

Stauromedusae of the genus *Manania* (= *Thaumatocypus*) (Cnidaria, Scyphozoa) in the northeast Pacific, including descriptions of new species *Manania gwilliami* and *Manania handi*¹

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Manania gwilliami n.sp. and *Manania handi* n.sp., stauromedusae belonging to the family Depastridae, are described from the west coast of North America. They are differentiated from the one species of the genus previously known from that area, *M. distincta* (Kishinouye, 1910) by shape, color, habitat, and geographic range. Specimens of *M. gwilliami* are generally red and those of *M. handi* are green; both lack the dark brown herringbone patterning of *M. distincta* medusae. *Manania gwilliami* is widely distributed from Mexico to Canada in exposed shallow-water coastal habitats, whereas *M. handi* has been found only off the San Juan Islands and Vancouver Island in protected shallow water. The occurrence of *M. distincta* in the northeast Pacific has been sporadic. The name *Manania* is a senior synonym of *Thaumatocypus*.

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On trouvera ici la description de *Manania gwilliami* n.sp. et de *Manania handi* n.sp., stauroméduses de la famille des Depastridae provenant de la côte ouest de l'Amérique du Nord. Les nouvelles espèces se distinguent de la seule autre espèce du genre dans cette région, *M. distincta* (Kishinouye, 1910), par leur forme, leur taille, leur habitat et leur répartition géographique. Les spécimens de *M. gwilliami* sont généralement rouges, alors que ceux de *M. handi* sont verts; ni l'une ni l'autre espèce ne possèdent les dessins en chevrons qui caractérisent *M. distincta*. *Manania gwilliami* est bien répandue, du Mexique au Canada, dans des habitats côtiers peu profonds et exposés, alors que *M. handi* n'a été trouvée qu'au large des îles San Juan et de l'île de Vancouver, dans des eaux peu profondes et bien protégées. *Manania distincta* ne fréquente le nord-est du Pacifique que sporadiquement. Le nom de *Manania* est un synonyme plus ancien de *Thaumatocypus*.

[Traduit par la revue]

Introduction

Stauromedusae, an order of sessile, polyp-like scyphozoans, contains 14 genera and about 40 species (Kramp 1961; Larson 1988). Although these animals occur worldwide, they are most abundant and diverse in shallow, temperate seas, where they live permanently or temporarily attached to sea grass, algae, and rocky substrata. Being often cryptically pigmented and mostly small, they are generally inconspicuous.

Their life cycle is poorly known. Upon fertilization of the small eggs, which are shed into the water during summer, worm-like, crawling planulae develop (Otto 1976). They metamorphose into small stauromedusae that mature in less than 1 year. It is unclear how long these cnidarians live, or how littoral populations in cold waters survive the winter, since stauromedusans are seldom seen at that time (Hirano 1986a; Larson 1988).

Stauromedusae feed mainly on small crustaceans, especially gammaridan amphipods and harpacticoid copepods (Larson 1987; Hirano 1986a). In tide pools of the northeast Pacific, they can reach densities of 25/m² (R. J. Larson, unpublished data). The medusae described in this paper are sometimes

common, and so may play an important role in sublittoral ecosystems, a subject that deserves study.

Before the 1950s, little was known about the stauromedusan fauna of the northeast Pacific. As a graduate student at the University of California, Berkeley, G. F. Gwilliam studied the taxonomy, biogeography, morphology, and neurobiology of seven species found from British Columbia to California. Although he recorded several new species and proposed valuable nomenclatural changes, unfortunately the conclusions he reached in his dissertation (1956) were never published. An attempt during the 1970s by P. Corbin, of England, to document the same fauna likewise was not published.

Subsequent to recent collection of specimens by both of us, Gwilliam gave some of his original material and an unpublished manuscript by himself and C. Hand to D.G.F. From these specimens and data we describe two new species belonging to the genus *Manania* Clark, 1863.

Materials and methods

Specimens were collected by hand at low tide or by scuba diving. Before fixation, some were relaxed in isotonic MgCl₂ for 24 h, then quickly fixed in hot (50°C) Bouin's fluid, whereas others were relaxed more quickly and fixed in formalin. Paraffin sections 8 or 10 µm thick were stained, generally with hematoxylin and eosin. Measurements of cnidae, which were examined in smash preparations of fixed tissue, were made on undischarged capsules.

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Taxonomy

Manania gwilliami sp. nov.

(Figs. 1, 2, 3A)

Description

Goblet-shaped (Fig. 1A), to 4 cm total length. Calyx as long as wide, clearly demarcated from stalk, with scattered nematocyst warts. Stalk narrow; circular to quadrangular in cross-section (Fig. 1B); highly contractile, from 1/2 to 3–4 times calyx length; four-chambered throughout (Fig. 1B).

Arms short, tending to occur as four interradi pairs. Secondary tentacles 15–30 per arm, short, capitate, outermost ones with enlarged adaxial glandular pads (Fig. 1C). Primary tentacles (anchors) eight, similar to abaxial secondary tentacles but smaller; each with a small, dark pigment spot near margin.

Mouth quadrate with frilled lips.

Coronal muscle well developed, entire, at subumbrellar margin. Radial subumbrellar muscles eight, in adradia, extending to arm tips.

Subumbrellar nematocyst vesicles along margin, most numerous in perradii where they cover most of gonad surface. Gonads eight, in four perradial pairs. Each pair with obliquely oriented folds.

Color of subumbrella, calyx, and stalk variable, ranging from tan to magenta. Those from type locality mostly dark red (Fig. 3A). Subumbrellar nematocyst clusters vivid white. Gonads cream to tan with narrow, dark brown pigment band extending radially over subumbrellar surface.

Cnidom

"Atrichous" isorhizas (lacking visible spines) 12–20 × 2–4 μ m; microbasal euryteles A 10–13 × 8–9 μ m; microbasal euryteles B 3–12 × 4–5 μ m (Figs. 2A–2C).

ETYMOLOGY: The specific epithet *gwilliami* honors G. F. Gwilliam, who first recognized this species in his unpublished Ph.D. dissertation (1956), where he referred to it as *M. "enerereuths"* because of its red coloration.

TYPE LOCALITY: Barkley Sound, Vancouver Island, British Columbia, Canada.

Material examined

HOLOTYPE: California Academy Sciences, Department of Invertebrate Zoology (CASIZ) 063346, Barkley Sound, Vancouver Island, 2–15 m depth, June 1985, S. Smith coll.

PARATYPES: California Academy of Sciences (CASIZ): 24 specimens, No. 063347, Barkley Sound, Vancouver Island, 2–15 m, June 1985, S. Smith coll.; 1 specimen, No. 065187, Barkley Sound, Vancouver Island, 6 June 1985, R. Van Syoc coll.; 1 specimen, No. 065186, Bodega Head, California, 10 m, 23 May 1964, R. Sikora coll.; 10 specimens, No. 065184, Bodega Head, California, 10 m, 23 May 1964, R. Sikora coll.; 1 specimen, No. 065185, Punta Banda, Baja California, 12 m, no date, Scripps Institution of Oceanography coll.; 1 specimen, No. 060169, San Miguel Island, California, 15 m, 30 August 1985, Channel Islands Research Program coll. Moss Landing Marine Laboratory Museum: 1 specimen, Acc. No. C0083, Barkley Sound, Vancouver Island, 2–3 m, 9 June 1976, E. Anderson coll. Royal British Columbia Provincial Museum (RBCPM) (all specimens from the west coast of Vancouver Island): 1 specimen, No. 981-216, Cape Sutil, 20–25 m, 24 August 1981, P. Lambert coll.; 1 specimen, No. 985-409-11, Brooks Peninsula, 12 m, 5 June 1985, P. Lambert and G. Green coll.; 2 specimens, No. 980-331, Cape Parkins,

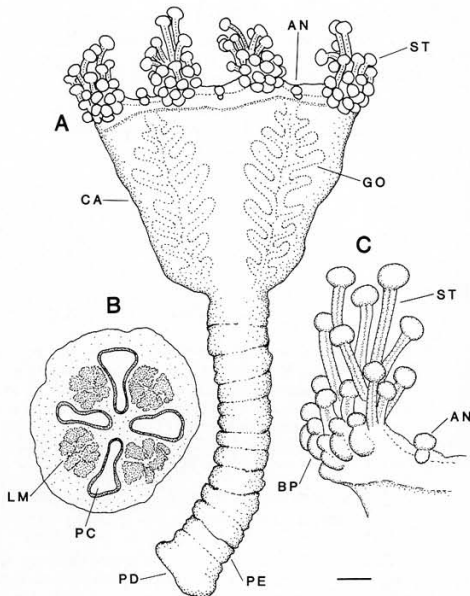


FIG. 1. *Manania gwilliami*. AN, anchor; BP, basal pad; CA, calyx; GO, gonad; LM, longitudinal muscle; PC, peduncular canal; PD, pedal disc; PE, peduncle; ST, secondary tentacle. (A) Side view of holotype. Scale bar = 0.5 mm. (B) Cross section of stalk. Scale bar = 1.0 mm. (C) Side view of calyx margin. Scale bar = 1.0 mm.

Quatsino Sound, 10 m, 29 June 1980, P. Lambert and G. Green coll.; 2 specimens, No. 980-350, Mate Island, Barkley Sound, 12 m, 11 July 1980, G. Green coll.; 5 specimens, No. 976-1047-1, Wizard Inlet, Barkley Sound, 15 m, 14 July 1976, P. Lambert coll.; 11 specimens, No. 976-1045-1, Bamfield, Barkley Sound, 12 m, 13 July 1976, P. Lambert coll.; 3 specimens, No. 973-189-2, Austin Island, Broken Group, Barkley Sound, 0–10 m, 31 July 1973, A. Peden and B. Cooke coll.; 4 specimens, No. 973-163-2, Howell Island, Broken Group, Barkley Sound, 12 m, 5 July 1973, A. Peden, B. Cooke, and P. Lambert coll.; 4 specimens, No. 973-158-4, Howell Island, Broken Group, Barkley Sound, 18 m, 30 June 1973, A. Peden and P. Lambert coll.

OTHER MATERIAL EXAMINED: *In situ* color photographs: Effingham Island, Barkley Sound, 6 m, August 1982, J. Cosgrove; Port Renfrew, Vancouver Island, June 1978, B. Cooke; Jansen Reef, British Columbia, March 1978, N. McDaniel; Beg Island, British Columbia, July 1978, N. McDaniel. *Ex situ* color photographs: Stillwater Cove, Pebbel Beach, California, July 1977, J. Cooper.

Distribution and natural history

Manania gwilliami seems to be the most widespread species of *Manania* on the North American Pacific coast, and to be particularly abundant in British Columbia. As well as the numerous specimens from the west coast of Vancouver Island, the RBCPM collection contains two juvenile specimens (976-

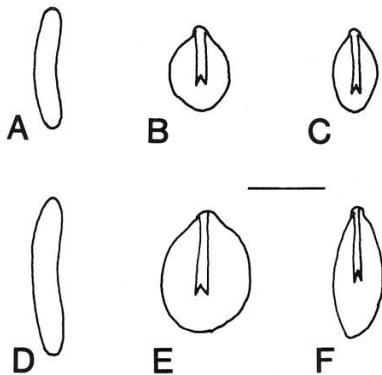


FIG. 2. Cnidae of *Manania gwilliami* (A–C) and *M. handi* (D–F) (from Gwilliam 1956). (A and D) Atrich; (B and E) A eurytele; (C and F) B eurytele. Scale bar = 10 μ m.

1031-3) probably belonging to this species from Rivers Inlet, Queen Charlotte Sound, B.C. (collected 23 March 1976, at 10 m, by B. Cooke and P. Lambert). Based on the material examined and records in G. F. Gwilliam and C. Hand (unpublished data), *M. gwilliami* is also known from northern California to Baja California. It probably occurs along the coast of Oregon and Washington but has been overlooked there.

These stauromedusae attach to rocks and alge in surf-swept areas generally at 2–15 m depth, and rarely in very low tide pools. Their red coloration makes these animals cryptic in areas with abundant coralline algae. In strong directional currents, a medusa may incline, resting on stalk and calyx. In oscillating current the long stalk can twist and untwist (N. McDaniel, personal communication, 1988). This flexibility may allow the animals access to waters above the boundary layer that would be prohibited by a shorter, rigid stalk. The anchors (and probably the abaxial secondary tentacles) serve to reattach a medusa if its pedal disc becomes detached from the substratum, as might be expected to happen relatively frequently in the turbulent habitats from which *M. gwilliami* is known. The anchors are also involved in capture of prey, which probably consists largely of crustaceans, as evidenced by copepods and amphipods in the gastric cavity of some specimens S. Smith, personal communication, 1985).

Manania handi sp. nov.

(Figs. 2, 3C, 3D, 4)

Description

Trumpet-shaped (Fig. 4), to 4 cm total length. Calyx longer than wide, indistinctly demarcated from stalk, with scattered nematocyst warts. Stalk short, from one-half to equal to the entire calyx in length; narrow, contractile, circular to quadrangular in cross-section; four-chambered throughout.

Arms short, appearing as four interradial pairs. Secondary tentacles 15–25 per arm, capitate, outermost ones with enlarged basal glandular adhesive pads. Primary tentacles eight, similar to abaxial secondary tentacles but smaller; small, dark spot on adaxial side of each primary tentacle near margin.

Mouth quadrate with frilled lips.

Muscles as in *M. gwilliami*.

Subumbrellar nematocyst vesicles along margin, most numerous in perradii where they extend toward gonads. Gonads similar to those of *M. gwilliami*.

Color of subumbrella, calyx, and stalk translucent yellowish green (Figs. 3C, 3D). Four linear, interradial "windows" of lighter green outlined by a thin brown margin occur along almost entire length of calyx. Gonads cream colored. Subumbrellar nematocyst vesicles vivid white.

Cnidom

"Atrichous" isorhizas (lacking visible spines) 17–21 \times 2–3 μ m; microbasic euryteles A 14–17 \times 3–10 μ m; microbasic euryteles B 15–18 \times 4–8 μ m (Figs. 2D–2F).

ETYMOLOGY: The specific epithet *handi* honors Cadet Hand, noted coelenterate biologist, major professor of G. F. Gwilliam, and coauthor with Gwilliam of an account of this species that was not published. Gwilliam (1956) referred to this species as *M. "prasinus"* because of its green coloration.

TYPE LOCALITY: False Bay, San Juan Island, Washington, U.S.A.

Material examined

HOLOTYPE: CASIZ No. 065183, False Bay, San Juan Island, Washington, intertidal, 21 May 1955, G. F. Gwilliam coll.

PARATYPE: U.S. National Museum of Natural History: 1 specimen No. 54517, Diana Island, Trevor Channel, Bamfield, Vancouver Island, 3 m depth on *Zostera*, mid-May 1976, Coelenterate Biology class coll.

OTHER MATERIAL: *Ex situ* color photographs Barkley Sound, Vancouver Island, May 1976, R.J.L.; Barkley Sound, Vancouver Island, October 1983, K. Larson; black and white photograph of a specimen identified as *Thaumatoscyphus hexadradatus* in Kozloff (1983, Fig. 344).

Distribution and natural history

Individuals of this species have been found off Vancouver Island (Barkley Sound and Victoria, B.C.), and off San Juan Island, WA. They attach to sea grass (*Zostera*) and algae in semiprotected subtidal habitats, often sympatrically with stauromedusae of the genus *Haliclystus*. Their coloration make them cryptic on sea grass.

Discussion

Taxonomic and nomenclatural issues at the generic level

The genus *Manania* was established by H. James-Clark (1863) (whose name has subsequently been commonly rendered as H. J. Clark, but who referred to himself as H. James-Clark (1863)) to contain *Lucernaria auricula* Fabricius, 1780, also known as *Halimocyathis lagena* (O. F. Müller, 1776). Müller's name is unavailable because it was part of a non-Linnaean polynomial ("Holothuria lagenam referens..."). Therefore the valid name for this taxon is *Manania auricula* (Fabricius, 1780). Clark (1863) recognized this species as sufficiently distinct from *Halimocyathus platypus* Clark, 1863, type species of that genus, to merit a separate genus.

Identity of the type specimen of *L. auricula* appears to be in doubt. P. Corbin (personal communication, 1975) determined that the material from Greenland, now housed in Denmark, that served as the basis for that name contains specimens of two species, *Manania auricula* and *Manania* (= ? *Stenoscyphus*) *hexaradiata* (Broch, 1907). Therefore, a lectotype must be selected from those specimens. That might be facilitated if Corbin's suggestion (personal communication, 1975)

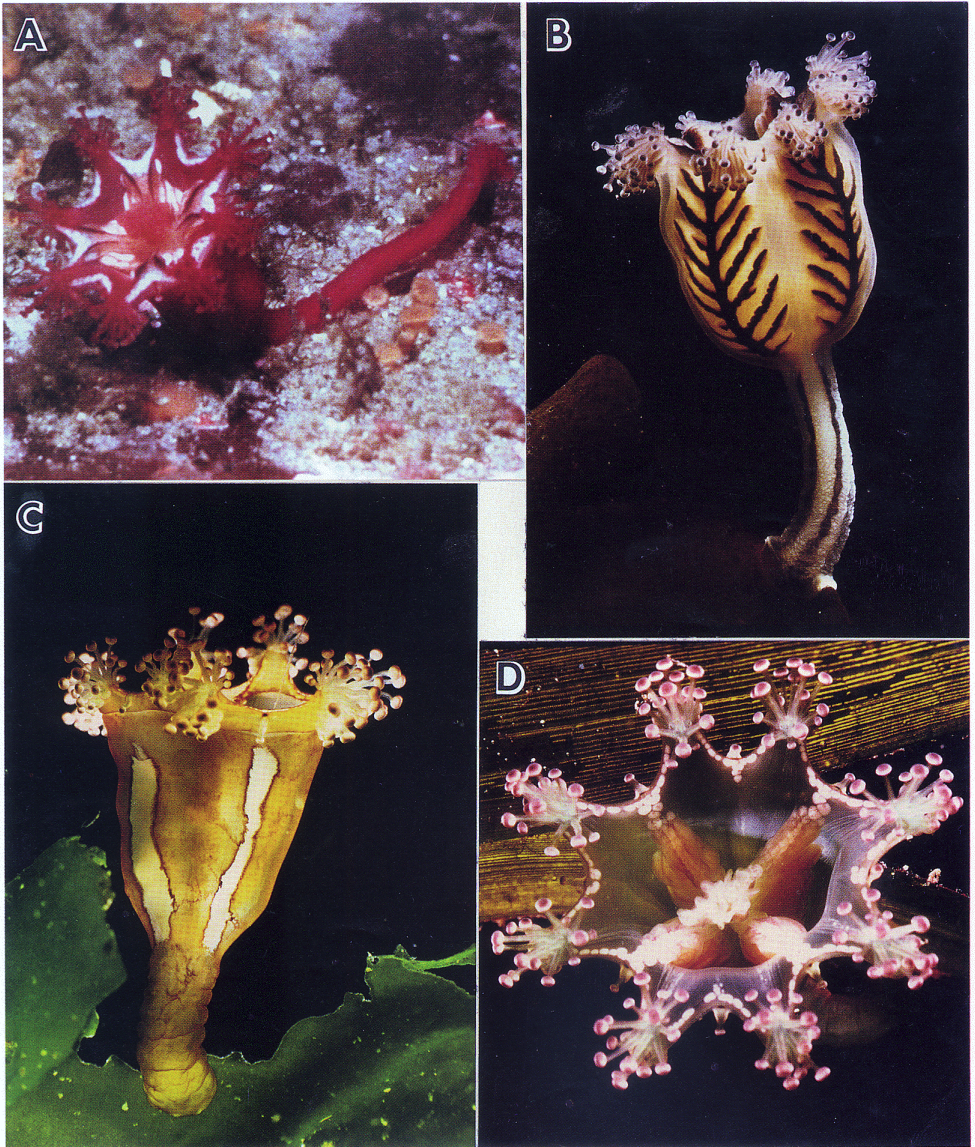


FIG. 3. *Manania* spp. (A) *Manania gwilliami*. *In situ*. Port Renfrew, Vancouver Island, June 1978. Taken by B. Cooke, RBCPM Photo File 5295. (B) *Manania distincta*. *In situ*. Cape Perpetua, Oregon, July 1974. Taken by R. J. Larson. (C) *Manania handi*. *Ex situ*. Barkley Sound, Vancouver Island, October 1983. Taken by K. Larson. (D) *Manania handi*. *Ex situ*. Barkley Sound, Vancouver Island, May 1976. Taken by R. J. Larson.

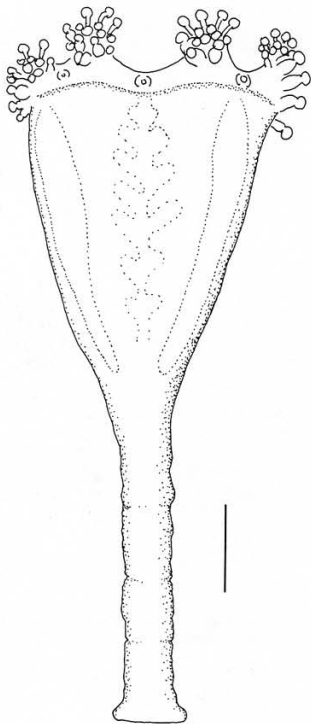


FIG. 4. *Manania handi* (from Gwilliam 1956). Scale bar = 0.5 mm.

were borne out that a more complete description of *L. auricula* may exist among unpublished manuscripts by Fabricius in the Danish Royal Library.

In his description of the new genus and species *Thaumatoscypus distinctus*, Kishinouye (1910) did not distinguish the taxa from any already named. Carlgren's (1935) table of taxonomically significant characters (e.g., nature and position of coronal muscle, number of peduncular chambers) for all 13 stauromedusan genera he recognized did not include *Manania*. Each listed taxon was characterized by a unique suite of characters except for *Halimocythus lagena* and *Thaumatoscypus distinctus*, which had identical diagnoses. Carlgren (1935) concluded that *H. lagena* really belongs to *Thaumatoscypus*. Despite this, Kramp (1961) recognized *Thaumatoscypus* with the single species *T. distinctus*, and *Halimocythus* with *H. lagena* and *H. platypus*. He, too, did not mention *Manania*.

Carlgren's (1935) table also included *Brochiella hexaradiata*, which had been made type species of the new genus *Brochiella* by Krumbach (1925). Uchida (1929) had placed it with a query in *Thaumatoscypus*, and Carlgren (1933) also questioned whether morphology of the peduncular canal was sufficiently distinctive and invariant to support recognizing the genus *Brochiella*, but Carlgren (1933, 1935), as well as Kramp (1961) continued to recognize the two genera as distinct, while Naumov (1961) synonymized them.

We agree with Gwilliam (1956) and Corbin (personal communication, 1975) that recognition of *Manania* as the senior synonym of *Thaumatoscypus* and *Brochiella* is justified. *Manania*, a member of the family Depastridae, is diagnosed as follows: with an entire mesogleal coronal muscle passing on exumbrellar sides of primary and secondary tentacles. Tentacles (both primary and secondary) capitate; primary and outermost secondary tentacles with abaxial glandular pads. Peduncle well developed with four interradial muscles in septa; chambers one or four throughout or in part.

Diagnosis of the family Depastridae Haeckel, 1879 (= Depastridae plus Halicyathidae Haeckel, 1879) is as follows: without well-defined marginal lobes; anchors (primary tentacles) small, simple; abaxial secondary tentacles with glandular pads; peduncle with four longitudinal muscles, and one or four chambers, or four in part. It belongs in suborder Cleistocarpida Clark, 1863, which is defined as follows: stauromedusae with perradial stomach pouches divided into inner and outer mesogonial pockets by a partition (claustrum).

Subfamily Thaumatoscypinae, erected by Carlgren (1935) for the genera *Thaumatoscypus* and *Halimocythus*, currently contains only the genus *Manania*. Its diagnosis is therefore identical with that for the genus. If recognizing it as a subfamily is desirable to parallel other subfamilies in the Depastridae, it must continue to be termed Thaumatoscypinae, according to International Code of Zoological Nomenclature Article 40(a), since our formal generic synonymization is subsequent to 1960, and no other family-group name is involved.

Taxonomy at the species level

Five species of *Manania* had been described before this paper, three in *Thaumatoscypus*: *T. distinctus* Kishinouye, 1910, *T. uchida* Naumov, 1961, and *T. atlanticus* Berrill, 1962. The others are *M. hexaradiata* and *M. auricula*. As with nearly all stauromedusae, characters used in their taxonomy are strictly morphological. The most useful for initial separation is number of chambers in the stalk (Table 1). Hirano's (1986b) synonymization of *M. uchida* with *M. distincta* seems unsupportable on this basis, but, as she remarked, further study is necessary to determine if this character is affected by age or environment. In any event, *M. distincta* is uniquely patterned (see below).

Manania hexaradiata has only one chamber. The three nominal species with four proximal chambers that coalesce distally into a single canal, i.e., *M. atlantica*, *M. auricula*, and *M. uchida*, seem to lack characters that clearly separate them, and have overlapping geographical ranges. Their taxonomic status should be critically examined, with particular attention to features such as those that distinguish among the three species discussed below, all of which also have similar peduncular canal morphology and overlapping ranges.

The only species of *Manania* with four chambers throughout, other than the two described here, is *M. distincta* (Kishinouye, 1910) (Fig. 3B), which was described from the Kurile Islands, and has subsequently been recorded from elsewhere in northern Japan (e.g., Uchida and Hanaoka 1933; Uchida 1954). Specimens of it were apparently first collected in the eastern Pacific by R.J.L. (unpublished data), who found two medusae attached to algae in the intertidal at Cape Perpetua, Oregon, in July 1974. (The specimens were subsequently lost.) Two additional specimens from Gillen Harbour, Estevan Group, B.C., collected by A. Parkinson at 6–18 m, 16 August 1974, bear catalog No. RBCPM 974-564-3, and

TABLE 1. Geographic distribution and number of peduncular canals in species of *Manania*

	Geographic range	Peduncular canals	References*
<i>Manania hexaradiata</i>	Arctic, N Atlantic	1 throughout	2, 5
<i>Manania atlantica</i>	N Atlantic	4/1†	6, 7
<i>Manania auricula</i>	N Atlantic	4/1†	1
<i>Manania uchida</i>	Arctic, NW Pacific	4/1†	5
<i>Manania distincta</i>	N Atlantic	4 throughout	3, 4, 5, 8
<i>Manania gwilliami</i> n.sp.	NE Pacific	4 throughout	4, 8
<i>Manania handi</i> n.sp.	NE Pacific	4 throughout	4, 8

*1, Clark 1863; 2, Broch 1907; 3, Kishinouye 1910; 4, Uchida 1929; Uchida and Hanaoka, 1933; 4, Gwilliam 1956; 5, Naumov 1961; 6, Berrill 1962; 7, Berrill 1963; 8, this report.

†Four proximally and one distally.

one specimen from Torch Bay, Alaska (collected by A. R. Palmer, 6 m, 10 June 1978) is in the synoptic collection at the University of Washington Friday Harbor Laboratories, catalog No. 2391. *Manania distincta* is rarely seen on the west coast of North America, and probably occurs sporadically.

These three North Pacific species are distinguished by differences in coloration and, to a lesser extent, by calyx shape, peduncle length, habitat, and geographic distribution. Specimens of *M. distincta* are light tan to cream in color, with a dark brown herringbone pattern extending from the lumen between the members of each perradial gonad pair down the stalk to the pedal disc. Medusae of *M. gwilliami* are usually red with contrasting white subumbrellar nematocyst vesicles, and those of *M. handi* are green with linear interradial "windows." It has been our experience, and that of Gwilliam and Hand also, that these color patterns are consistently present and distinguishable. Stalks of both *M. distincta* and *M. gwilliami* are rather elongate in life, and clearly demarcated from the calyx, giving the animals a goblet shape. The trumpet-shaped medusae of *M. handi* have shorter, indistinctly demarcated stalks. Individuals of the last species are found in protected areas, mostly on *Zostera*, and have been identified only from San Juan and Vancouver islands. By contrast, those of the other two species inhabit the open coast where there is considerable wave action, and are more widespread: the range of *M. distincta* is northern Japan to Oregon, and that of *M. gwilliami* is British Columbia to Baja California.

Preserved material may be difficult to identify because of tissue shrinkage and loss of pigmentation. However, the dark herringbone pattern of *M. distincta* remains for some years after fixation. Nematocyst size ranges for these three species of *Manania* mostly overlap and are therefore of limited taxonomic value (Gwilliam 1956).

Acknowledgements

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