have octocorals been observed growing on living tissues of other octocorals. However, an example of a soft coral or stoloniferous octocoral growing on the exposed or dead axis (internal skeleton) of a holaxonian gorgonian is that of Alcyonium fauri (Williams 1992: 278, fig. 13A, E). Similarly, the stoloniferous octocoral, Carijoa sp., was observed growing on the bared axis of living Pacifigorgia colonies in the eastern Pacific Ocean (O. Breedy, pers. comm.). In addition, we would expect a mechanism to prevent such a phenomenon as the overgrowth of healthy living tissue by another large organism, as a means of protection and maintenance of overall colonial health and uninhibited growth.

Presumably, acrozooids are morphologically independent from the rest of the parent colony and therefore are able to live and develop as incipient colonies after separation. Most importantly, they are not attached to other zooids by lateral canals (solenia) nor are they imbedded in a common coenenchyme, as are autozooids, siphonozooids, and mesozooids. Since it is postulated that acrozooids are asexual buds and therefore incipient colonies, the growth of an acrozooid leading to the development of a new colony presumably takes place only after separation from the parent colony and after settlement of the acrozooid at a new location, which is independent from the parent colony.

Several precedents for asexual reproduction by colony fragmentation, fission, or budding are known in other octocorals such as soft corals and gorgonians (Ofwegen et al. 2009: 179). Two such examples (observed on coral reefs in the Philippines by the 1st author) are of the ellisellid gorgonian *Junceella* spp. (Fig. 10) and the alcyoniid soft coral *Sarcophyton* spp. (Benayahu, et al. 2004: 556, figs. 13-15), which were respectively observed to exhibit vegetative (asexual) budding at the distal terminus and peripheral margin of the colony. In these examples, a coenenchymal mass containing several autozooids gradually pinches off from the parent colony and settles on suitable substratum to establish a new colony. Acrozooids differ in that they are presumed to be vegetative buds which represent independent polyps, and are not associated with a coenenchymal mass or other kinds of zooids.

Vegetative or asexual reproduction, also known as clonal propagation, was previously described in various alcyonacean octocorals via a variety of modes (Hartnol 1975, Highsmith 1982, Lasker 1983 1984 1988 1990, Walker and Bull 1983, Benayahu and Loya 1985 1987, Dinesen 1985, Farrant 1985, Jackson 1985, McFadden 1991, Dahan and Benayahu 1997, Simpson 2009), but ours is the 1st record of this phenomenon in pennatulacean octocorals.

The presumption provided here of the newly described kind of pennatulacean polyp that is representative of clonal propagation is viewed not as a record, but as a suggested mode of clonal propagation that needs future verification.

Acknowledgments: The color illustration for figure 1A is by J. Machnicki in 2010 of the California Academy of Sciences (San Francisco, CA, USA). We are grateful for the generous donation of the Hearst Foundation which made possible the 2011 Hearst Philippines Expedition of the California Academy of Sciences. We thank 2 anonymous reviewers for their critical reading of the manuscript.

REFERENCES

- Bayer FM, M Grasshoff, J Verseveldt. 1983. Illustrated trilingual glossary of morphological and anatomical terms applied to Octocorallia Leiden, The Netherlands: Dr. W. Backhuys, 75 pp.
- Benayahu Y. 1998. Lobe variation in *Sinularia nanolobata* Verseveldt, 1977 (Cnidaria: Alcyonacea). Bull. Mar. Sci. 63: 229-240.
- Benayahu Y, Y Loya. 1985. Settlement and recruitment of a soft coral: Why is *Xenia macrospiculata* a successful colonizer? Bull. Mar. Sci. **36**: 177-188.
- Benayahu Y, Y Loya. 1987. Long-term recruitment of softcorals (Octocorallia: Alcyonacea) on artificial substrata at Eilat (Red Sea). Mar. Ecol. Progr. Ser. 38: 161-167.

- Benayahu Y, M-S Jeng, S Perkol-Finkel, C-F Dai. 2004. Soft corals (Octocorallia: Alcyonacea), from southern Taiwan.
 II. Species diversity and distributional patterns. Zool. Stud. 43: 548-560.
- Bleeker P. 1859. Over eenige nieuwe soorten van Zeeveders of Pennatulina (polypi natantes) van den Indische Archipel. Natuurk. Tijdschr. voor Nederl. Ind. 20: 399-404.
- Brafield AE. 1969. Water movements in the pennatulid coelenterate *Pteroides griseum*. J. Zool. **158**: 317-325.
- Broch H. 1910. Diagnosen von neuen oder weniger bekannten Pennatulidae. Zool. Anz. **36:** 60-65.
- Dahan M, Y Benayahu. 1997. Reproduction of Dendronephthya hemprichi (Cnidaria: .Octocorallia): yearround spawning in an azooxanthellate soft coral. Mar. Biol. **129:** 573-579.
- Dinesen ZD. 1985. Aspects of the life history of a stolonbearing species *Efflatounaria* (Octocorallia: Xeniidae). Proc. 5th Int. Coral Reef Congr. **6:** 89-94.
- Fabricius K, P Alderslade. 2001. Soft corals and sea fans - a comprehensive guide to the .tropical shallow-water genera of the Central-West Pacific, the Indian Ocean and the Red Sea. Townsville, Australia: Australian Institute of Marine Science, 264 pp.
- Farrant PA. 1985. Reproduction in the temperate Australian soft coral Capnella gaboensis. Mar. Biol. 92: 381-392.
- Goldberg WM, KC Makemson, SB Colley. 1984. Entocladia endozoica sp. nov., a pathogenic chlorophyte: structure, life history, physiology, and effect on its coral host. Biol. Bull. 166: 368-383.
- Gosliner TM, DW Behrens, GC Williams. 1996. Coral reef animals of the Indo-Pacific - animal life from Africa to Hawai'i exclusive of the vertebrates. Monterey, CA: Sea Challengers, 314 pp.
- Hartnoll RG. 1975. The annual cycle of *Alcyonium digitatum*. Estuar. Coast. Shelf Sci. **3:** 71-78.
- Herklots JA. 1858. Notices pour servir à l'étude des polypiers nageurs ou pennatulides. Bijdr. Dierk. **7:** 1-31.
- Hickson SJ. 1916. The Pennatulacea of the Siboga Expedition, with a general survey of the order. Siboga Expeditie Monogr. 14: 1-265.
- Highsmith RC. 1982. Reproduction by fragmentation in corals. Mar. Ecol. Progr. Ser. **7:** 207-226.
- Hoeksema BW. 2007. Delineation of the Indo-Malayan centre of maximum marine biodiversity: the coral triangle. *In* W. Renema, ed. Biogeography, time and place: Distributions, barriers and islands, Springer Dordrecht, the Netherlands, pp. 117-178.
- Jackson JBC. 1985. Distribution and ecology of clonal and aclonal benthic invertebrates. *In* JBC Jackson, LW Buss, RE Cook, eds. Population biology and evolution of clonal organisms. New Haven, CT: Yale Univ. Press, USA, pp. 297-355.
- Jungersen HFE. 1888. Über Bau und Entwicklung der Kolonie von *Pennatula phosphorea* L. Zeit. wiss. Zool. **47**: 626-649.
- Kükenthal W. 1909. Beobachtungen an einigen Korallentieren des Adriatischen Meeres. Aus der Natu, **5:** 321-328.
- Kükenthal W. 1915. Pennatularia. Berlin: Verlag von R. Friedländer und Sohn. Das Tierreich **43:** 1-132.
- Lasker HR. 1983. Vegetative reproduction in the octocoral Briareum asbestinum (Pallas). J Exp. Mar. Biol. Ecol. 72: 157-169.
- Lasker HR. 1984. Asexual reproduction, fragmentation, and

skeletal morphology of a plexaurd gorgonian. Mar. Ecol. Progr. Ser. **19:** 261-268.

- Lasker HR. 1988. The incidence and rate of vegetative propagation among coral reef Alcyonarians. Proc. 6th Int. Coral Reef Symp. **2:** 763-768.
- Lasker HR. 1990. Clonal propagation and population dynamics of a gorgonian coral. Ecology **71**: 1578-1589.
- Niedermeyer A. 1911 Studien über den Bau von *Pteroides* griseum (Bohadsch). Arb. zool. Inst. Univ. Wien zool. Sta. Triest **19:** 99-164.
- Niedermeyer A. 1912. Über den Verschlussmechanismus der Stielporen bei *Pennatula* und *Pteroeides*. Zool. Anz. **39**: 190-196.
- McFadden CS. 1991. A comparative demographic analysis of clonal reproduction in a temperate soft coral. Ecology 72: 1849-1866.
- Simpson A. 2009. Reproduction in octocorals (Subclass Octocorallia): a review of published literature. Version 16 July 2009. In Deep-Sea Corals Portal. Available at http:// www.ucs.louisiana.edu/~scf4101/Bambooweb Accessed 12 Dec. 2012.
- Sutherland KP, JW Porter, C Torres. 2004. Disease and immunity in Caribbean and Indo-Pacific zooxanthellate corals. Mar. Ecol. Progr. Ser. 266: 273-302.
- van Ofwegen LP, O Breedy, S Cairns. 2009. Octocorallia -Octocorals. *In*: V. Häussermann and G. Förstera, eds. Marine Benthic Fauna of Chilean Patagonia. Nature in Focus, Santiago de Chile: 177-214.
- von Kölliker RA. 1869-72. Anatomisch-Systematische Beschreibung der Alcyonararien. Erste Abtheilung. Die Pennatuliden. Abh. Senckenb. naturforsch. Ges. 7: 111-255; 487-602; 8: 85-275 (also issued in 1872 with consecutive pagination, 1-485).
- Walker TA, GD Bull. 1983. A newly discovered method of reproduction in gorgonian coral. Mar. Ecol. Progr. Ser. 12: 137-143.
- Williams GC. 1986. Morphology, systematics, and variability of the southern African soft coral *Alcyonium variabile* (J. Stuart Thomson, 1921) (Octocorallia, Alcyoniidae). Ann. S. Afr. Mus. **96:** 241-270.
- Williams GC. 1989. The pennatulacean genus Cavernularia Valenciennes (Octocorallia: Veretillidae). Zool. J. Linn. Soc. 95: 285-310.
- Williams GC. 1990. The Pennatulacea of southern Africa (Coelenterata, Anthozoa). Ann. S. Afr. Mus. 99: 31-119.
- Williams GC. 1992. The Alcyonacea of southern Africa. Stoloniferous octocorals and soft corals (Coelenterata, Anthozoa). Ann. S. Afr. Mus. **100**: 249-358.
- Williams GC. 1995. Living genera of sea pens (Coelenterata: Octocorallia: Pennatulacea): illustrated key and synopses. Zool. J. Linn. Soc. Lond. **113**: 93-140.
- Williams GC. 2011. The global diversity of sea pens (Cnidaria: Octocorallia: Pennatulacea). PLoS ONE 6: 1-11.
- Williams GC, SD Cairns. 2011. Systematic list of octocoral genera. Octocoral Research Center website - Genera (Systematic List). Available at http://researcharchive. calacademy.org/research/izg/OCTOCLASS.htm Accessed 12 Dec. 2012.
- Williams G, C Mattison. 2006. Microscope slide or SEM stub preparation for octocoral sclerites or other invertebrate spicules. Octocoral Research Center website - Research Techniques. Available at http://researcharchive. calacademy.org/research/izg/OctoResearchTech.htm Accessed 12 Dec. 2012.