

CARYBDEA ALATA AUCT. AND MANOKIA STIASNYI, RECLASSIFICATION TO A NEW FAMILY WITH DESCRIPTION OF A NEW GENUS AND TWO NEW SPECIES

LISA-ANN GERSHWIN

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The species recognition criteria have been confused for cubomedusae, leading to underestimates of biodiversity and nomenclatural errors in the group. At least nine different species have been described with crescentic gastric phacellae, T-shaped rhopalial niche ostia, and/or 3 velarial canals per octant; all were subsequently included in the synonymy of the oldest name, *Carybdea alata*, which lacks both a type specimen and an unambiguous identity. To stabilize the nomenclature of the group, the new genus *Alatina* is proposed based on a common form for which type material and DNA sequences are available. Two species from northern Australia are herein described for the genus. The other nine species previously associated with the name *Carybdea alata* are herein reevaluated and determinations are made as to their validity. The validity of another species, *Manokia stiasnyi*, has been questioned, and was not previously appreciated as belonging to this morphogroup. Reexamination of the holotype confirms that the taxon is distinct, and allied to *Alatina*; a redescription is provided. A new family, Alatinidae, is proposed to accommodate *Alatina* and *Manokia*. The family Carybdeidae and the genus *Carybdea* are redefined. □ Taxonomy, Irukandji syndrome, Cubozoa, box jellyfish, Australia.

Lisa-ann Gershwin, School of Marine Biology and Aquaculture, James Cook University, Townsville, Queensland, 4811, and Australian Institute of Marine Science, Townsville, Queensland, 4810, Australia [email: lisa.gershwin@jcu.edu.au]; 18 March 2004.

Carybdea alata Reynaud, 1830, has been the most problematical of all cubozoan species, from nomenclatural and practical perspectives. The species was erected for a medusa collected somewhere in the South Atlantic, on the basis of a watercolour by Reynaud in Lesson (1830). It was widely disregarded as unrecognizable, until the name was revived by Vanhöffen (1908) in the interest of stability. Unfortunately, Vanhöffen failed to assign a particular specimen or suite of characters to the name, and the species originally assigned that name is unrecognizable. By the time of Kramp's Synopsis (1961), the nominal species *C. alata* was recognized by its crescentic phacellae and three well developed scales enclosing the rhopalial niches. Other authors additionally recognized three velarial canals per octant as diagnostic (Mayer, 1910; Bigelow, 1938). The problem is that many different forms share these characters, even though they barely resemble one another overall. This makes identification very easy for the lay person, but it does not reflect biological reality and makes for confusion that has yet to be resolved.

At least nine different nominal species have been described with crescentic phacellae and/or three canals per octant and/or three well

developed covering scales. Haeckel (1880) recognized six species with these characters, including five new ones (*Procharybdis tetraptera*, *Procharybdis turricula*, *Carybdea pyramis*, *Carybdea philippina*, and *Carybdea obeliscus*). Agassiz & Mayer (1902) added *C. grandis*, based on its very large size. Mayer (1906) added *C. moseri*, based on short basal stalks of the pedalia and differently shaped pedalian wings, though Bigelow (1909) regarded it as a young stage of *C. grandis* and Mayer (1910) concurred. Menon (1930) added *C. madraspatana*, based on its apical concavity and greater number of velarial canals. Kramp (1961) lumped them all under the oldest available name, *C. alata*. Historical confusion and instability concerning *alata*-group relationships have apparently been based on failure to recognize the crescentic phacellae as common to more than one species, and reluctance to regard geographically variable characters as informative.

Manokia stiasnyi (Bigelow, 1938), also possesses crescentic phacellae and three well developed covering scales, though the former character was not previously appreciated. The species was defined on the basis of its branched tentacles and its similarity to *Carybdea alata* was

not noted. Different authors have held different opinions about the validity of this species without examining the type specimen (Southcott, 1967; Kramp, 1968). I have examined the holotype, and believe the species is worthy of recognition.

It is difficult to say how many different species under the name *Carybdea alata* can be distinguished worldwide, because typically every specimen with crescentic phacellae has been lumped into the one nominal species, with typically very little discussion about other characters. However, at least three different species exist in the southwestern Pacific off Australia and New Guinea, and that these differ from several earlier described forms. To stabilize the nomenclature of *Carybdea alata* auct., I propose reclassification of species with crescentic phacellae and T-shaped rhopaliar niche ostia, defined on the basis of a well characterized type species for which type specimens and DNA sequences are available. Thus, I propose *Alatina* nov. with *A. mordens* sp. nov. and *A. rainensis* sp. nov. The other nine species previously associated as *Carybdea alata* are re-evaluated and determinations are made as to their validity. Problematical *Manokia stiasnyi* (Bigelow, 1938) is redescribed based on the type specimen. Together, *Alatina* and *Manokia* appear to form a natural group separate from *Carybdea* and other carybdeids. For this group I propose *Alatinidae* fam. nov.; the separation of the groups is supported by 18S rDNA analysis (personal observations). Revised definitions of the *Carybdeidae* and *Carybdea* are given.

MATERIALS AND METHODS

All taxonomic observations and measurements were made on preserved material, unless otherwise noted. Measurements were made with Max-Cal digital calipers to the nearest 0.01mm; in some cases, an available absolute measurement was clearly not the correct full measurement (e.g., in the case of a brittle, folded specimen), denoted with + following the measurement. Bell height (BH) was measured from the apex of the bell to the velarial turnover. Diagonal bell width (DBW) was measured across diagonally opposite pedalia on a flattened specimen, at the height of the pedallial lamella. Interrhopalial width (IRW) was measured between adjacent rhopalia, with the specimen flattened. Tentacle base width (TBW) was

measured across the widest diameter at the uppermost part of the tentacle, immediately below the pedallium. Pedallial dimensions are as follows: length (PL) from the subumbrellar lamella to the tentacle insertion, width (PW) and canal width (CW) at the vertical midpoint. Sex was determined, when possible, by biopsy. Female gonads have obvious ova; male gonads have a conspicuous "finger-print" appearance of many fine more-or-less parallel lines. Phacellae were examined by making a small incision in the upper corners of the bell, and then pulling back a small amount of mesoglea to expose the phacellae in situ, or by opening up the full length of the body wall to expose the stomach. Nematocysts were examined and measured with a Leica DMLB compound microscope and Leica IM-50 Image Manager v. 1.20 for Windows; all observations and photographs were made through a 40x objective, unless otherwise specified. Nematocysts were identified following the keys of Calder (1974), Mariscal (1971) and Williamson et al. (1996). Translations of the original German descriptions of *M. stiasnyi* and Haeckel's species were made with Globalink Power Translator 6.0 for Windows.

Throughout the text, "*alata*" has very restricted meaning. *Carybdea alata* refers to the species named by Reynaud, or to specific contextual meanings of other authors, but *Carybdea alata* auct. refers collectively to the species grouped under this name by various other authors. The term "*alata*-group" refers to the loosely defined collection of described and undescribed forms that have been identified as *Carybdea alata* by traditional criteria (including museum collections and published identifications), but are not yet clearly internal or external to *Alatina*.

ABBREVIATIONS: Australian Institute of Marine Science (AIMS); Great Barrier Reef (GBR); Institut Royal des Sciences Naturelles de Belgique, Brussels (IRSNB); James Cook University (JCU); Museum of Comparative Zoology, Harvard (MCZ); Museum of Tropical Queensland, Townsville (MTQ); Queensland Museum, Brisbane (QM); South Australian Museum, Adelaide (SAM); and United States National Museum, Washington DC (USNM). In synonymies I follow Matthews (1973); "v" indicates that I have seen the material referenced and "v*" indicates that I have seen the type.

TABLE 1 (facing). Comparison of main diagnostic characters in the *Carybdeida*.

Species	Phacellae	Rhopalial niche ostium	Pedial canal	Velarial canals (per octant)	Principal tentacular nematocysts	Other distinguishing features
<i>Alatina</i> spp.	Crescentic, with long cirri	T-shaped	Simple, rounded or angular	3, typically simple, or only slightly branched distally	Euryteles, isorhizas	Tall, narrow, flimsy body; very wide pedalial wings; lacking perradial mesenteries
<i>Carukia barnesi</i>	Lacking	Frown-shaped	Simple	2, simple	Lemon-shaped tumiteles	Neckerchief-like tentacle bands; with rhopalial "horns"; narrow pedalia
<i>Carybdea rastonii</i>	Multiple-stalked oblique row	Heart-shaped	Knee	2, dendritic	Football-shaped euryteles and small ovoid isorhizas	Single row of nematocyst freckles on outer pedalial wing; pedalia scalpel-shaped
<i>Carybdea marsupialis</i>	Multiple-stalked epaulette	Heart-shaped	Knee	3-4, dendritic	Unknown	Single row of nematocyst freckles on outer pedalial wing; pedalia scalpel-shaped
<i>Carybdea sivickisi</i>	Crescentic, cirri singly rooted	Vertical oval	Simple	2, paw-like	Football-shaped euryteles, large and small ovoid isorhizas	Adhesive pads on top of exumbrellar; single row of nematocyst bars on outer pedalial keel; narrow pedalia
<i>Carybdea xaymacana</i>	Single-stalked epaulette	Heart-shaped	Knee	2, of two types	Large club-shaped euryteles, small ovoid isorhizas	Single row of nematocyst freckles on outer pedalial wing; pedalia scalpel-shaped
"Darwin carybdeid"	Lacking	Frown-shaped	Thorn	4, paw-like with long, parallel fingers	Club-shaped type 4 microbasic p-mastigophores	With rhopalial "horns"; with well developed perradial mesenteries; pedalia broadly rounded
<i>Manokia stiasnyi</i>	Crescentic	T-shaped	Small nub at bend	4, simple and undulating	Subspherical euryteles	Tentacle bands with lateral extensions; with scalpel-shaped pedalia
"Morbakka"	Lacking	Frown-shaped	Thorn	Feather-like, too many to count	Club-shaped type 4 microbasic p-mastigophores; football shaped isorhizas	2 eyes per rhopalium; with perradial lappets and rhopalial "horns"; with well developed perradial mesenteries; pedalia relatively narrow
<i>Tamoya haplonema</i>	Vertical	Frown-shaped	Thorn	Numerous	Unknown	6 eyes per rhopalium; lacking perradial lappets and rhopalial "horns"; with well developed perradial mesenteries; pedalia long and well rounded on both sides
<i>Tripedalia</i>	Single-stalked epaulette	Shallow frown-shaped	Simple	3-4, simple	Euryteles, stenoteles and spherical & non-spherical isorhizas	Two or three pedalia per corner; with weak perradial mesenteries; pedalia narrow

SYSTEMATICS

Phylum CNIDARIA Verrill, 1865
 Subphylum MEDUSOZOA Petersen, 1979
 Class CUBOZOA Werner, 1973
 Order CARYBDEIDA Maas, 1909 sensu
 Werner, 1984
 Family ALATINIDAE nov.

TYPE GENUS. *Alatina* gen. nov.

DIAGNOSIS. Gastric phacellae crescentic, comprised of long cirri arranged more or less parallel in a single plane; with T-shaped rhopalial niche ostia, comprised of a single upper covering scale and 2 lower, well developed covering scales; with 3 or 4 more or less simple velarial canals per octant; with a shallow stomach, completely lacking perradial mesenteries.

Alatina gen. nov.

TYPE SPECIES. *Alatina mordens* sp. nov.

ETYMOLOGY. From the specific name of *Carybdea alata* Reynaud, 1830, with the suffix *-ina* (diminutive, Latin). Feminine.

DIAGNOSIS. 3 velarial canals per octant; tentacles simple.

REMARKS. *Alatina* spp. are easily distinguished from other carybdeids by several conspicuous features, especially the crescentic phacellae and their long cirri, the hemispherical adaxial pedalial wings, the T-shaped rhopalial niche ostia, the three simple or end-branched velarial canals per octant, and the flimsy gelatinous consistency of the body. In contrast, *Carybdea* spp. have epaulette-shaped or linear phacellae of short cirri, scalpel-shaped pedalia, heart-shaped rhopalial niche ostia, 2-4 branched velarial canals per octant, and a relatively springy bell consistency that holds its shape in water. *Tripedalia* spp. have multiple simple pedalia. *Tamoya* is characterized by having vertical phacellae in the interradial corners of the stomach wall. *Carukia* and several other undescribed forms are characterized by lacking phacellae altogether. *Tripedalia*, *Tamoya* and *Carukia* all have frown-shaped rhopalial niche ostia (Table 1). Species of *Carybdea* are detailed because there is historically great confusion on how to tell them apart. A revision of *Carybdea* with additional species is to be published elsewhere, and is beyond the scope of this paper.

Regrettably, it is impossible to say with certainty which of the Atlantic forms is the true *C. alata* of Reynaud, but it is clear that not all forms of *C. alata* auct. should be considered the same species. One must start sorting out the confusion somewhere, and because I have multiple local specimens at my disposal, along with their DNA, it seems most prudent to begin with these. It is my hope that by establishing a workable system in which to incorporate other species, it will eventually be possible to differentiate the large number of regionally distinct forms.

Alatina moseri (Mayer, 1906) from Hawaii is redescribed based on type and non-type material. The other eight species of *Alatina* are treated briefly and compared (Table 2). Although some remain unidentifiable, most forms previously described and associated with *C. alata* auct. should be considered valid until proper comparison of material from the different type localities can be made.

Alatina mordens sp. nov.
 (Figs 1, 2)

Unidentified species, v?Mulcahy, 1999: 88 [Irukandji syndrome case requiring life support]; v?Little et al., 2001: 178 [case history of sting, life support required for 8 days]; ?Taylor et al., 2002: 175 [Irukandji syndrome with persistent symptoms over 7 months].

MATERIAL EXAMINED. HOLOTYPE: QMG55282, Moore Reef, GBR, QLD (approx. 16°52.160'S 146°12.353'E), coll. 13 November 1998; immature male, BH 80.79, DBW 64.42, IRW 30.07, TBW 2.45; forwarded by J. Seymour; captured within minutes of severe Irukandji sting reported by Mulcahy, 1999 (Fig. 1A).

PARATYPES: SAMH1013, same data as holotype; BH 74.09, DBW 54.22, IRW 25.29, TBW 1.89 (Fig. 1B). SAM H1053, Osprey Reef, Coral Sea, QLD (approx. 13°54.190'S 146°38.985'E), 29 January 2000; BH uninterpretable due to damage, DBW 47.75, IRW 24.06, TBW 1.94; forwarded by P. Colwell; captured within minutes of Irukandji stings; examined live and preserved. QMG317058, Agincourt Reef, GBR (approx. 16°01.907'S 145°51.203'E), coll. 24 April 1998, forwarded by R. Hore; BH 80.44, DBW 64.05, IRW 30.93, TBW 2.13. QM G317059, same data as QMG317058; BH 59.22, DBW 41.24, IRW 22.40, TBW 1.05. AIMS 2003-10, Agincourt Reef, GBR, 28 April 2003; BH ca. 75, DBW ca. 55; forwarded by R. Hore, captured following superficial sting of 12 year old boy. QM G55288, Agincourt Reef, GBR, 25 August 2003; immature male, 85mm BH, 65mm DBW, 32mm IRW; forwarded by R. Hore.

TABLE 2 (facing). Comparison of *Alatina* species. Data based on original descriptions and figures.

	Maximum BH	Bell nematocysts	Velarial canal # per octant	Velarial canal form	Pedial canal bend	Pedial nematocysts	# of eyes	Other characters
<i>A. alata</i> comb. nov.	?	?	?	?	?	?	?	
<i>A. grandis</i> comb. nov.	230mm	Apparently absent	3	Short, branched tree-like	90°	Apparently absent	1 in adults; 3 in juvs	
<i>A. madraspatana</i> comb. nov.	110mm	Small	5	Branched	Simple	Sometimes; small	6 (1 lensed)	Apical concavity
<i>A. mordens</i> n. sp.	96mm	Small	3	Simple, bifurked, trifurked at tip	Rounded	Minute	2 median	Pedial wings wide
<i>A. moseri</i> comb. nov.	80mm	Present	3	Simple/bifurked	Simple	Absent or 1 row oblong	4	Paired cirri in phacellae
<i>A. obeliscus</i> comb. nov.	35mm	?	3	Simple beside frenula, forked beside pedalia	?	?	?	Tentacles thickened at end
<i>A. philippina</i> comb. nov.	30mm mature	Apparently absent	3	Simple, short	Simple to angular	Apparently absent	?	Split phacellae; long pedalia
<i>A. pyramis</i> comb. nov.	30mm mature	Apparently absent	3	Simple, wide	Apparently simple	Apparently absent	6?	Pedial wings narrow, frizzy lips
<i>A. rainensis</i> n. sp.	18mm mature	Minute	3	Simple	90°	Absent	4	Butterfly-form gonads
<i>A. tetraptera</i> comb. nov.	30mm mature	Apparently absent	Lacking	Lacking	Simple	Apparently absent	1	Split wing-like phacellae; very long, large pedalia
<i>A. turricula</i> comb. nov.	170mm	Apparently absent	Apparently absent	—	Simple to angular	Apparently absent	?	Overhanging pedial wings

OTHER MATERIAL EXAMINED, [JCU1] Unregistered specimen at JCU Cairns, QLD, same data as holotype; BH 61.32, DBW 53.53, IRW 22.83, TBW 1.77 (Fig. 1C). [JCU 2] Unregistered specimen at JCU Cairns, QLD, coll. Agincourt Reef, GBR, 6 July 1991; BH 96.06, DBW 69.72, IRW 31.77, TBW 1.75. Approximately 20 specimens frozen or in ethanol, caught at various times at Agincourt Reef, GBR, 2000-2004, examined casually before being forwarded for venom analysis.

TYPE LOCALITY. Moore Reef, outer Great Barrier Reef.

ETYMOLOGY. Latin *mordax*, biting; in reference to the painful sting.

DIAGNOSIS. Bell tall, tapered, apically truncate, with exumbrellar nematocyst freckles; with crescentic phacellae, comprising many tufts of long cirri which branch only near the root; with 3 straight, simple to triforked velarial canals in each octant, bearing a row of 1-5, typically 1-3, small, round nematocyst freckles on root area; with broadly rounded adaxial pedalia keels; with simple rounded pedalial canal.

DESCRIPTION OF HOLOTYPE. Bell much taller than wide, with overall shape of a truncate tall pyramid, of thin and flimsy gelatinous consistency (Fig. 1A-C). Apex much narrower than velarial aperture; flat to slightly rounded. Exumbrella with sparsely scattered minute, unraised, round nematocyst freckles; with interradial furrows shallow and wide, extending along entire bell height. Adradial furrows lacking. Phacellae (Fig. 2A) 4, interradial, crescentic, broad, with numerous long gastric filaments arranged in a more or less parallel fashion in a single plane. Rhopalial niches (Fig. 2B) 4, perradial, flush with exumbrellar bell wall, shallowly convex on subumbrellar wall; with T-shaped ostia, i.e., 1 covering scale above and 2 well-developed scales below. Upper covering scale thickened, protruding slightly from bell wall, broadly convex in contour; lower scales well developed, with vertical opposing edges, separated by a furrow continuing to velarium; upper and lower scales separated horizontally by a discontinuity on each side of ostium. Rhopalial horns lacking. Rhopalial stem without warts. Rhopalial lens and eyespot morphology indeterminable in holotype without dissection; due to very large size of lower eye, rhopalium appearing as a single black spot to unaided eye. Pedalia (Fig. 2C) 4, interradial, with short stalk; with large round adaxial keel approximately 3-4x pedalial canal width, overhanging at point of tentacle insertion; with narrow abaxial keel approximately 2x canal width; with few scattered

minute nematocyst freckles. Pedalial canals bowed slightly toward abaxial keel, narrow, laterally flattened; with rounded to slightly angular bend near point of origination from bell, straight or slightly tapered into tentacle. Velarium wide, with nematocysts confined to single row of small, round warts on adperradial velarial canals only. Velarial canals (Fig. 2D) 3 per octant, simple throughout most of length, may be biforked or triforked at distal end; 4-6 extensions reaching margin or nearly so in each octant; canal roots (velarial extensions of gastric pouches) 3 per octant, narrow, extending onto velarium approximately halfway to margin. Perradial lappets lacking. Frenulum a single, narrow, stiff sheet, extending only about halfway onto velarium, with a narrow strip of thickened tissue extending almost to velarial margin. Gonads attached along entire length of interradial septa; leaf-like, extending laterally into radial stomach pouches; narrow in this immature male specimen. Tentacles (Fig. 2E) 4, 1 per pedalum, hollow, round in cross section, with nematocysts in alternating bands (larger, smaller, larger, etc.); preserved, tentacle constricted approximately every 10 bands, giving segmented appearance, though unclear whether this is an artifact of contraction and preservation; length in life unknown. Stomach small, flat, extending into 4 large coelenteric pouches, divided by interradial septa. Interradial septa without minute perforations. Manubrium short. Color: preserved in formalin, the gonads, tentacles, rhopalial, and phacellae opaque whitish; body slightly cloudy.

The exact nature of several characters could not be ascertained in the holotype without dissection, which was considered inadvisable, e.g., the phacellae (number of roots, branching pattern of cirri bundles), the eyes (number and arrangement), the manubrium (cross section shape, length and shape of lips), and mesenteries (length and state of development). With strong side light, I was able to determine with reasonable confidence that the mesenteries do not extend down along the middle regions of the bell wall; however, it is not unusual for taxa to have weakly developed mesenteries in the perradii of the manubrium which only extend a short distance. Whether this is the case in *A. mordens* cannot be determined from the holotype. It is unfortunate that the number of roots to the phacellae could not be examined; this will likely be an important species discriminator. In paratype QMG55288, these missing characters were scored as follows: phacellae with

about 20 roots per group; cirri long, bundled near the base in clusters of several; eyes 4 per rhopalium, two lensed median plus one slit-eye on each side; manubrium open and amorphous; lips wide triangular; mesenteries completely absent in flap or cord form. Some specimens of this species have only two median eyes and no lateral eye spots, while one specimen has the normal cubozoan 6 eyes (2 median lensed eyes, 4 lateral eye spots); it would appear that the lateral eye spots are somewhat variable, but the lower main eye is always unusually large in comparison to other Carybdeida. The gonads of sexually ripe specimens are overlapping and pleated (Fig. 1B). In life, the body is completely transparent and colorless, and the tentacles are bright pink.

STATOLITH (Fig. 2F, paratype #AIMS 2003.10). Tear-drop-shaped, with a medially incised, truncate basal border, deep garnet reddish in colour; enclosed in lower portion of rhopalium, situated immediately behind the main lens rather than below it. The statolith is orientated truncate-side down for standardized comparison with statoliths of other species; however, *in situ* the truncate side is orientated up toward the rhopalial stalk and the flat side facing the camera in the photograph is the unexposed side, facing the back of the main eye *in situ*.

CNIDOME (Fig. 7A, B; from paratype QMG55288). The tentacular nematocysts are exclusively lemon-shaped euryteles, with an arithmetic mean of $22.96\mu\text{m}$ long by $12.77\mu\text{m}$ wide (range $19.30\text{--}27.25\mu\text{m}$ long \times $11.10\text{--}14.85\mu\text{m}$ wide, $N=57$). The bell nematocysts are exclusively large spherical isorhizas with a short, loosely coiled tubule, averaging about 12 per nematocyst freckle; the arithmetic mean size is $30.34\mu\text{m}$ (range $28.25\text{--}31.71\mu\text{m}$, $N=24$). Nematocysts of the lips and gastric cirri were not observed, despite efforts to find them.

NUCLEOTIDE SEQUENCES. Most of the 18S rDNA gene has been sequenced for 4 specimens (L. Peplow, unpubl. data).

DISTRIBUTION. Anecdotal reports from throughout the northern outer Great Barrier Reef (GBR) region; confirmed from Moore and Agincourt Reefs, on the outer GBR, and from Osprey Reef in the Coral Sea.

REMARKS. This species is distinguished from other carybdeid genera in nearly every scorable character (Table 1). Only rudimentary comparison can be made with other species that

have previously been associated with *C. alata* auct., due to insufficient descriptions and lack of comparative material (Table 2).

The relationships of *Alatina* spp. will not be fully understood until fresh collections are made from type localities and rigorous morphological and molecular comparative studies are made. Particular attention should be given to the number of roots to the gastric phacellae, the branching pattern or lack thereof to the velarial canals, the number of lensed eyes and eye spots at maturity, and patterns of exumbrellar, pedalial, and velarial nematocyst clusters.

LIFE CYCLE. Unknown. However, Arneson & Cutress (1976) described the life cycle of *C. alata* from Puerto Rico. Similarities may emerge when the life history of *A. mordens* is resolved, presumably being closely related.

ECOLOGY. Unknown. However, another species of uncertain identity in the *Alatina* clade, studied in Hawaii, occurs in large numbers 9–10 day after the full moon (Thomas et al., 2001). Preliminary study indicates that *A. mordens* has a similar predictability (R. Hore, pers. comm. June 2004).

SEASONALITY. Collection records indicate that *A. mordens* can be encountered any time of the year on the outer Great Barrier Reef, contrary to local folklore which holds that one is only at risk of stings during the summer months, and then only onshore. Furthermore, collection records do not appear to correlate season with size or maturity, indicating that perhaps *A. mordens* breeds and grows all year.

MEDICAL NOTES. *Alatina mordens* may pose a serious human health risk; however, correlations are ambiguous and experimental evidence supporting or refuting this hypothesis is lacking. There are several known cases of severe Irukandji symptoms following envenomation on the outer reef, with similar case histories and *A. mordens* being captured or sighted at the time. Typically, this species is encountered at night, when it swarms near lights used for scuba diving; some stings occur when scuba divers return to the boat and swim up into a swarm of jellyfishes. Severe envenomations in cases involving diving may be mistaken for decompression sickness (Williamson, 1985; Hadok, 1997). The outer reef symptoms typically onset quickly (ca. 5–10 minutes), and resemble a more severe version of the Irukandji Syndrome than is typically

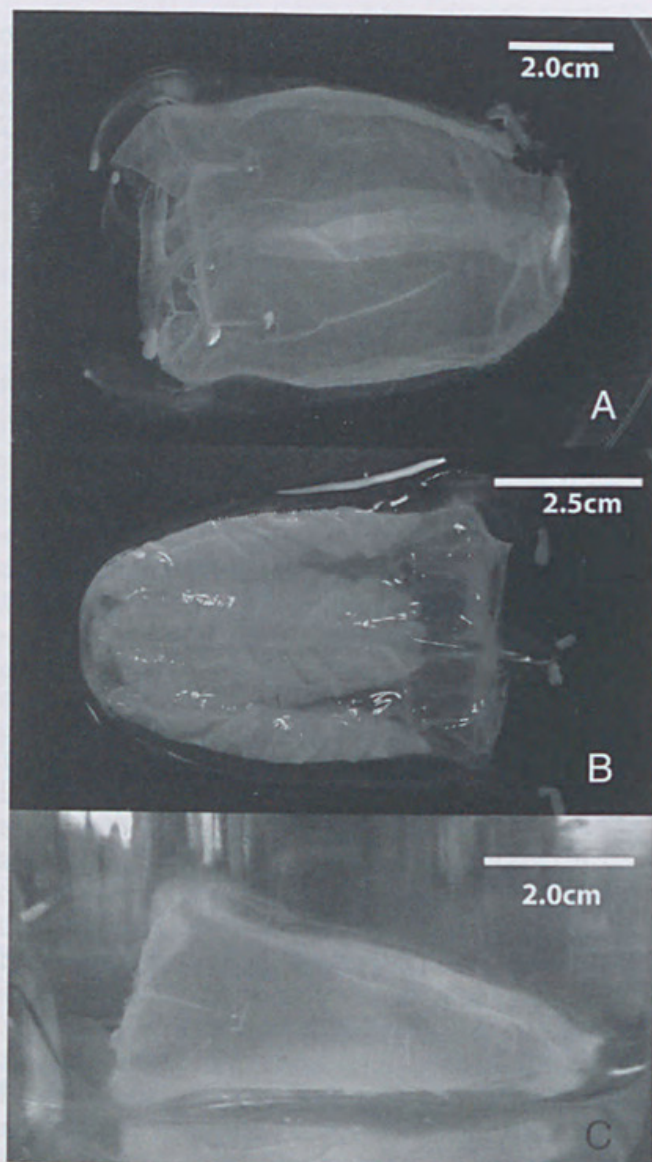


FIG. 1. *Alatina mordens* gen. et sp. nov., different forms of general appearance. A, Holotype QMG55282, laying flat, with immature gonads. B, Paratype SAM H1013, laying flat, with ripe, pleated gonads. C, Unregistered JCU specimen from Moore Reef, GBR, normal pyramidal appearance, as in life.

associated with coastal envenomation, often involving severe hypertension (unpubl. data).

In at least one outer reef case, the victim saw herself get stung by a large jellyfish in the water (Anonymous, pers. comm., Dec. 1998); three specimens retrieved at the time of the incident comprise the holotype, a paratype (SAMH986), and the first of the two JCU non-type specimens listed above. The patient was critically ill for more than a week following envenomation (Mulcahy, 1999; Little et al., 2001). A single nematocyst recovered from the victim's skin was later (Little & Seymour, 2003) attributed to an

unnamed species in the Queensland Museum collection previously identified by me. The nematocyst from this sting event (Little & Seymour, 2003) cannot be differentiated from those characteristic of *A. mordens* (Fig. 7); thus, the possibility that this species was responsible for the sting must be considered.

In another case from which the same species was recovered, 5 divers were stung at Osprey Reef the night of 29 January 2000, while surfacing into the swarm at the end of the dive; the onset of symptoms was rapid (ca. 5 minutes) and all required medical treatment (P. Colwell, pers. comm., Feb. 2000). A single specimen was captured from those that were swarming at the time, and was forwarded to me for study (SAM H1053). A third case of similar circumstances at Hastings Reef on New Years Eve 1999, involving 2 victims, was also reported (P. Colwell, pers. comm., Feb. 2000); no specimens were retained. Other anecdotal cases exist in which similar jellyfish were sighted but not captured, and which involved severe Irukandji syndrome (unpubl. data). While the evidence from multiple sting events lends support to this species being the stinging agent, it is important to note that this species is only possibly the cause of these cases of Irukandji syndrome; testing this hypothesis experimentally should be considered a high priority for stinger management.

There is also some indication that *A. mordens* is not especially dangerous. Paratype #AIMS 2003.10 was captured following a superficial sting to a 12 year old boy, in which no systemic symptoms were reported (R. Hore, pers. comm., Sept., 2003). In another incident, a 38 year-old woman was stung on the arm, with no systemic symptoms; her husband saw the jellyfish and a biologist familiar with *A. mordens* saw what he believed to be this species in the water shortly after (R. Hore, pers. comm., Oct., 2003).

Several explanations exist which may account for the differential symptoms. First, it is possible that a different species than *A. mordens* is responsible for the stings. This seems unlikely because the same species was recovered from multiple sting events with similar sting characteristics. Second, it is possible that different intensities of stings or different susceptibilities in the sting victims have led to very different outcomes. While differential susceptibilities and severities should not be ignored, it seems unlikely that these alone would fully explain the wide range of symptoms from

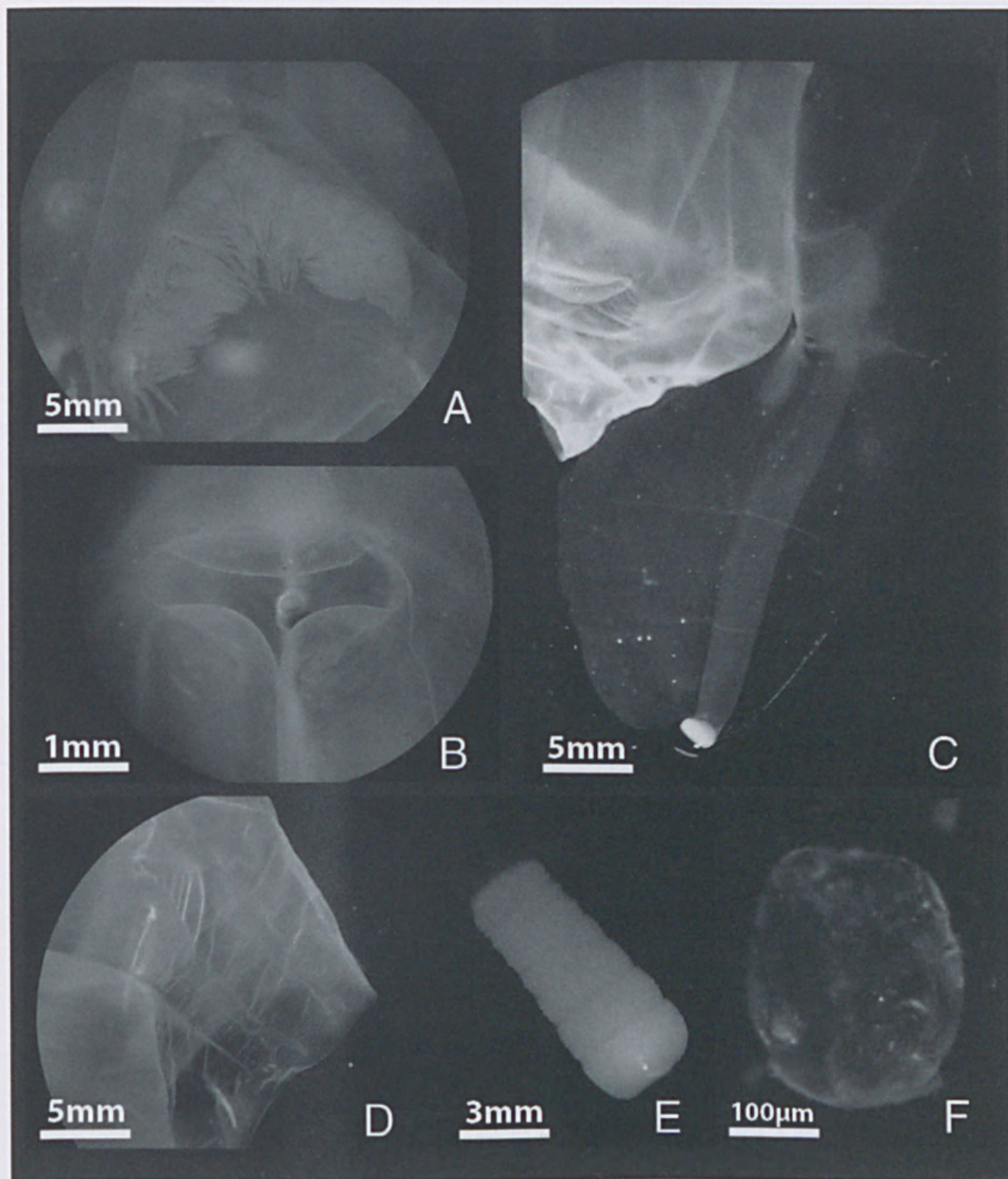


FIG. 2. *Alatina mordens* gen. et sp. nov. A, Crescentic phacellus with long cirri. B, Expanded lower covering scales, producing a T-shaped rhopalial niche. C, Pedalium, with greatly rounded adaxial keel. D, Velarial canals. E, Contracted tentacle, with regular constrictions. F, Statolith, dissected out of rhopalium; note that the statolith in this figure is orientated as it is in life, i.e., with the truncate border facing upward, whereas for inter-species comparison the truncate border is standardized to be the base.

mild to potentially lethal, all in previously healthy individuals. Third, it is possible that the medusae go through ontogenetic, seasonal, or reproductively-related changes in toxicity. No

data currently exist as to whether this is or is not the case, but it should be a priority for collaborative study by ecologists, toxinologists and taxonomists.

STING MANAGEMENT. A thorough treatment of stings and sting management is given by Williamson et al. (1996). When swimming in areas where cubozoans may occur, common-sense sting precautions should be employed, such as wearing protective clothing over exposed skin areas, e.g., a Lycra body suit. There is no medical or scientific evidence that commercial sting repellants or swimming like a turtle are effective methods of sting prevention. If stung, the best-known treatment for minimizing further envenomation is to pour vinegar liberally over the sting area for 30 seconds; this has been shown to be effective for a wide range of cubozoan stings (Williamson et al., 1996). If tentacles are present on the skin, they can then be safely removed. For severe stings, or those thought to be potential Irukandji envenomations, the patient should be made comfortable and medical treatment sought as quickly as possible.

There are many sources dispensing advice on jellyfish sting treatments, many of which are simply inaccurate. Contrary to popular belief, rubbing with sand or washing with freshwater often do more harm than good, causing additional nematocysts to discharge into the victim's skin. Metholated spirit is still often said to work well, but has been scientifically shown with *Chironex fleckeri* to cause immediate, massive discharge of nematocysts rather than to inhibit discharge (Hartwick et al., 1980); thus, it should not be used. There is also a common misbelief that vinegar stops the effect of the sting (i.e., relieves the pain, stops the illness) – this is untrue. It only disables undischarged nematocysts from discharging, eliminating further envenomation; vinegar should be used in all cases where stings from dangerous cubozoans are suspected.

There is no cause for alarm with the recognition of *A. mordens*. Most stings attributable to *A. mordens* occur at night, when the medusae are attracted to artificial lights (R. Hore, pers. comm., 2000; P. Colwell, pers. comm., 2000). Perhaps the most urgent action that should come from formally recognizing this species and its potential for harm, is the quest for an antivenom for severe cases of Irukandji syndrome. The only jellyfish antivenom that has been developed is for *Chironex fleckeri*, and this was shown by Fenner et al. (1986) to be ambiguous in managing

Irukandji envenomation. Recent efforts to develop an antivenom to the Irukandji syndrome have been hampered by the sporadic occurrence of *Carukia barnesi*, combined with its small size (and thus, low venom yield per animal). *Alatina mordens* may provide a more stable subject, as it occurs all year and has a much larger, more robust body and tentacles, and thus more venom yield. However, *C. barnesi* and *A. mordens* do not appear to be closely related to one another, so the relationship between their venoms is unclear.

***Alatina rainensis* sp. nov.**
(Figs 3, 4)

MATERIAL EXAMINED. HOLOTYPE: QMG55286, Raine Island, Great Barrier Reef, 11°35'34"S 144°02'12"E, Dec. 2002, collected by J. Seymour; gravid female, 17.78mm BH, 15.95mm DBW, 8.05mm IRW, 0.64mm TBW, 8.82mm PL, 4.29mm PW, 0.72mm CW.

PARATYPE: QMG55287, same locality as holotype; gravid female, 17.22mm BH, DBW not taken prior to sectioning, 7.93mm IRW, 0.58mm TBW, 8.68mm PL, 3.75mm PW, 0.68mm CW.

TYPE LOCALITY. Raine Island, outer Great Barrier Reef.

ETYMOLOGY. From Raine Island.

DIAGNOSIS. Body height at maturity small; gonads butterfly-form, attached in the central portion of the interradial only; phacellae with cirri rooted singly or in pairs.

DESCRIPTION OF HOLOTYPE. Bell taller than wide, with domed apex; with wide, shallow interradial furrows, lacking circum-aboral groove (Fig. 3A). Adradial furrows absent. Exumbrella sparsely sprinkled with minute unraised nematocyst freckles, absent on pedalia and velarium. Pedalia 4, interradial, with long stalk; inner keel quite rounded, outer keel more or less straight (Fig. 3B). Pedalial canals somewhat quadrate in cross section through stalk portion, flat through remainder; running along lower edge of pedalial lamella to about halfway, then leaving it perpendicularly, producing a 90° bend. Canal of fairly even width throughout length, bowing somewhat adaxially in a large shallow curve; straight at tentacle insertion. Tentacles 4, 1 per pedalum, round in cross section; straight-sided at the base. Tentacular banding pattern of two types: proximally, every 10th or 11th band smaller than others, thus giving tentacle a segmented appearance; distally, bands more or less alternate smaller with larger. Gonads butterfly-shaped, approximately ½ BH in length,

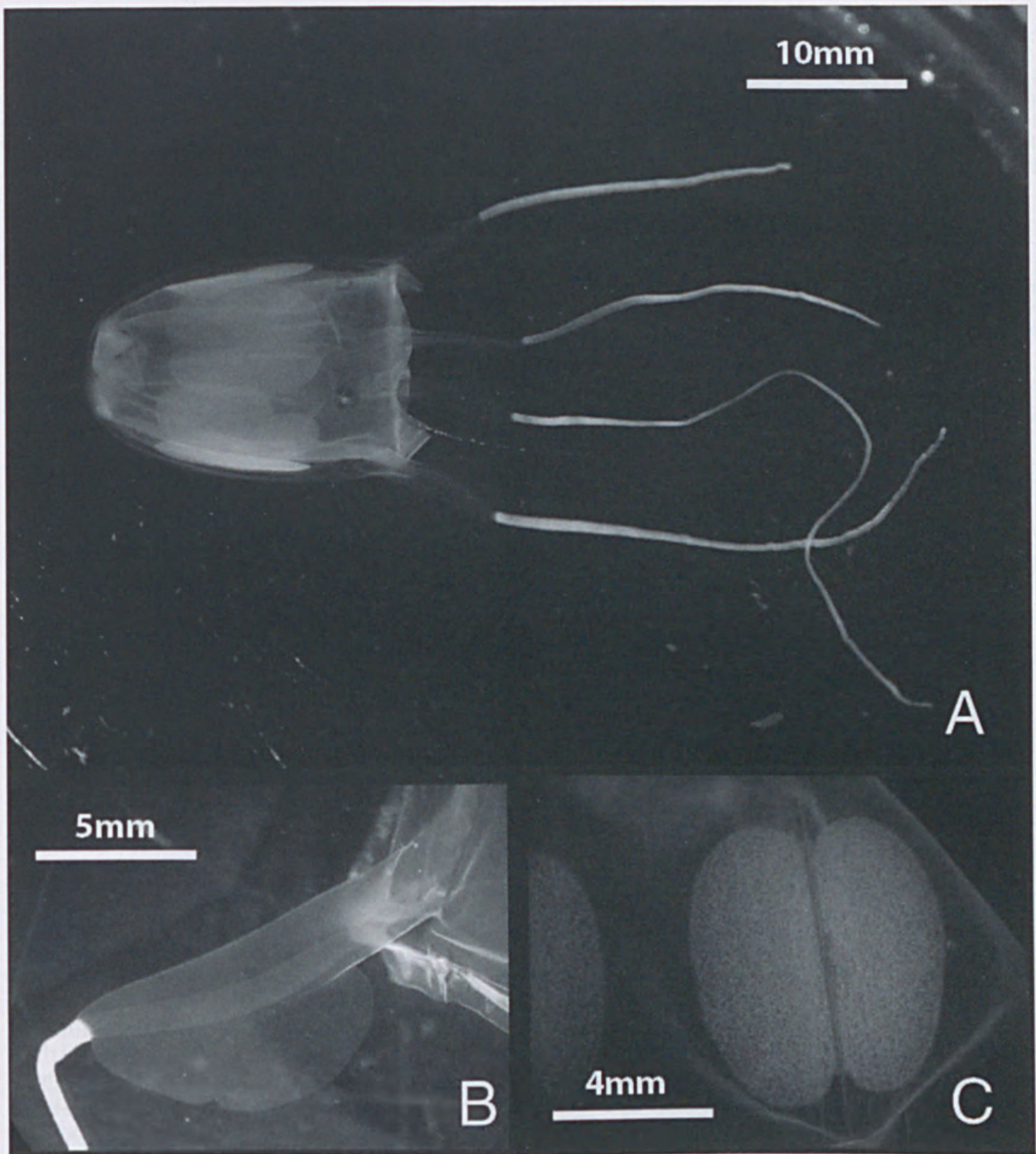


FIG. 3. *Alatina rainensis* sp. nov. A, holotype specimen, laying flat. B, Pedalium, with long stalk. C, Gonads, showing "butterfly" appearance.

but restricted to centre portions of interradial, approaching neither stomach nor pedalia, overlapping slightly at perradial; not pleated (Fig. 3C). Interradial septa with extremely minute perforations. Velarium narrow; with three canals per octant, simple throughout length (Fig. 4A).

Perradial lappets lacking. Frenulae composed of a single narrow sheet of tissue, extending on to velarium nearly to margin. Rhopalial niche ostium T-shaped, with a shallow M-shaped covering scale above, and two shallow scales below, open at both sides between upper and

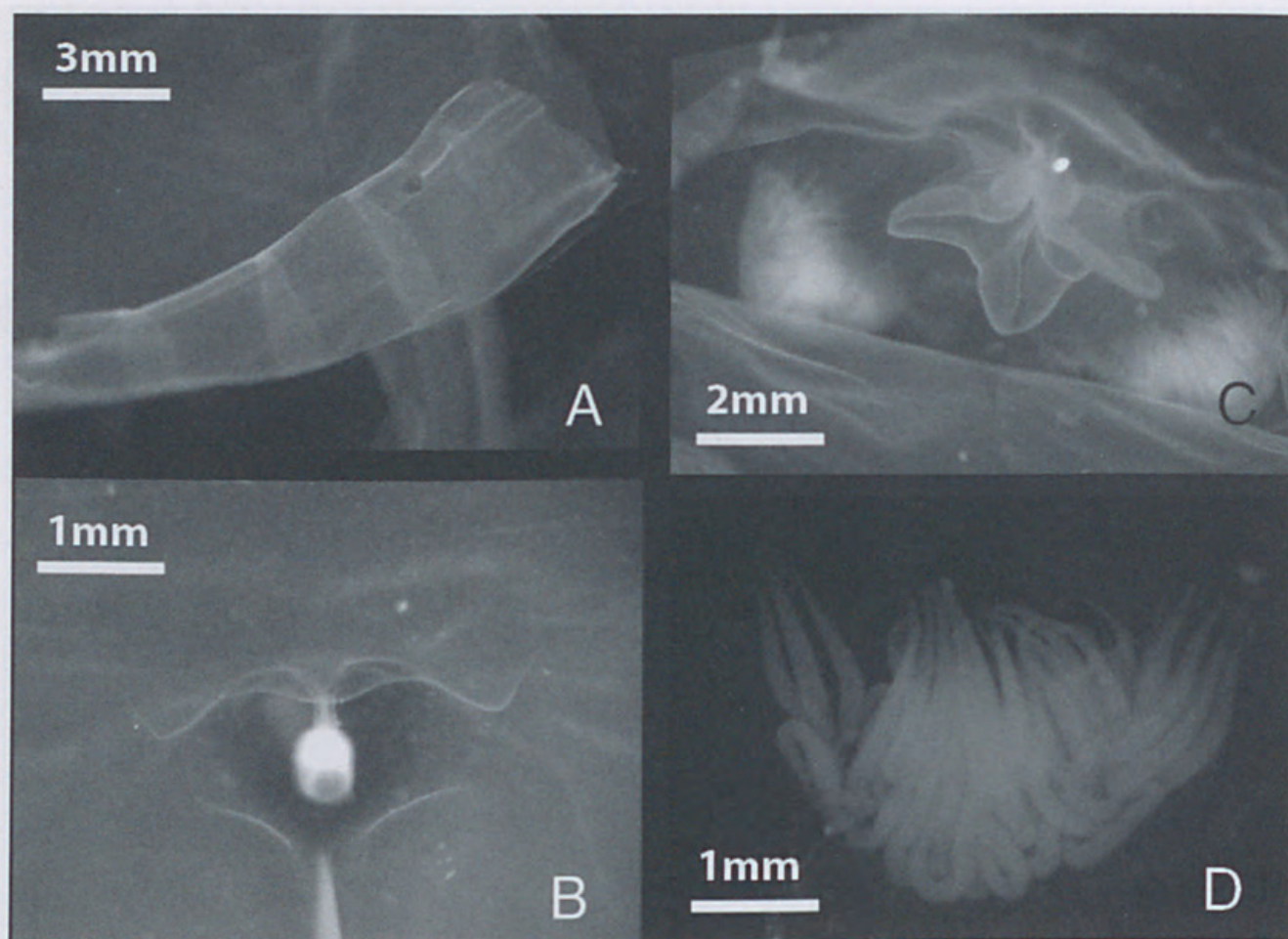


FIG. 4. *Alatina rainensis* sp. nov. A, Portion of velarium showing 3 simple canals per octant. B, Rhopaliar niche with W-shaped upper scale and poorly developed lower scales. C, Bell wall dissected away to show short, flat stomach. D, Phacellus, dissected out of stomach.

lower scales; lower scales separated by a deep furrow extending to velarium (Fig. 4B). Rhopaliar niche flush with exumbrellar wall; subumbrellar window bulging considerably. Rhopalia with 4 eyes, 2 median lensed eyes plus 2 elongate lateral eye spots. Lower of two lensed eyes large, round; upper laterally flattened into a strip distal to and cupping the lens. In preserved specimen, faint shadows occur where the 2nd pair of eye spots should be; thus, unknown whether eye spots faded or lacking. Statolith situated behind main eye, not below it; statolith shape indeterminable in preserved specimen. Rhopalia horns and warts lacking. Stomach small, shallow, completely lacking mesenteries (Fig. 4C). Manubrium very short, quadrate in cross section; mouth cruciform with 4 rounded lips. Gastric phacellae crescentic in interradii, opening toward midline; cirri approximately 50 per phacellus, long, simple, rooted singly or in pairs (Fig. 4D). Color in life not reported; preserved, the gonads,

phacellae, and tentacles whitish, rhopalia dark brown, all other parts transparent and colourless.

CNIDOME (Fig. 7D-H; from holotype and paratype). The tentacular nematocysts are of two primary types and two very small secondary types. The largest are isorhizas, with a sub-spherical capsule and tightly packed tubule occupying the whole inside; the tubule morphology could not be determined due to lack of discharged capsules. The arithmetic mean of these undischarged capsules is $20.12 \times 15.72 \mu\text{m}$ (range $16.42\text{--}23.78 \mu\text{m}$ long by $13.50\text{--}18.34 \mu\text{m}$ wide, $N=42$; Fig. 7G). The other primary nematocysts are medium-sized microbasic euryteles, with a relatively narrow lemon-shaped capsule, with a distinct nipple at the distal end, and a distinctly visible shaft but poorly defined tubule; the arithmetic mean of these undischarged capsules is $17.37 \times 11.51 \mu\text{m}$ (range $14.99\text{--}19.70 \mu\text{m}$ long by $10.43\text{--}13.11 \mu\text{m}$ wide,

N= 37; Fig. 7E, undischarged, Fig. 7F, discharged). The secondary nematocysts include a smaller size class of ovoid isorhizas (arithmetic mean $7.35 \times 6.17 \mu\text{m}$, range $6.19\text{--}8.24 \mu\text{m}$ long by $5.58\text{--}6.7 \mu\text{m}$ wide, N=13; not figured) and a nearly spherical type with a short, straight shaft and no visible tubule, presumed to be microbasic amastigophores (arithmetic mean $6.84 \times 6.40 \mu\text{m}$, range $6.19\text{--}7.16 \mu\text{m}$ by $6.02\text{--}6.80 \mu\text{m}$, N=6; Fig. 7E).

The exumbrellar nematocyst freckles have about 20–30 small spherical isorhizas per cluster, with an arithmetic mean of 9.67 (range $9.22\text{--}10.47 \mu\text{m}$, N= 22; Fig. 7H). Other loose nematocysts were found on a bell fragment from the apical portion of the paratype's dissected exumbrella; these included large sub-spherical isorhizas similar to those found on the tentacles (mean of $21.89 \times 17.89 \mu\text{m}$), microbasic euryteles ($16.55 \times 13.01 \mu\text{m}$), and large subovate microbasic p-mastigophores (mean of $28.28 \times 13.82 \mu\text{m}$). It is presumed that the isorhizas and euryteles were transferred from the tentacles during instrument handling, but whether the mastigophores were even from this species is not known; this type of nematocyst is characteristic of several undescribed species of Irukandjis. The nematocysts of the gastric cirri are extremely small euryteles, averaging $7.71 \times 5.45 \mu\text{m}$ (range $6.53\text{--}8.96 \mu\text{m}$ long by $4.61\text{--}6.55 \mu\text{m}$ wide, N=24; Fig. 7D). Nematocysts were not observed on the lips, despite exhaustive searching.

VARIATION. The paratype differs from the holotype in the more strongly alternate tentacle banding pattern lacking the 10-band groupings.

DISTRIBUTION. The type locality.

REMARKS. *A. rainensis* differs from all other carybdeids in its unique combination of crescentic phacellae and butterfly-form gonads. The crescentic phacellae are typically associated with the *Alatina* group, but the butterfly-form gonads are typically associated with the distantly related *Tripedalia* group. However, this species does not appear to be an evolutionary intermediate between the two groups, because the rhopalial niche ostia and windows, as well as the velarial canals, are also of the *Alatina* form. Thus, the species seems clearly of *Alatina* affinity, and the odd gonad shape appears to be convergent.

***Alatina moseri* (Mayer, 1906) comb. nov.**
(Fig. 5A)

Carybdea moseri v. Mayer, 1906: 1135–1136, pl. 1, fig. 2–2c; n. sp., description and illustrations; Bigelow, 1909: 19–20; young stage of *C. grandis*; Bigelow, 1938: 144, junior synonym of *Carybdea alata*; Chu & Cutress, 1954: 9, cause of dermatitis, Hawaii; Kramp, 1961: 304; in synonymy of *Carybdea alata*.
Carybdea moseri Mayer, 1915: 171, probably young of *C. alata* var. *grandis*; Mayer, 1917: 189 [in part], fig. 3; only half-grown stage of *C. alata*.
Carybdea alata var. *moseri* Mayer, 1910: 512; probably a variety or young stage of *C. grandis*; probably identical with *C. philippina*; Light 1914: 196; = *C. philippina*, Philippines; Stiasny, 1919: 34, 37–38, fig. 5, Sumatra; Bigelow, 1938: 144, in synonymy of *C. alata*.

MATERIAL EXAMINED. SYNTYPE: USNM #21800, Str. Albatross, sta 3829, Avalu Pt., Lanai Island, Hawaii; 23 specimens; poor condition, uninterpretable.

OTHER MATERIAL EXAMINED: USNM #22311, Albatross Station 3931, from Honolulu to Laysauld, Hawaiian Islands, 2535 fathoms; 1 specimen in very fine condition, 39.43mm BH, 29.88mm DBW, 13.88mm IRW, 1.19mm TBW. USNM #29632, Albatross Station 3829, South coast of Molokai Island, Hawaii, 1 April 1902, at surface; 2 specimens in very fine condition, A) 85.37mm BH, 51.47mm DBW, 26.82mm IRW, 74.67mm AR, 1.47mm TBW, B) 73.34mm BH, 43.30mm DBW, 22.88mm IRW, 62.48mm AR, 1.87mm TBW (Fig. 5A).

TYPE LOCALITY. Avalu Pt., Lanai Island, Hawaii.

DIAGNOSIS. Nematocysts present or absent on exumbrella and pedalia, lacking on velarium, with two median and two lateral eyes, with phacellae comprised of numerous cirri pairs, velarial canals 3 per octant and either simple or of two forms.

REVISED DESCRIPTION. Bell to about 85mm BH, 27mm wide, tall, narrow; with bluntly rounded apex, without circumaboral groove; with thin but rigid body (Fig. 5A). Exumbrella lacking nematocysts and warts in most specimens. Interradial and adradial furrows lacking. Pedalia 4, approximately 1/4 BH, nearly as wide as long, with widely rounded adaxial keel and narrow abaxial keel. Pedalial canals simple at bend; not flaring at tentacle insertion, flat throughout length. Tentacles 4, simple, round in cross-section, with equal-sized nematocyst rings; straight-sided at the base. Phacellae in crescentic rows at interradii; cirri long, arranged in parallel manner, rooted together in pairs. Mouth with 4 simple lips. Rhopalial niche flush with exumbrella; T-shaped, with a single broadly rounded covering scale above and two well developed scales below. Rhopalia with 2 round median eyes with lenses and 2 lateral, elongate

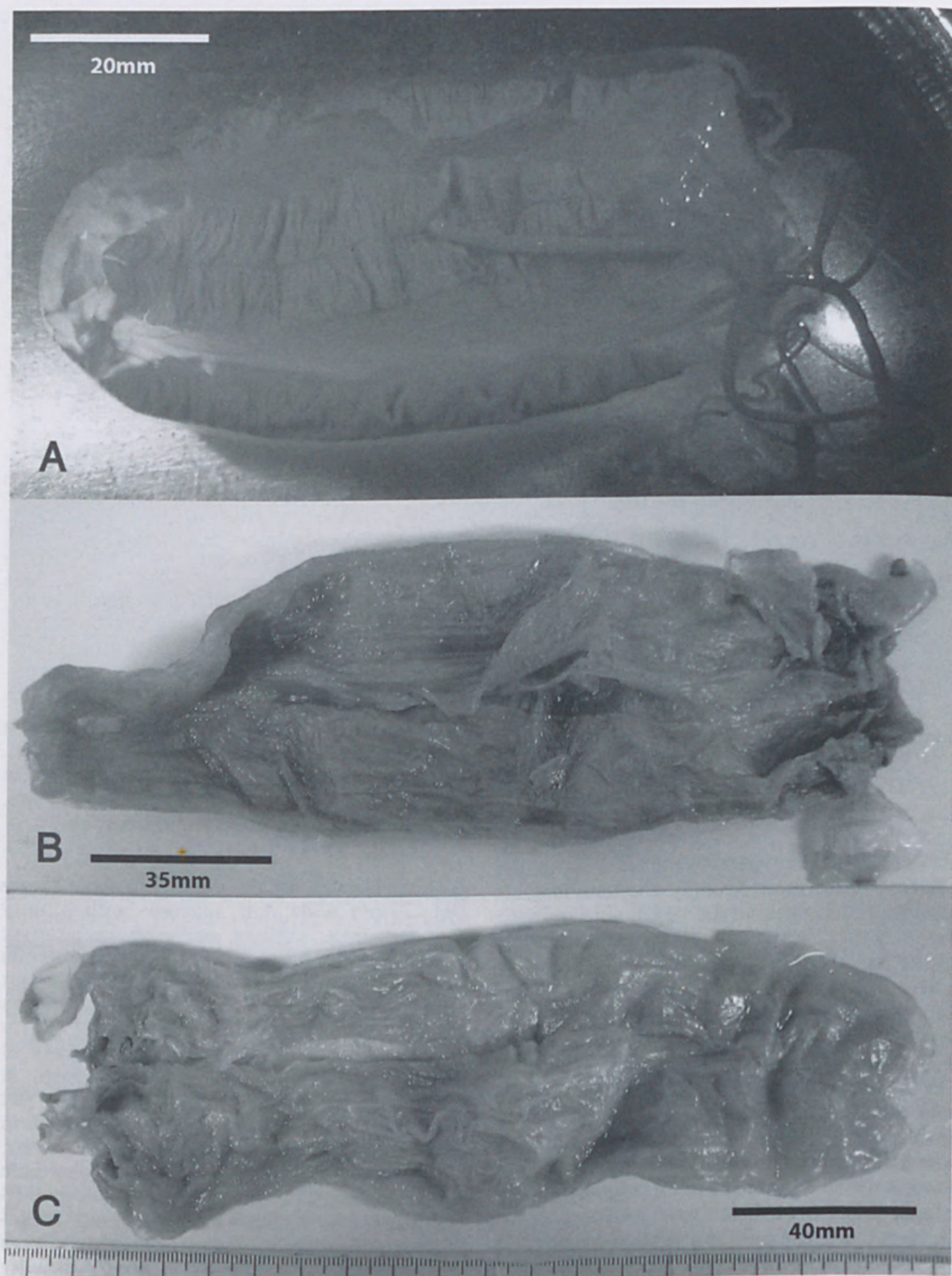


FIG. 5. *Alatina moseri* (Mayer, 1906) comb. nov., and *A. grandis* (Agassiz & Mayer, 1902) comb. nov. A, *A. moseri*, non-type specimen from Molokai Island (USNM 9632). B, (MCZ1043); C, (MCZ342). *A. grandis*, non-type specimens from the Hawaiian Islands, caught in 1861 and identified by Bigelow (1909:20).

eye spots slanting upward away from between the two median eyes. Statolith disintegrated, uninterpretable in preserved specimens. Rhopalial horns lacking. Velarium wide; nematocyst warts lacking. Velarial canals 3 per octant, simple and unbranched. Perradial lappets lacking. Frenulum very broadly webbed when viewed laterally, narrow and pointed along velarium; nearly reaching velarial edge. Gonads attached along entire length, reaching from stomach to level of rhopalial canal. Interradial septa perforations lacking. Stomach wide and shallow. Mesenteries lacking. Color in life unknown; preserved body hyaline, tentacles pink, eye spots dark brown, gonads milky yellow.

VARIATION. USNM29632-A has nematocyst freckles in a single row of the outer pedalial keel, and also a few scattered upon the exumbrellar surface. Relationship of this specimen to others is not well understood. Velarial canals nearest the pedalia are biforked in USNM22311.

DISTRIBUTION. Hawaiian Islands.

REMARKS. Placed in *Alatina*, based on crescentic gastric phacellae, 3 velarial canals per octant, and broadly rounded abaxial pedalia wings. However, it may be distinguished from the other species by several characters. First, the gastric cirri are rooted in pairs, whereas in other forms they are typically rooted in bunches. Second, the velarial canals are straight and unbranched, similar to most species in the *alata*-group but differing from others such as *A. grandis* comb. nov. and at least two undescribed forms. Third, the rhopalial of *A. moseri* have only 4 eyes, 2 median eyes with lenses and 2 lateral ocelli. This feature was also described for immature specimens of *A. grandis* (Agassiz & Mayer, 1902). And indeed, several workers have thought that *A. moseri* is merely the young of *A. grandis* (Bigelow, 1909: 19; Bigelow, 1938: 138, 144-145; Mayer, 1910: 507, 512; Mayer, 1915: 171; Mayer, 1917: 189). However, *A. moseri* specimens have fully mature gonads, so they are unlikely to be the young of another species. Bigelow (1938: 138, 145) thought that *A. moseri* might be a dwarf race of *A. grandis*. There is limited value in recognizing races among diagnosably different forms.

Mayer (1906) thought this species might be the same as *Carybdea* sp. of Semper (1860: fig. 9) from the Philippines, subsequently named by Haeckel (1880) as *Procharybdis turricula*.

Oddly enough, Mayer (1910: 512) and Stiasny (1919: 37) both confused Semper's and Haeckel's forms, attributing Haeckel's *C. philippina* to Semper's fig. 9, whereas Haeckel gave the name to Semper's fig. 8. To whichever one Mayer intended to refer, he (Mayer, 1910: 512) stated that *C. moseri* and Semper's form were "probably identical." Light (1914: 196) regarded the two species as identical. I have translated Haeckel's descriptions, and studied them and Semper's figures extensively; I am unable to find any characters that definitively characterize either of Semper's species, whereas *A. moseri* is diagnosable based on the peculiar paired phacellae bunches, having only four eyes, and the lack of exumbrellar nematocysts.

Unfortunately, there are some discrepancies between the reported station data and the data on the specimen labels; it is difficult to say with certainty what is accurate. First, station 3931 was not included in the published list, but was indicated on the label in Mayer's writing as being *Charybdea moseri* n. sp. Second, specimens from station 3829 are indicated on two samples, USNM29632 and 21800, unfortunately with different localities. Furthermore, the specimen numbers do not match those published. Specifically, Mayer listed 10 specimens from station 3829, collected 1-2 April at Avalu Point, Lanai Island. However, neither of the two lots of specimens is a match. USNM29632 matches the date, 1 April, but gives the locality as Molokai Island, and contains 2 specimens. USNM21800 matches the locality, Avalu Pt., Lanai Island, but there are 23 specimens. The remaining samples could not be found. Mayer (1906: 1136) indicated USNM21800 as type, which is unfortunate, since the specimens are now completely fragmented and uninterpretable. He indicated in handwriting on the specimen labels in USNM29632 that that lot was to be the type, but he did not indicate this in publication. Lots USNM29632 and 22311 are in excellent condition.

OTHER NOMINAL SPECIES OF *ALATINA*

Alatina alata (Reynaud, 1830) comb. nov., is completely unrecognizable based on the original description and illustration, but because of the prevalence of the name in the literature, should be stabilized by declaration of a neotype; a full redescription of a South Atlantic specimen will serve as the basis for identification of the taxon in the future. Accordingly, an application to the

ICZN to conserve *A. alata* will be submitted as soon as a suitable neotype is located.

Alatina obeliscus (Haeckel, 1880) comb. nov., seems to fall within the *Alatina* group, based on its large phacellae. However, its exact identity with respect to its congeners cannot be determined. Even with a specimen to study, it is unlikely that the species could be properly diagnosed, based on its uneven development of the velarial canals, and the size of Haeckel's specimen (35mm BH, 20mm BW), both of which indicate that it was very likely a juvenile. Assuming it is one of the branched-canal species, it would be relatively easy to diagnose, but only with mature specimens. Haeckel described a "button-form" thickening at the end of the tentacles. This is found occasionally in specimens that have spent too long in captivity in sub-optimal conditions (e.g., too warm, too confined, poor circulation; Gershwin, unpubl. data), and does not appear to be a diagnostic species character. Because this species is unlikely to be recognizable under any circumstances, the name is best abandoned.

Alatina philippina (Haeckel, 1880) comb. nov., was described based on a line drawing by Semper (1860, pl. 39, fig. 8). At a mature bell height of 30mm, one might expect that the species would be diagnosable, but Semper's line drawing and Haeckel's description are too vague to allow for differentiation of this species from any other. It seems closest to *A. tetraptera* (Haeckel, 1880) comb. nov., based on the long pedalia and wing-like phacellae. However, whether the two are synonymous or not cannot be concluded from available information. Thus, in the interest of stability, it seems most conservative to abandon the name.

Alatina pyramis (Haeckel, 1880) comb. nov., appears distinctive based on features from Haeckel's (1880) description and illustrations. First, being only 30mm tall and having full gonads, the only other *Alatina* spp. in this adult size range would be *A. rainensis* sp. nov., which has butterfly-shaped gonads, and *A. tetraptera*, which has peculiarly long pedalia and wing-shaped phacellae. Second, *A. pyramis* is the only species with frizzy lips. Third, the pedalia are considerably narrower than is typically found in other species of *Alatina*. I have no doubt that when this species is encountered again, it will be immediately recognizable based on these combined characteristics.

Alatina tetraptera (Haeckel, 1880) comb. nov., seems to fall within the *Alatina* group, based on the large pedalia with "mighty" wings and the phacellae with long cirri. Furthermore, the rhopalial niche ostia were described as "heart-shape," which could be easily mistaken for T-shaped if the specimen were not well preserved. Finally, only a single large eye was observed on the rhopalia, which is characteristic of some *Alatina* spp. Haeckel classified this species into *Procharybdis*, based on the absence of the velarial canals and frenulum. I am unsure what to interpret from the missing velarial structures, but it would be wrong to regard the species as anything other than distinct based on the split, wing-like phacellae (Haeckel, 1880: pl. 25, fig. 4) and the extremely long, uniquely shaped pedalia (pl. 25, fig. 3). These two characters are not known in any other cubozoan, except possibly the later-described *A. pyramis*. This species has not been recognized in the scientific literature for almost 100 years, but it seems appropriate to revalidate it awaiting fresh material that can be studied for a proper redescription. At a mature bell height of 30mm, with the structures described, I think this species would be recognizable if found again.

Alatina turricula (Haeckel, 1880) comb. nov., described from a line drawing by Semper (1860, pl. 39, fig. 9), is unrecognizable. It is clear from the widely rounded pedalia in the original illustration that this medusa is a member of the *Alatina* group. Furthermore, due to its extremely tall body (170mm), it is possible that it is referable to *A. grandis*. However, this is merely speculation, as it is impossible to diagnose with certainty from the drawing and vague description. There are no structural characters described that would serve to differentiate this species from any of the others; thus, it seems most conservative to permanently abandon the name.

Alatina grandis (Agassiz & Mayer, 1902) comb. nov.: The type material of this species from the Paumotu, has apparently been lost; neither MCZ nor USNM know of its whereabouts. Specimens from the Society Islands (MCZ1043 and MCZ 342), identified by H. Bigelow as *C. grandis*, match the original description but are too poorly preserved to be usefully interpretable. One (MCZ 342, BH 170.93, DBW 57.78, IRW 33.56+), bears the following collection data: Pacific Ocean, Society Islands, coll. A. Garrett, 29.ix.1861; originally preserved in alcohol, now preserved in formalin (Fig. 5C). The other (MCZ

1043, BH 184.55, DBW 59.55, IRW 33.18), was apparently collected at the same time, and delivered to the MCZ by A. Garrett in 1864 (Fig. 5B). The species seems distinctive based on its extremely large size, and in having only one median eye and short, branched velarial canals.

Alatina madraspatana (Menon, 1930) comb. nov., is described as having up to 5 branched velarial canals per octant, an apical concavity, and 6 eyes on each rhopalium, one of the median bearing a lens. This combination of characters is unique, and thus, the species is regarded herein as valid. However, I remain curious about the velarial interpretation, as it seems rather odd for an *Alatina* to have 5 velarial canals per octant.

Manokia Southcott, 1967

***Manokia stiasnyi* (Bigelow, 1938) (Fig. 6)**

Charybdea spec. v*Stiasny, 1930: 3-5, figs 1-7; occurrence in New Guinea, and description of species; Stiasny, 1937: 216; brief comparison of branched tentacles.

Carybdea stiasnyi v*Bigelow, 1938: 136; sp. nov., in reference to Stiasny's (1930) description; Kramp, 1961: 306; Southcott, 1963: 51; tentacle comparison; Kramp, 1968: 69 [doubtful species].

Manokia stiasnyi Southcott, 1967: 667; new genus comb. nov.

Charybdea stiasnyi vPayne, 1960: 6, 28, 32-33.

MATERIAL EXAMINED. HOLOTYPE: IRSNB IG 9223, Manokwari, New Guinea, 10 March 1929; male, 23.59mm BH, 20.11mm DBW at the top of the pedulum, 21.66mm DBW at the widest point, 10.24mm IRW, 1.32mm TBW, 12.52mm Pedalial length, 2.23mm pedalial width at widest part.

TYPE LOCALITY. Manokwari, New Guinea.

REVISED DESCRIPTION. Body barrel-shaped, widest in middle region, with conspicuous apical depression (Fig. 6A). Interradial furrows deep, nearly meeting pedalia. Adradial furrows deep, demarcating rhopalial region and interradian thickenings. Bell with scattered gelatinous nematocyst warts, extending onto velarium but warts not specific to any canal or pattern. Pedalia 4, interradian, scalpel-shaped, with relatively narrow inner keel, lacking nematocyst warts or freckles. Pedalial canals flat throughout length, with slight upward-pointing nub projecting into sub-lamellar space; straight at tentacle insertion. Tentacles 4, interradian, round in cross section, with evenly-sized nematocyst bands. Nematocyst bands drawn out adaxially into short, blunt extensions, approximately 8 per tentacle (Fig. 6B); one tentacle having extensions in 2 alternating rows, other tentacles having them

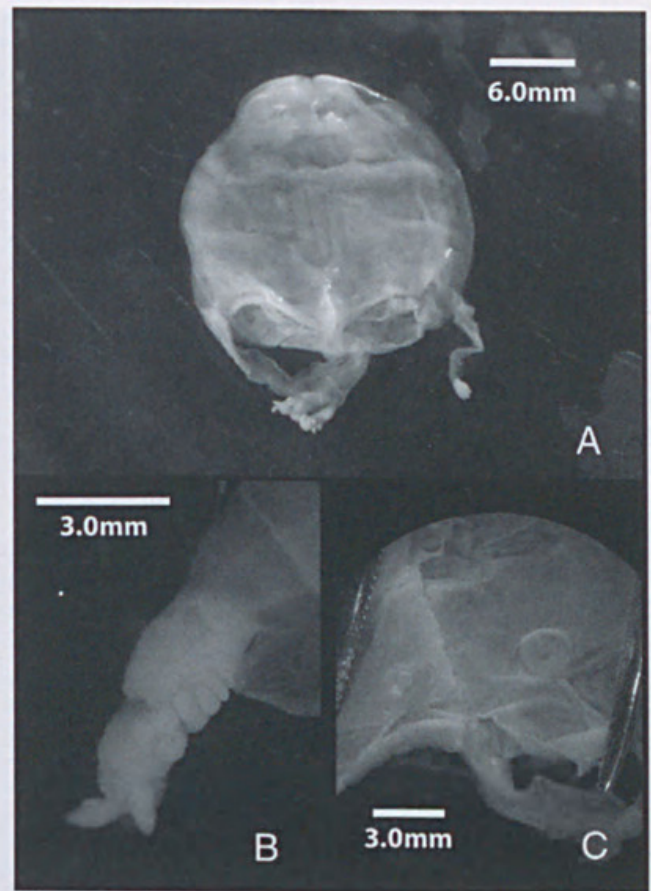


FIG. 6. *Manokia stiasnyi* (Bigelow, 1938). A, holotype specimen. B, One tentacle, showing peculiar branching pattern. C, Subumbrellar view of rhopalium, with convex windows.

in more or less a single row. Rhopalial niche flush with surrounding bell wall; with T-shaped ostia, comprised of a single thickened covering scale above and two well developed covering scales below. Upper scale with a median flap hanging down into ostium in front of rhopalium. Rhopalial horns absent. Subumbrellar wall of rhopalial niche made of a thick window of un-muscle mesoglea, hemispherically convex on subumbrellar side, concave on rhopalial niche side (Fig. 6C). Rhopalia with two median lensed eyes, distal-most larger than proximal, and two pairs of unevenly sized lateral eye spots, distal pair larger than proximal pair. Phacellae crescentic, with numerous long cirri, arranged more or less parallel; number of trunks in each phacellus indeterminable without damaging specimen, but appears to be between 5 and 10. Stomach shallow, with short manubrium; specimen with large amphipod high inside the subumbrellar cavity. Mouth shape indeterminable without damaging specimen. Mesenteries lacking. Frenulae well developed,

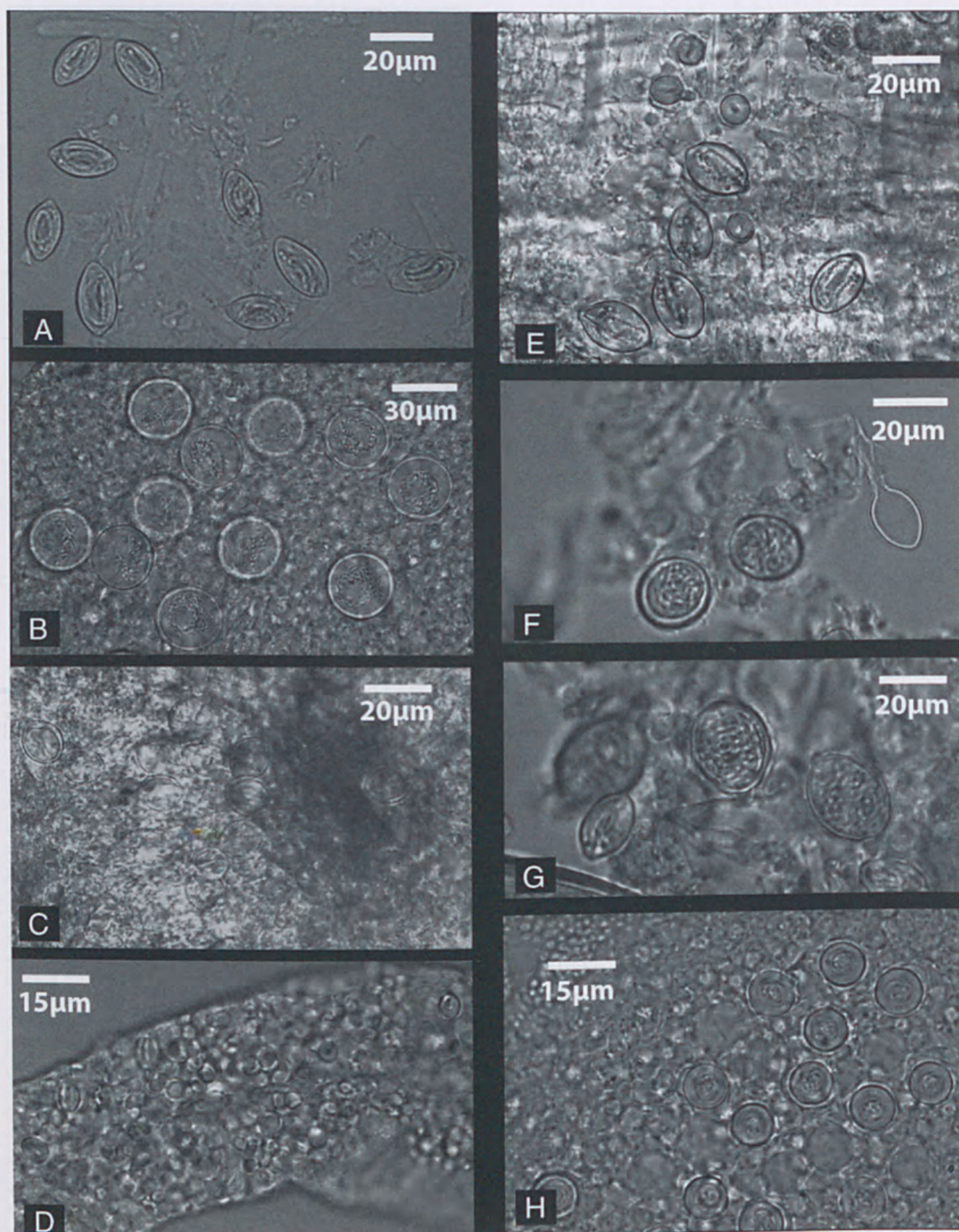


FIG. 7. Nematocysts of Alatinidae. A, *A. mordens*, tentacle. B, *A. mordens*, bell wart. C, *M. stiasnyi*, tentacle. D, *A. rainensis*, gastric cirrus. E-G, *A. rainensis*, tentacle. H, *A. rainensis*, bell wart. See text for complete descriptions and measurements.

but short, reaching only approximately halfway to velarial margin. Perradial lappets absent. Velarium 2.71 mm wide, with 4 undulating, unbranched canals per octant. Gonads leaf-like, attached along nearly whole length of interradial septa, projecting laterally into coelenteric cavity. Colour in life unknown.

CNIDOME (Fig. 7C). The tentacles of *Manokia stiasnyi* have a mononidome of sub-spherical euryteles with a thick capsule wall, with an arithmetic mean of 15.23 μ m long by 12.43 μ m wide (range 13.42–16.53 μ m long by 11.54–13.63 μ m wide, N=12). Nematocysts from other parts of the body were not examined due to brittleness of the specimen.

REMARKS. Stiasny (1930) commented that the exumbrella of this species was smooth, lacking nettle-warts. However, this is inaccurate. The holotype specimen has a few scattered warts, and while most of these have become flattened through the passage of time, several are still raised. I could not observe any particular pattern to their arrangement, but they are present on the velarium as well as the body.

The tentacles are worthy of discussion, as they have always been the chief character used to separate this species from others. The tentacles are typically said to be branched (Stiasny, 1930; Bigelow, 1938; Kramp, 1961; Southcott, 1967). However, the tentacles are not branched in the conventional sense, and referring to them as such is somewhat misleading. In branched tentacles, one would expect that the central lumen would be branched, in order to maintain the flow of nutrients and various fluids. However, in the tentacles of the present specimen, it is the nematocyst bands that are branched rather than the tentacle itself. Therefore, the "branches" are not true branches, but rather, merely elongations of one side of the tentacular nematocyst bands. Each band is drawn out a short distance adaxially like a little tail, with these extensions primarily arranged in two vertical rows. This character is somewhat reminiscent of the neckerchief-shaped tentacle bands of *Carukia barnesi*, but the resemblance is apparently only superficial. In *M. stiasnyi*, the bands are apparently normal around most of the tentacle, and only extended in a bluntly rounded, almost herniated manner along the adaxes. In *C. barnesi*, the bands are widely spaced, and the adaxial extensions are quite remarkably triangular in form, extending distally.

The peculiar branching of the tentacles led Stiasny (1937: footnote p216) to think that the medusa might be the young of an unusual chirodropid he identified as *Chiropsalmus quadrigatus*. His specimen from the Maldives had numerous filaments on the tips of the tentacles. He misunderstood Mayer's (1910) redescription of *C. quadrigatus*, thinking that each pedalial finger should bear numerous tentacles, rather than a single one. In fact, *M. stiasnyi* bears no resemblance whatsoever to *C. quadrigatus*, nor does Stiasny's Maldivian specimen; the latter will be formally described in a forthcoming chirodropid revision.

Two particular characters suggest a strong affinity to the *Alatina* species group, namely, the T-shaped rhopalial niche ostia and the crescentic-shaped phacellae of long cirri. Although similar, the ostia are also quite different, in that the upper covering scale has a central flap that hangs down, rather than the typical straight scale of *Alatina*. The two lower covering scales are quite robust, and the indentation between them extends down to the velarium.

Southcott (1967) erected *Manokia* based on the branched tentacles, 4 undulating velarial canals per octant, and horizontal phacellae. He commented that the branched tentacles alone would be insufficient basis to establish a new genus, because they could simply be aberrant; however, the velarial canals were quite distinct. He went on to compare the canals with those of *Carybdea rastonii* and *C. marsupialis*, citing that those of *M. stiasnyi* are more numerous but simpler in nature. However, any species in the *Alatina* group would have been a closer comparison (though *M. stiasnyi* still would have proven unique). The crescentic phacellae and T-shaped rhopalial niche ostia are more reminiscent of *Alatina*, as are the more or less simple velarial canals and lack of mesenteries.

Kramp (1968) remarked that Bigelow's species was doubtful, but did not elaborate why. Less than a decade earlier, he had considered it valid (1961). The point is moot anyway, for re-examination of the specimen has revealed a combination of characters unlike those of any other known species.

GENERAL DISCUSSION

The species of the *Alatina* group all share the conspicuous characters of crescentic phacellae and T-shaped rhopalial niches. However, the

internal and external relationships of this group have been debated in the past. Traditionally, *C. alata* auct. was diagnosed by focussing on the crescentic phacellae, with varieties sometimes based on size differences (Mayer, 1910; Kramp, 1961). Other characters occasionally used for diagnosis have been inconsistent and often misinterpreted, for example, rhopalial niche shape (Mianzan & Cornelius, 1999). However, Gershwin (2001) and Gershwin & Collins (2002) showed that analysis of numerous characters in jellyfishes can highlight relationships that were previously overlooked with narrower analyses. Numerous forms of *Carybdea alata* from disparate locations, all with crescentic phacellae, differ with regard to umbrellar and velar nematocysts, number and degree of branching of the velarial canals, number of eyes, number of phacellae roots, shape of the rhopalial niche ostium scales, and tentacle banding patterns. No doubt additional differences will be found with closer morphological study, cnidome comparison, and molecular analysis of these and other forms.

Within the *Alatina* clade, the most attention historically has fallen on the interpretation of *Alatina grandis*. According to Bigelow (1938), *C. grandis* was the first in the group to be positively identifiable, because *C. alata* as described by Reynaud (1830) is unrecognizable and the name was revived by Vanhöffen (1908) for stability. Unfortunately, Vanhöffen failed to assign a particular specimen or suite of characters to the name; thus, we are left with the name of an unrecognizable species, and stability was not served. Bigelow went on to conclude that all the forms within the *C. alata* group are but one species, with *C. grandis* being the adult form. However, three decades earlier, Bigelow (1909) thought that *C. grandis* was valid and that the Pacific complex of *C. philippina*, *C. grandis*, and *C. moseri* could be easily separated as follows: *C. philippina* matures at only 30mm BH, whereas *C. moseri* does not begin to develop gonads until 60mm BH; *C. moseri*, in turn is closely allied with *C. grandis*, being separable, if at all, on the velarial canals being simple in the former, branched in the latter. More often than not, *C. grandis* has been interpreted as a gigantic variety of *C. alata* (Mayer, 1910, 1915, 1917; Light, 1921; Thiel, 1928), although Kramp (1961), without comment, regarded *C. grandis* and all the nominal species in the group as junior synonyms of *C. alata*.

While most authors have argued over which crescentic-phacellae forms should be considered species and which should be considered varieties, *alata* also became the subject of a large and confusing misunderstanding that spanned 14 decades and never was completely resolved. Agassiz (1862) assigned Reynaud's *C. alata* to *Tamoya*, rather than to his *Marsupialis*, for reasons that are wholly unclear. *Tamoya haplonema*, the type species, could not possibly be confused with *C. alata* under any reasonable circumstances. Haeckel (1880) moved it back to *Carybdea*, a combination which has been widely adopted since. However, Uchida (1929) identified his local large carybdeid as *Tamoya alata*. It is clear from his illustrations how he arrived at the *Tamoya* part of his identification, but there is no indication of how he came to think that they were *alata*. His medusae were not *alata*-like in the sense of the crescentic phacellae and T-shaped rhopalial niche ostia. He further misidentified the small species *C. sivickisi* to be the young of his *T. alata*; in fact, *C. sivickisi* shares only the crudest resemblance to any *Alatina*, in that both have 4 tentacles. All other characters, from the rhopalial niche ostia to the phacellae, from the velarial canals to the pedalia, are quite different. Over 40 years later Uchida remained confused on *Carybdea alata*, for he erroneously assigned to this species a single specimen from Cape Town with *C. marsupialis*-type gastric phacellae and *T. haplonema*-like rhopalial niche ostia (Uchida, 1970). Apparently Uchida's error was what led Branch and his colleagues (1994) to erroneously identify the common Cape Town carybdeid as *C. alata*, and Pagès et al. (1992) to identify it as *T. haplonema*, when it should have been recognized as a new species (Gibbons & Gershwin, unpubl. data).

In the process of sorting out which of the *Alatina* species should be retained and which are unrecognizable, many other new species are likely to be found. For example, a single Indonesian specimen (SAMH967) from the Te Vega Expedition, and specimens from Sri Lanka (QMG317054, G317055) and Madagascar (QM G317053), all match the standard descriptions for *C. alata* auct. but differ in numerous other structural characters. Sorting out the true biodiversity of the *Alatina* group will require fine feature study of a large number of specimens from regions throughout the world's tropics.

Removal of several species from *Carybdea* and the Carybdeidae, in particular the well published

C. alata auct. and the obscure *M. stiasnyi*, in effect redefines both *Carybdea* and the Carybdeidae. I thus propose the following revised descriptions, pending a comprehensive revision. I am further excluding *C. sivickisi* from *Carybdea*, and the Irukandjis and *Tamoya* from the Carybdeidae, based on overwhelming morphological and molecular comparison; the full explanation and reclassification for these exclusions is beyond the scope of this paper, but is forthcoming (Gershwin, unpubl. data).

Carybdeidae. Carybdeida with gastric phacellae; with poorly defined rhopaliar niche covering scales; with nematocyst clusters on the pedalia; with unbranched tentacles.

Carybdea. Carybdeidae with epaulette-shaped or linear phacellae, comprised of short gastric cirri; with heart-shaped rhopaliar niche ostia; with usually two, sometimes 3-4, dendritically branched velarial canals per octant; with scalpel-shaped pedalia, typically with nematocyst clusters on the outer keel.

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