

Reinterpretation of some tentacular structures in actinodendronid and thalassianthid sea anemones (Cnidaria: Actiniaria)

A. Ardelean

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Adorian Ardelean, Division of Invertebrate Zoology, University of Kansas Natural History Museum and Biodiversity Research Center, And Department of Ecology and Evolutionary Biology, University of Kansas, Lawrence, KS 66045 USA (e-mail: adorian@ku.edu).

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The oral disc of an actinodendronid sea anemone is drawn out into a variable number of highly branched tentacular structures that make the anemone resemble a tree. These tentacular structures have been considered either lobes or branched tentacles. The term lobe has been applied to various structures of the oral disc in sea anemones; I distinguish between temporary lobes, permanent marginal lobes, and permanent tentacular lobes. I use the number of mesenterial pairs involved in a tentacular structure as evidence that tentacular structures in Actinodendronidae should be considered tentacles, not lobes. According to this interpretation, actinodendronids have only one tentacle communicating with each intermesenterial space, both endocoels and exocoels. The similarity between tentacular structures in members of Actinodendronidae and Thalassianthidae is only superficial; the tentacular structures in these families are not homologues as they have been previously considered.

Introduction

The family Actinodendronidae is a group of three exclusively tropical Indo-Pacific sea anemone genera: *Actinodendron* Blainville, 1830, *Megalactis* Ehrenberg, 1834, and *Actinostephanus* Kwietniewski, 1897. As a distinguishing feature, the oral disc of an actinodendronid is drawn out into a variable number of highly branched tentacular structures that make the sea anemone resemble a tree and distinguish an actinodendronid from a member of any other sea anemone family.

The peculiarity of tentacular structures and the arrangement of tentacles in sea anemones are important family-level taxonomic characters. Although of great importance in the taxonomy and systematics of sea anemones, the definition of lobes and tentacles is missing from the list of technical terms in the catalogue of Carlgren (1949: 7-10) as well as from Stephenson (1921, 1928), Hyman (1940), and Doumenc & Van-Praët (1987).

Morphology of tentacular structures and arrangement of tentacles in actinodendronids is not well understood; these structures have been interpreted both as lobes and as branched tentacles. They were termed tentacles by Quoy & Gaimard (1833), Blainville (1830, 1834), Ehrenberg (1834), Kwietniewski (1897), Haddon (1898), and Carlgren (1900a), as arms by Carlgren (1900a, 1940, 1949), as tentacle-like lobes by Haddon (1898), and as arm-like projections by Stephenson (1921) and Doumenc & Van-Praët (1987). Haddon (1898) called the same structures “elongated non-retractile lobes” in *Actinodendron*, lobes of disk and tentacles in *Megalactis*, and tentacles in *Actinostephanus*.

Carlgren (1949: 67) interpreted actinodendronids to have the “oral disc thrown into long, tentacle-like arms (lobes)” that “bear either dendritic tentacles or conical simple ones.” According to this interpretation, actinodendronids have multiple tentacles arising from each endocoel (the interval between the two members of a pair of mesenteries) and exocoel (the interval between mesenteries belonging to different pairs). If each tentacular structure is considered a single tentacle, however, actinodendronids would have only one tentacle per endocoel and one tentacle per exocoel.

Morphology and arrangement of tentacles are very important in phylogeny. In phylogenetic analyses it is important to have a good character argumentation and to avoid homoplasy as much as possible (Cracraft, 1967). Tentacular structures of Actinodendronidae considered as lobes will place these sea anemones in close relationship to sea anemones with more than one tentacle per endocoel (e.g. Stichodactylidae, Phymanthidae, Thalassianthidae). If the tentacular structures of actinodendronids are branched tentacles, these sea anemones would have only one tentacle per endocoel or exocoel. This character argumentation will change the topology of trees resulted from phylogenetic inference and the placement of the family Actinodendronidae within the current classification.

Lobed structures of the oral disc occur also in sea anemones of the families Actinernidae, Metridiidae, Stichodactylidae, and Thalassianthidae (Carlgren, 1949). The generic term “lobe” encompasses various structures of the oral disc, from temporary folds in Stichodactylidae to tentacular structures in Thalassianthidae. In thalassianthids, the tentacular structures, which are superficially similar to those in Actinodendronidae, have been consistently considered to be permanent lobes (Andres, 1883; Haddon, 1898; Carlgren 1900a, 1949). The oral disc has, on these lobes or surrounding them, branched or globular tentacles.

Because of superficial similarities, historically, actinodendronids have been classified with sea anemones that have branched tentacles (Milne Edwards 1857; Andres, 1883). Haddon (1898: 488) created the family Actinodendronidae for the genera *Actinodendron*, *Megalactis*, *Actinostephanus*, and *Acremodactyla*, sea anemones with “oral disk produced into a number of long tentacle-like arms, which bear variously disposed dendritic or globular tentacles.” *Thalassianthus* and *Actinaria*, the sister groups in earlier classifications of *Actinodendron*, were placed by Haddon (1898: 482) with *Heterodactyla* and *Cryptodendrum* in the family Thalassianthidae, based on the presence of permanent lobes of the oral disc and the presence of branched and globular tentacles. Both families Actinodendronidae and Thalassianthidae were considered by Haddon (1898: 465) to have more than one tentacle per endocoel and were included in the order Stichodactylinae. Carlgren (1900a, 1900b) classified in subtribe Stichodactylinae all the sea anemones with more than one tentacle on at least some of the endocoels (i.e. Stoichactidae, Thalassianthidae, Actinodendronidae, Phymathidae, Aureliidae, Heteranthidae, and Homostichanthidae). Stephenson (1921: 533) accepted Stichodactylinae as a homogeneous group but suggested it be subordinated under Endomyaria, sea anemones with an endodermal marginal sphincter muscle. This suggestion was adopted in the catalogue of Carlgren (1949), in which all the families previously classified under subtribe Stichodactylinae were classified under subtribe [sic] Endomyaria.

Material and methods

Abbreviations. KUNHM – Kansas University Natural History Museum (USA), USP – University of the South Pacific (Fiji), MNHN – Museum National d'Histoire Naturelle (France).

Specimens of actinodendronids and thalassianthids were investigated alive by diving, or in aquaria, and as preserved material. The results from this study are based on examination of more than 400 museum lots and photographs of actinodendronids. Listed below are specimens featured in this publication.

Material.— **Fiji:** Great Astrolabe Reef, Dravuni Island: USP 4887, *Actinodendron glomeratum* Haddon, 1898, 178°31.43'E, 18°45.28'S, depth 5 m, on sandy bottom with sea grass, leg. A. Ardelean and D.G. Fautin, June 2000; USP 4888, *Actinodendron glomeratum* Haddon, 1898, 178°31.43'E, 18°45.28'S, depth 3 m, on sandy bottom with sea grass and *Halimeda* spec. leg. A. Ardelean and D.G. Fautin, June 2000; West of Yaukulevu Island: USP 4892, *Heteractis aurora* (Quoy and Gaimard, 1833), 18°45'S, 178°3'E, depth 3 m, on sandy bottom, leg. A. Ardelean and D.G. Fautin, June 2000; **New Caledonia:** MNHN 2486, *Isactinernus quadrilobatus* Carlgren, 1918, Volcans Hunter et Matthew "Alis" Campagne Volsmar, Orstom, Sta. DW5, depth 600-700 m, 1 June 1989. **Papua New Guinea:** Madang: *Actinaria* spec., 145°50.36'E, 5°10.20'S, depth 1 m, in coral thickets, photo document A. Ardelean, June 2000; KUNHM 1660, *Cryptodendrum adhaesivum* Klunzinger, 1877, 145°49.34'E, 5°09.55'S, depth 3 m, juvenile, on *Acropora* spec., leg. A. Ardelean and D.G. Fautin, June 2000; KUNHM 1659, *Heterodactyla* spec., depth 1.5 m, leg. A. Ardelean and D.G. Fautin, June 2000; Motupore Island: KUNHM 1661, *Actinodendron plumosum* Haddon, 1898, 147°17.07'E, 9°31.22'S, depth 1.5 m, on sand with tall sea grass, leg. A. Ardelean and D.G. Fautin, June 2000.

Actinodendronid specimens were recorded in situ on Hi8 videotape using a Canon ES6000A video camera in an Amphibico underwater housing. Live material was collected underwater by hand. Geographic coordinates were read with an Eagle 12-channel GPS receiver at the point of collection. Some animals were kept in aquarium for three weeks; no food was given. Photographs were made in the aquarium using a Nikon Coolpix 950 digital camera. Archived videotapes and photographs are in the collection of KUNHM. Specimens were relaxed with magnesium sulfate in seawater, then preserved in 10% seawater formalin. After at least two months, they were transferred to 10% freshwater formalin solution.

Results and discussion

The term lobe of the oral disc in sea anemone morphology can apply to at least three structures that I distinguish as: temporary lobes, permanent marginal lobes, and permanent tentacular lobes.

In some anemones (e.g. *Cryptodendrum*, *Entacmaea*, *Heteractis*, *Stichodactyla*), the circumference of the oral disc is much larger than that of the distal column, so the edges of oral disc contract unevenly and form temporary lobes, each involving large numbers of mesenterial pairs (fig. 1).

The margin of the oral disc in *Actinernus* and *Synactinernus* is drawn out into four or eight triangular permanent marginal lobes, which are formed by participation of column and oral disc, and involve more than one pair of mesenteries (fig. 2A). In most

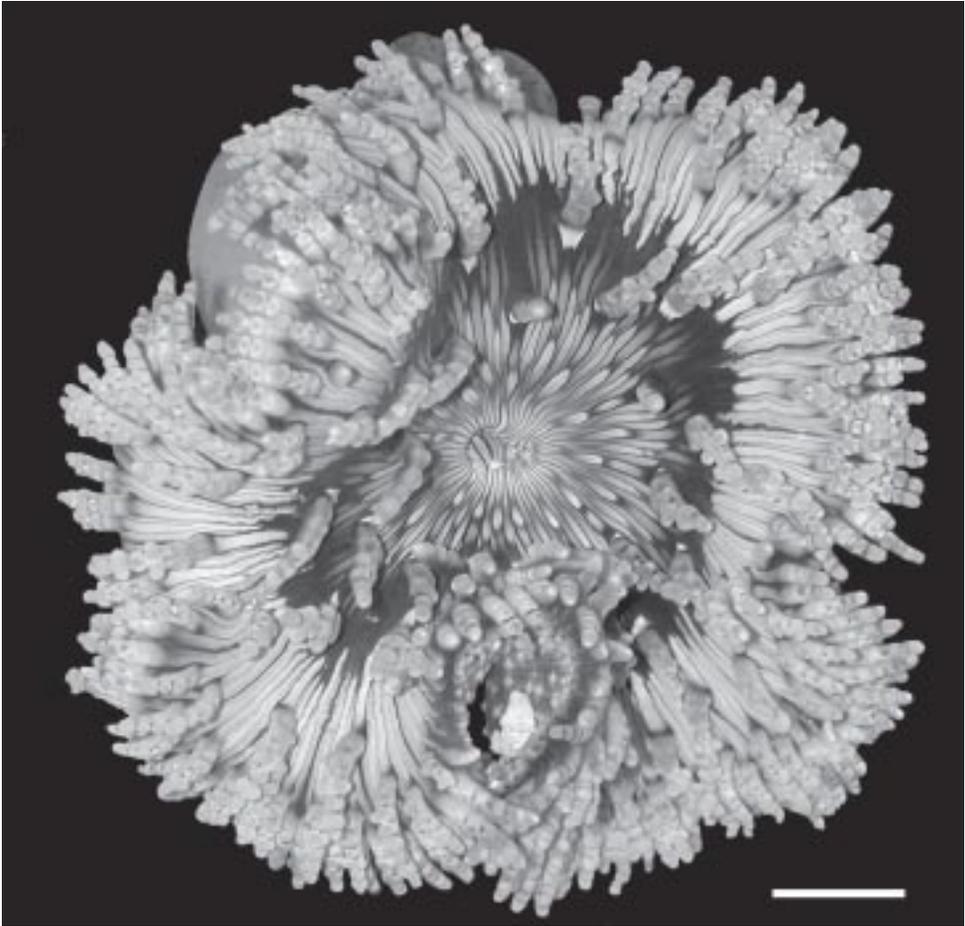


Fig. 1. Temporary lobes in a live specimen of *Heteractis aurora* (Quoy & Gaimard, 1833) from Great Astrolabe Reef, Fiji. Scale bar 10 mm.

species of *Metridium*, the margin of the oral disc has undulate permanent marginal lobes built from the oral disc and the column (fig. 2B).

In contrast, thalassianthids have permanent tentacular lobes formed from the projections of the oral disc alone and involving at least one endocoel and its adjacent exocoel (fig. 3). In some cases two types of lobed structures appear in the same animal (e.g. temporary lobes and permanent tentacular lobes in *Actineria*) (fig. 4). A transformation series of oral disc morphology in Thalassianthidae suggests that tentacular structures in this family are lobes of the oral disc (fig. 5). In *Cryptodendrum* (fig. 5A), the oral disc has no lobed tentacular structures; the tentacles bearing nematospheres are marginally disposed on the endocoels; ramified tentacles occur in the region between nematospheres and mouth. In *Heterodactyla* and *Thalassianthus*, the oral disc has permanent tentacular lobes. The relative position of tentacles bearing nematospheres is similar to that in *Cryptodendrum*: the nematospheres are disposed on the abo-

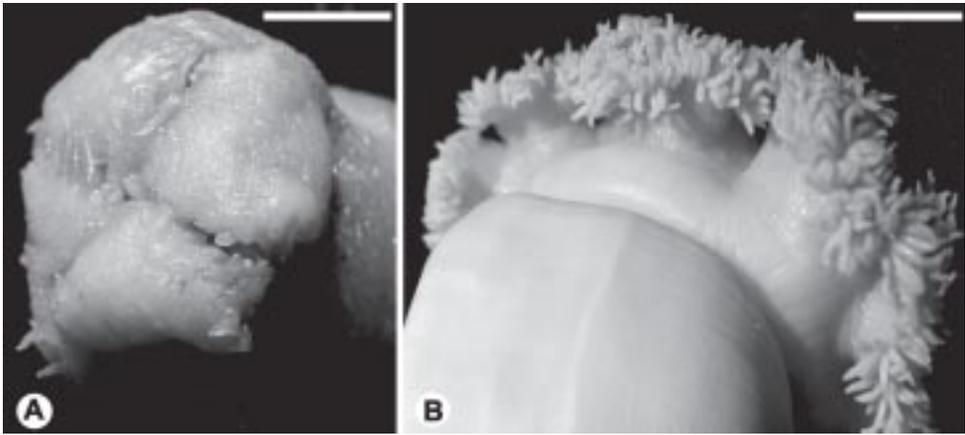


Fig. 2. Permanent marginal lobes. A. Triangular lobes in *Isactinernus quadrilobatus* Carlgren, 1918, MNHN 2486. Scale bar 10 mm. B. Undulating lobes in *Metridium farcimen* (Tilesius, 1809). Scale bar 10 mm.

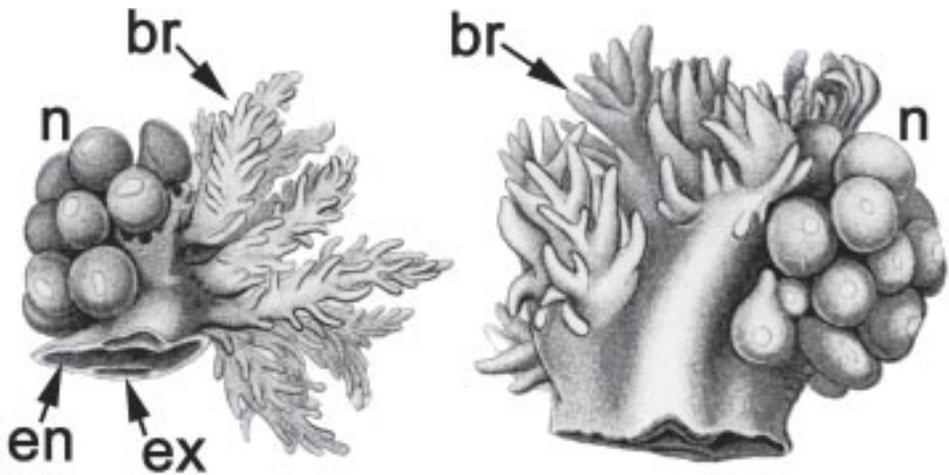


Fig. 3. Morphology of a permanent tentacular lobe in *Thalassianthus aster* Leuckart in Rüppel, 1828 (left) (Figure 6, plate IV in Carlgren, 1900a) and *Heterodactyla hemprichii* Ehrenberg, 1834 (right) (Figure 10, plate IV in Carlgren, 1900a). br – branched tentacle; en – endocoel; ex – exocoel; n – nematosphere.

ral face of the tentacular structures (toward the margin); ramified tentacles are disposed on the oral face of the tentacular structures and continue in radial rows on the oral disc toward the mouth (fig. 5B-C).

Removal of a tentacular structure reveals some functional correlates. If one is removed from a live specimen of *Heterodactyla*, the pore in the oral disc will remain open at least 24 h (pers. obs. on KUNHM 1659 and KUNHM 1660). The pore in the oral disc does not close because a tentacular structure extends over one endocoel and its adjacent exocoels. A tentacular structure in species of *Actinodendron* can easily

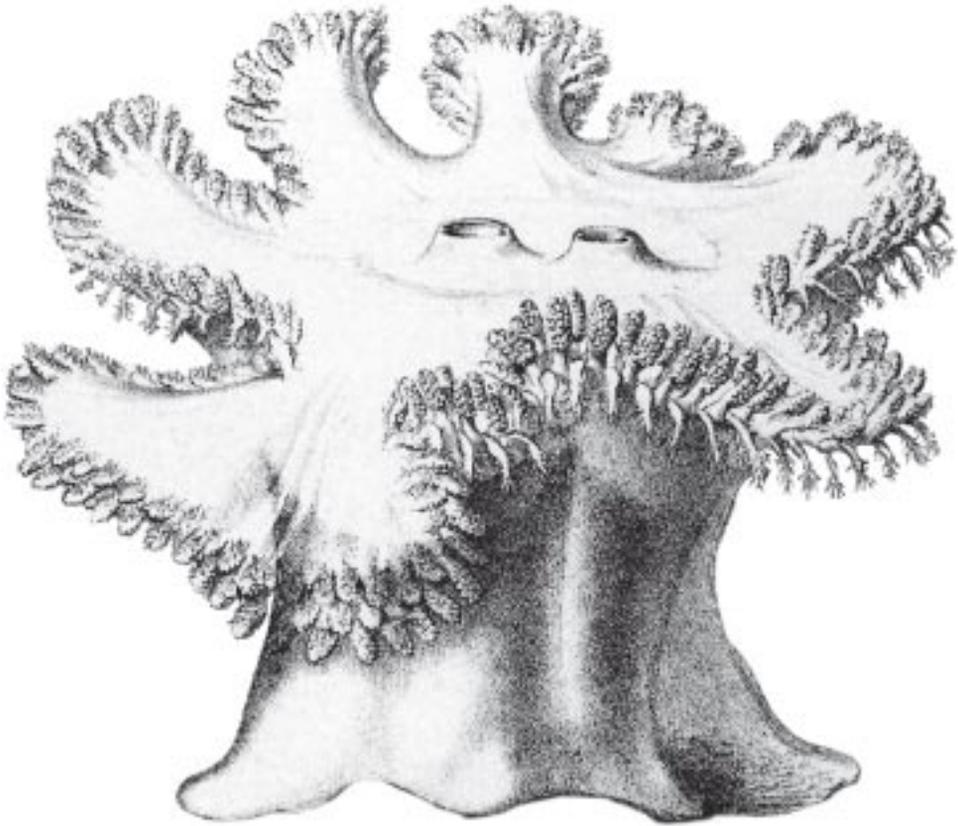


Fig. 4. Lobed structures in *Actineria dendrophora* Haddon and Shackleton, 1893: temporary lobes and permanent tentacular lobes. Modified from figure 7, plate 25 (Haddon, 1898).

detach from the oral disc (Moosleitner, 1992: 38; Fautin pers. comm.; pers. obs.). This is true for each branch of a tentacle in a specimen of *Actinodendron*. When this happens, the remaining pore can close in a matter of minutes (fig. 6). This is possible because circular muscular fibers are present throughout the length of a tentacle (fig. 7). I found no sphincter muscles at the base of tentacles like in other sea anemones that can autotomize their tentacles (e.g. *Liponema*, *Bolocera*) (Carlgren, 1949). I interpret these structural details as evidence that tentacular structures in Actinodendronidae are branched tentacles.

Tentacular structures in actinodendronids involve only one endocoel or exocoel. These structures have an almost circular base, very similar to the attachment region of an unbranched tentacle to the oral disc (fig. 7). I found, contrary to Haddon (1898: 489), that the tentacular structures of actinodendronids are fully retractile and can contract generally or locally; the same finding is alluded to in Moosleitner (1992: 38).

In conclusion, I interpret a tentacle as any projection of the oral disc that occurs between one pair of mesenteries or between mesenteries of two adjacent pairs. A

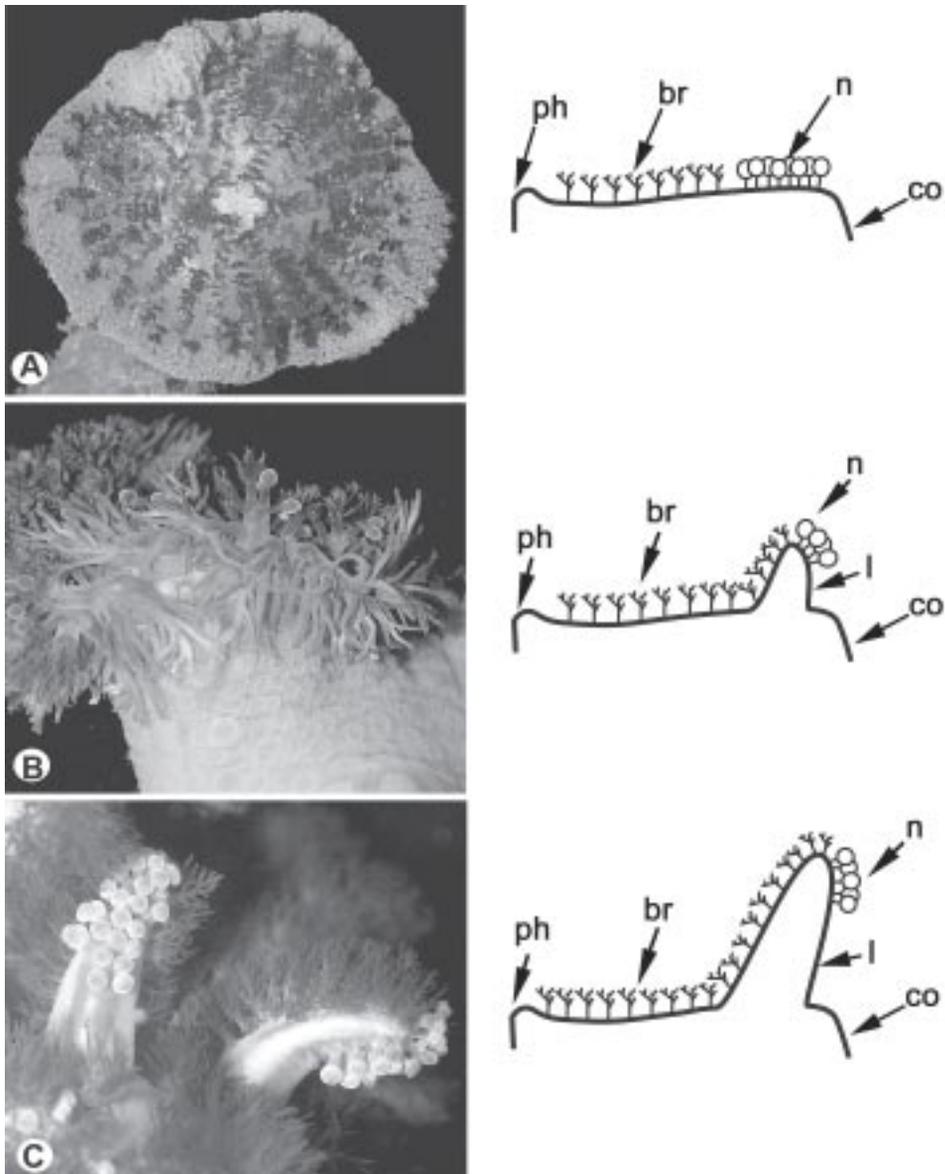


Fig. 5. Transformation series of lobe morphology in Thalassianthidae. A. *Cryptodendrum adhaesivum* juvenile, KUNHM 1660. B. *Heterodactyla cf. hemprichii*, KUNHM 1659. C. *Actinera* spec. br – branched tentacle; co – column; l – lobe; ph – actinopharynx; n – nemasphere.

lobe is a structure that involves at least one endocoelic interval and its adjacent exocoelic intervals. I distinguish several types of lobes of the oral disc in sea anemones. Based on comparative morphology, I find that the tentacular structures in Actinodendronidae should be called tentacles; actinodendronids have only one branched

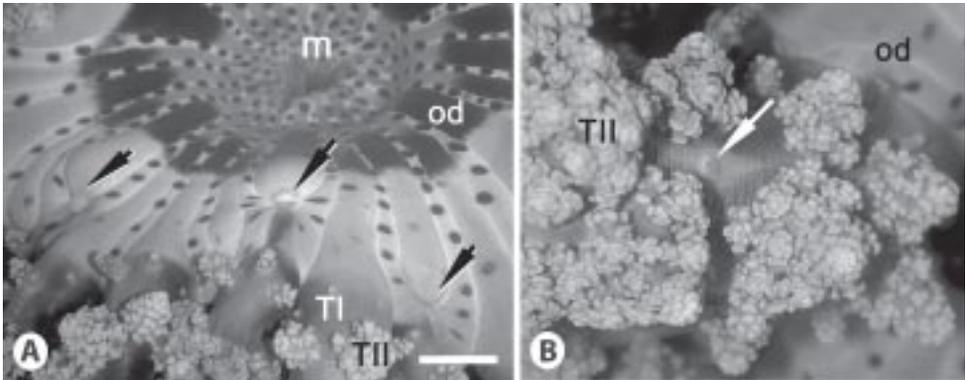


Fig. 6. *Actinodendron glomeratum* Haddon, 1898, USP 4887, Great Astrolabe Reef, Fiji. A. Oral disc with black arrows indicating where missing tentacles had been. B. Tentacle missing a secondary branch; white arrow indicates the place where the secondary branch is missing. od – oral disc; m – mouth; TI – primary branch; TII – secondary branch. Scale bar 10 mm.

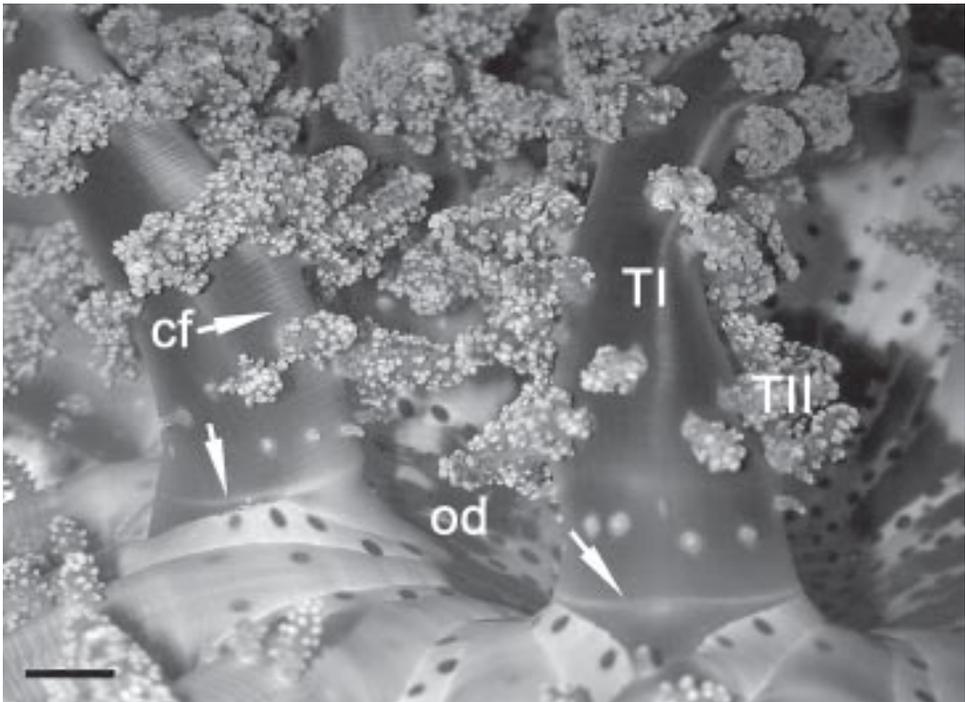


Fig. 7. Attachment region of tentacles to the oral disc in Actinodendronidae. *Actinodendron glomeratum* Haddon, 1898, USP 4888, Great Astrolabe Reef, Fiji. cf – circular fibers; od – oral disc; TI – primary branch; TII – secondary branch. Scale bar 10 mm.

tentacle on each endocoel and exocoel. Contrarily, the tentacular structures in Thalassianthidae, which are superficially similar to those in Actinodendronidae, should be called permanent tentacular lobes of the oral disc; thalassianthids have multiple tentacles on at least each endocoel. According to this interpretation, the actinodendronids may not be closely related with sea anemones that have more than one tentacle per endocoel or exocoel. Analysis on 16S ribosomal RNA gene sequences of actiniarians indicated that Actinodendronidae is not nested with the thalassianthids and stichodactylids (unpublished results). According to 16S data, Actinodendronidae is rather a sister group to a larger clade that includes on one side stichodactylids and thalassianthids and on the other side members of the family Actiniidae.

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