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Nematocysts of the Cubozoa

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Abstract

Nematocysts (stinging organelles) are an important part of cnidarian identification, but the cnidomes of many species remain poorly known because of identification difficulties and confusing nomenclature. Currently, the cnidomes of 20 cubozoan species are documented in whole or in part (including four undescribed species and five newly described species); 18 of these are re-examined in detail, and the cnidomes of 13 species are newly presented. Type material was used for these studies where possible. A new category of nematocyst is designated, namely '*p*-rhopaloid', characterized by having a v-shaped notch in the undischarged shaft, as in *p*-mastigophores, but having a lobed discharged shaft, as in rhopaloids; this type of nematocyst is found in both the Carybdeida and Chirodropida. Measurements, shape descriptions, and photographs are presented for all cnidomes studied. Also presented are a glossary to nematocyst terminology, descriptive sections on nematocyst nomenclature and preparation, and a key to the nematocysts of the

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Cubozoa. Special remarks sections for taxonomists and forensic specialists are given, along with a summary of phylogenetic patterns. This catalogue will be useful to taxonomists, envenomation physicians, and toxinologists, as well as anyone wishing to identify cubozoan specimens or stings.

Key words: Box jellyfish, Irukandji, sea wasps, cnidomes, cnidae, stinging organelles, stinging cells, Cnidaria, Cubomedusae, Carybdeida, Chirodropida, morphology, taxonomy, forensics

Ode to the nematocyst

Wondrous little organelle of death;
O to know your mysteries.
A coiled harpoon of lightning speed,
Revealing species' histories.

Banana-shaped or ovoid,
Large or small, or spheres.
Measured in tens of microns,
Powerful microns of fear.

Forty thousand G's of force,
Drilling into flesh;
Bathed in a golden toxin,
Spiny hypodermic of death.

Designed to conquer prey or foe,
But if you longer linger,
Fascinating capsules of beauty,
These treasures of St. Inger.

........................*St. Inger, the Patron Saint of Marine Envenomation*

Introduction

Cnidomes have been used as diagnostic taxonomic tools for many years in the Anthozoa and Hydrozoa (Östman, 1983; Gravier-Bonnet, 1987; Östman et al. 1987; Zamponi & Genzano, 1990; Hidaka, 1992; Acuna & Zamponi, 1997; Bouillon & Boero, 2000), but comprehensive data are lacking for the Cubozoa. To date, the cnidomes of only a few species are documented (Berger 1900; Cleland and Southcott 1965; Calder and Peters 1975; Rifkin and Endean 1983; Kinsey 1986; Moore 1988; Avian et al. 1997; Marques et al. 1997; O'Reilly et al. 2001; Carrette et al. 2002; Currie et al. 2002; Yanagihara et al. 2002; Oba et al. 2004). Several attempts at linking fatalities to species via nematocysts recovered from victims have been of limited utility due to lack of comparative knowledge

(Kingston and Southcott 1960; Schnadig et al. 1991; Huynh et al. 2003).

The purpose of this paper is to provide a comprehensive foundation for study and identification of cubozoan nematocysts. This tool will be useful to medical professionals needing to identify sting samples, taxonomists wishing to distinguish among species, and various researchers faced with the task of identifying fragmentary or disintegrated specimens.

This report focuses on mature medusa cnidomes; however, those seeking information on juvenile or polyp cnidomes are directed to the following resources: *Carybdea marsupialis* Linnaeus (Stangl et al. 2002); *Carybdea xaymacana* Conant (as *C. marsupialis*) (Studebaker 1972; Cutress and Studebaker 1973); *Tripedalia cystophora* Conant (Werner 1975; Chapman 1978; Werner 1984); *Carybdea sivickisi* Stiasny (Hartwick 1991); *Chironex fleckeri* Southcott (Yamaguchi and Hartwick 1980); "*Carybdea alata*" auct. (Arneson 1976; Arneson and Cutress 1976); and the Japanese "*Carybdea rastonii*" auct. (Okada 1927).

Nematocyst terminology

Nematocyst terminology can be somewhat bewildering to the non-expert; those wishing a more thorough explanation are directed to Östman (2000). Nematocysts are comprised of three parts, the capsule, the shaft (= basis, or butt; the stiff, thickened section first out of the capsule), and the tubule (the long flexible, narrow section that extends beyond the shaft). Macrobasic and microbasic (derived from the word "basis") simply refer to the length of the everted shaft compared to the length of the capsule. Traditional classifications refer to shafts about 3–4 times the length of the capsule as macrobasic, whereas microbasic refers to anything shorter. An everted shaft that is longer than the capsule length must twist tightly or fold back on itself to fit into the capsule when inverted. It has recently been suggested (N. Boero and J. Bouillon, lecture notes, 2000) that a more practical classification might regard the capsule length as a natural cut-off point, i.e., everted shafts longer than the capsule are macrobasic, whereas those shorter than the capsule are microbasic, i.e., if the shaft must twist or fold to fit into the capsule, how many times it twists or folds is simply a matter of scale. Macrobasic nematocysts have not previously been reported within the Cubozoa, but are present in *Tamoya haplonema* (see Plate 24). In cubozoans, three main categories of nematocysts are common: euryteles (sometimes called tumiteles in the Cubozoa), mastigophores, and isorhizas. These names also make a bit more sense when one understands their origins. Eurytele translates to "distally widened shaft". Mastigophore translates to "whip-bearing." Isorhiza translates to "equal root," in reference to nematocysts in which a thickened shaft is lacking and the tubule is of equal diameter throughout. Names with "trich" refer to the spination, i.e., atrichous (without spines), holotrichous (completely covered with same-sized spines), heterotrichous (spines of different sizes), basitrichous (spines only at the base), merotrichous (spines only in the middle), and apotrichous (spines only at the end).

Not all authors have used the same terminology for the same nematocyst types, although for the most part it has been more consistent than the nomenclature concerning medusa structural morphology. For example, not all authors accept Southcott's name "tumitele" for the tentacular nematocysts of some carybdeids (Southcott 1967; Matsumoto 1995; Hartwick unpublished), and only recently have the heterotrichous microbasic euryteles of *Chironex fleckeri* been reclassified as trirhopaloids (Rifkin and Endean 1983; Williamson et al. 1996; Carrette et al. 2002). A synopsis of the history of nematocyst nomenclature is given by Östman (2000), and a synopsis of the cnidomes of some cubozoan species is given by Shostak (1996).

The following is merely a brief glossary to some of the main terms that apply to cubozoan cnidomes as compiled from countless sources; for a more comprehensive understanding, refer to Weill (1934), Mariscal (1971), Calder (1974), Rifkin (Williamson et al. 1996), and Östman (2000).

Atrichous isorhiza: A type of nematocyst (= stinging organelle). [See 'Isorhizas'].

Cnidae: [See 'Nematocysts'].

Cnidome: The full complement of nematocysts characteristic of a species.

Eurytele: A type of nematocyst (= stinging organelle) common in all four medusozoan classes, but lacking in the Anthozoa; characterized by a single dilation on the distal end of the shaft. [See 'Rhopaloids'].

Freckles: Unraised nematocyst clusters on the exumbrellar surface, velarium, perradial lappets, or pedalia. Often historically referred to as "nematocyst warts," but herein redefined as follows: warts are nematocyst clusters which are underlain by gelatinous protuberances, whereas freckles are nematocyst clusters which are not underlain by gelatinous protuberances. [See 'Warts'].

Handkerchiefs: [See 'Nematocyst bands'].

Haplonemes: Without a well defined shaft; referring to a higher grouping including **Isorhizas.**

Heterotrichous/Holotrichous/Homotrichous/Atrichous: Refers to the spines on the tubule of the nematocyst. Nematocyst tubules may be atrichous (= without spines), homotrichous (also called holotrichous) (= spines the same throughout), or heterotrichous (= spines different throughout). The base of the tubule (or 'shaft') uses a different terminology: for terminology on the length of the shaft, see 'Macrobasic/microbasic'; for terminology on the shape of the shaft, see 'Mastigophores' and 'Rhopaloids'; for terminology on the spination of the shaft, see the discussion of 'Types' under 'Mastigophores'.

Isorhiza: A type of nematocyst (= stinging organelle) without a well-defined shaft, i.e., the discharged tubule is the same diameter throughout its length, or narrowing slightly toward the distal end. Nematocysts with the tubule slightly dilated proximally are termed 'anisorhizas'.

Macrobasic/Microbasic: Refers to the length of the discharged shaft (or basis, or butt) on nematocysts, i.e., the thickened base of the tubule. Traditionally, 'microbasic' was defined as 3 times or less the length of the capsule, whereas 'macrobasic' was defined as 4 times or more than the length of the capsule. However, I prefer to follow the convention of Bouillon and Boero, in which a single capsule length is the critical point; thus, microbasic is herein used to mean those nematocysts in which the discharged shaft does not exceed the length of the capsule, and thus does not need to twist or fold to fit inside, and macrobasic is herein used to mean those nematocysts in which the discharged shaft is too long for the capsule, and thus is forced to twist or fold to fit inside, regardless of the number of times. Most cubozoan nematocysts are microbasic.

Mastigophore: A type of nematocyst (= stinging organelle). These are thought to be the primary carrier of the lethal factor in the chirodropid taxa. *B*-mastigophores, in which the discharged shaft tapers gradually into the distal tubule, are not known in the Cubozoa, whereas *p*-mastigophores, with an abrupt demarcation between the shaft and tubule, are quite common. *P*-mastigophores are readily identifiable in the undischarged state, by the presence of a conspicuous v-shaped notch in the distal end of the shaft. *P*-mastigophores have been previously documented in three types: **Type I** [all spines orientated at right angles to the capsule axis], **Type II** [all spines orientated towards the capsule], and **Type III** [shorter spines orientated toward the capsule, longer spines orientated away]; a fourth form, recently designated **Type IV** [all spines long, orientated away from the capsule], is characteristic of the non-*Carukia* species of the Irukandji clade, e.g., *Malo maxima* Gershwin (2005b), *Gerongia rifkinae* (Gershwin and Alderslade 2005), 'Pseudo-Irukandji,' and 'Morbakka' (See Plates 18B, 21 A, B, 22B; Gershwin, 2005a; Gershwin, 2005b).

Neckerchiefs: [See 'Nematocyst bands'].

Nematocysts: The stinging organelles, also collectively called 'cnidae'. Nematocysts occur in a variety of shapes and sizes, and the ratios of different types can be diagnostic for some species. The main cnidae that occur in the Cubozoa are: Mastigophores, Isorhizas, and Euryteles. Nematocyst identification is properly done on the shafts and tubules of discharged capsules. [See also 'Macrobasic/Microbasic' and 'Heterotrichous/Holotrichous/Homotrichous/Atrichous' for explanation of the shaft terminology. For explanation of shaft morphology, see also 'Mastigophores' and 'Rhopaloids'].

Nematocyst bands: Fleshy raised bands on the tentacles of all cubozoan species, on which the nematocysts are concentrated. Nematocyst bands repeat throughout the length of the tentacle, and the pattern of banding is highly diagnostic in some species. In some cases the nematocyst bands are distinctive, as in the genus *Carukia*, where the bands may be of a 'handkerchief' or 'neckerchief' form, so called by Southcott (1967) who likened them to the trademark handkerchief worn around the neck by the movie actor John Wayne, with the triangular 'tail' that hangs down on one side. In a currently undescribed species, the nematocyst bands have a peculiar 'halo' form, with the nematocysts inserted end-on around the periphery of shelf-like bands.

Rhabdoids: A category of nematocysts, with the shaft of constant diameter; referring to a higher grouping including **Mastigophores**.

Rhopaloids: A category of nematocysts, with the shaft of unequal diameter. Rhopaloids come in three types: **Euryteles**, interchangeably used to refer to nematocysts in which the shaft is dilated at only one point along the length, or in which the shaft has only a single distal swelling; **Birhopaloids**, in which the shaft has two dilations with regular spines; and **Trirhopaloids**, with three dilations, the middle (largest) swelling bearing spines. **Stenoteles** and **Tumiteles** are other names that have been used.

Stenotele: A type of nematocyst (= stinging organelle) present in many hydrozoans and a few cubozoans, characterized by a constriction on the shaft, with large spines emitting from the constriction.

Tentacles: The whip-like filaments on which the primary stinging organelles occur, i.e., the dangerous part of the jellyfish. In cubozoans, the tentacles are attached to the body by means of pedalia; the tentacles are properly defined as the flexible, opaque part, whereas the pedalia are the transparent, gelatinous, stiff part at the base.

Tentacle bands: [See 'Nematocyst bands'].

Tumitele: A type of nematocyst (= stinging organelle) introduced by Southcott (1967) for some Carybdeida, characterized by the middle portion of the shaft being wider than it is at either end, with this swelling bearing spines. This type of nematocyst is not typically recognized by later workers, often lumped in with euryteles; however, the cylindrical shaft and distally-pointing spines are more similar to the Irukandji *p*-mastigophores.

Warts: Typically nematocyst clusters which are underlain by gelatinous protuberances on the exumbrellar surface. [See 'Freckles'].

Nematocyst preparation

Nematocysts can be permanently mounted for study by placing a bit of tentacle, bell snip, or cluster of cirri onto a glass slide, covering with one or two drops of warmed Glycergel (Dako Corp., California), and finishing with a cover slip; gently pressing or tapping with a blunt object will help squash the sample for easier study. For those wishing a cleaner sample, i.e., nematocysts separated from tissue, the simple disintegration isolation method of Bloom et al. (1998) works well. Fresh samples can be made to discharge with the addition of a drop of freshwater, saliva, or ethanol prior to adding the Glycergel; preserved nematocysts cannot be discharged. Since nematocyst identification is ultimately based on the shaft and tubule structures, fresh samples are preferable; however, capsule measurements are best made on undischarged capsules, which are more stable when preserved. Nematocysts are best examined under a compound microscope with a 40x or 100x objective.

For the table and corresponding plates herein, tissues were sampled from holotypes or neotypes, or specimens designated to become them, unless otherwise noted. 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 (i.e., 400x magnification). Nematocysts were identified following the keys of Calder (1974), Mariscal (1971), and Williamson et al. (1996), as well as the work of Carrette (2002) and Oba et al. (2004).

Nematocyst identification

Determination of nematocyst type was made based on information obtained from many nematocysts studied (sample sizes given in Table 1). Images were selected for the catalogue based on overall clarity and interpretability (e.g., capsule shape and size relative to others if applicable, tubule winding pattern, shaft length and undischarged shape, discharged spination pattern on shaft); however, not all features are observable in all images.

Every effort was made to study inverted and everted nematocysts; however, with fixed material, this was not always possible. In order to maintain continuity with past researchers' results, as well as to provide a means of comparison, the following conventions were used herein: nematocysts widely identified as euryteles (e.g., *Carybdea* spp.; *Alatina* spp.) or previously identified as tumiteles (e.g., *Carukia* spp.) were classified accordingly, unless new observations compellingly indicated otherwise; nematocysts with a v-shaped notch in the distal end of the undischarged shaft were classified as *p*-mastigophores (if the discharged shafts were cylindrical) or *p*-rhopaloids (if the discharged shafts were lobed; see below); nematocysts without a v-shaped notch in the undischarged shaft were classified as trirhopaloids if either they could be verified by discharged morphology, or they have been widely identified as such (e.g., chirodropids).

Remarks on Rhopaloids and Rhabdoids

Certain oval, football-shaped, egg-shaped or lemon-shaped nematocysts of cubozoans have been more or less interchangeably classified as euryteles (Calder and Peters 1975; Rifkin and Endean 1983; Avian et al. 1997; Marques et al. 1997; Yanagihara et al. 2002; Oba et al. 2004), stenoteles (Moore 1988) or tumiteles (Southcott 1967; Matsumoto 1995), whereas some recent workers have classified them as trirhopaloids (Williamson et al. 1996; Carrette et al. 2002; Oba et al. 2004). However, in some taxa (e.g., *Carybdea mora* (Plate 5A, B); *Chiropsoides buitendijki* Horst (Plate 29B)), these undischarged nematocysts appear to have two different forms, one with a fine tubule and a narrow shaft with a v-shaped notch at the distal end, and the other with a heavier tubule and a broader shaft with a less well-defined distal end. It is not currently clear whether these two forms represent different categories, or different developmental stages of the same category; herein, they are differentiated for clarity.

TABLE 1. Comparison of medusa cnidomes of cubozoan species; polyp cnidomes are not given here but may be found in the literature cited in the text. Where nematocysts were reported previously by other workers and again by me (herein), new reports are indicated by my initials (LG). Terminology follows Williamson et al. (1996). All measurements are in microns (µm), given as length x width.

	Tentacles	Exumbrellar warts	Gastric cirri	Manubrium	Citations
Alatina mordens, holotype	Lemon-shaped euryteles, 19.30-27.25 x 11.10-14.85, n=57	Spherical isorhizas, 28.25-31.71, n=24	Nematocysts not found	Nematocysts not found	Gershwin, 2005c; Herein
Alatina moseri, non-type, Hawaii	Ovoid heterotrichous microbasic eurytele, 24.4 (±SE 1.23) x 13.6 (±SE 0.61), and rhopaloids and isorhizas	Haplonemes and heteronemes	Not examined	Not examined	Yanagihara et al., 2002
Alatina rainensis, holotype	1) Egg-shaped microbasic euryteles, 14.99-19.70 x 10.43-13.11, n=37 2) Large & small oval isorhizas, 16.42-23.78 x 13.50-18.34, n=42; 6.19-8.24 x 5.58-6.78, n=13 3) Tiny sub-spherical microbasic ?amastigophores, 6.19-7.16 x 6.02-6.80, n=6	Spherical isorhizas, 9.22-10.47, n=22	Small euryteles, 6.53-8.96 x 4.61-6.55, n=24	Nematocysts not found	Gershwin, 2005c; Herein
Manokia stiasnyi, holotype	Sub-spherical euryteles with a thick capsule wall, 13.42-16.53 x 11.54-13.63, n=12	Not examined	Not examined	Not examined	Gershwin, 2005c; Herein
Carybdea marsupialis, non-type, Adriatic	1) Atrichous isorhiza haplonemes, 8.99-18.05 x 4.29-9.88 2) Heterotrichous microbasic euryteles, 17.02-42.26 x 12.11-23.99 3) Holotrichous isorhizas, 15.11-24.94 x 13.79-22.86	Not reported	Not reported	Not reported	Avian et al. 1997
Carybdea mora, neotype, Japan	1) Oval microbasic euryteles, 26.06-36.38 x 13.42-17.62, n=33; *p*-rhopaloids, n=6 2) Egg-shaped isorhizas, 10.74-13.84 x 6.11-8.08, n=5	Not examined	Not examined	Not examined	Herein
Carybdea rastonii, neotype, South Australia	Southcott, Matsumoto: Tumiteles Cleland & Southcott (pl. 2): Microbasic mastigophores LG: 1) Egg-shaped microbasic euryteles, 19.58-29.75 x 12.55-18.43, n=34 2) Egg-shaped isorhizas, 8.88-12.85 x 6.64-7.88, n=12	Holotrichous haplonemes LG: 1) Spherical isorhizas, 18.81-21.89, n=44 2) Tiny euryteles, ca. 10 diameter	LG: Sub-spherical euryteles, 10.09-12.48 x 8.41-9.21, n=9	LG: Nematocysts not found	Cleland & Southcott, 1965 (Pl. 2); Southcott, 1967; Matsumoto, 1995; Herein

to be continued

TABLE 1 (continued).

	Tentacles	Exumbrellar warts	Gastric cirri	Manubrium	Citations
Carybdea sivickisi, non-type, N. QLD specimen	1) Egg-shaped euryteles, 13.43-19.40 x 9.60-12.40, n=21 2) Egg-shaped isorhizas with full tubules, 15.82-18.77 x 9.60-11.52, n=16 3) Sub-spherical *p*-mastigophores, 10.58-11.94 x 9.60-10.60, n=6 4) Tiny oval isorhizas, 9.02-11.41 x 4.38-5.96, n=4	Not examined	Not examined	Not examined	Herein
Carybdea xaymacana, non-type SW Australian specimen, and non-type Puerto Rican specimen	Berger (Caribbean form): Two kinds, larger and smaller, similar to *Tripedalia cystophora* LG (SW Australian form): 1) Elongate lemon-shaped euryteles, 26.27-37.02 x 11.67-15.40, n=43 2) Small oval isorhizas, 9.17-11.93 x 5.41-6.95, n=8 (Caribbean form): Elongate lemon-shaped euryteles, 28.73-32.67 x 12.20-15.31, n=17	LG, SW Australian form: Spherical isorhizas, 12.48-15.96, n=23	Nematocysts not found	Nematocysts not found	Berger, 1900; Herein
Carybdea n. sp. A, holotype, California	1) Large oval euryteles, 21.05-28.28 x 11.60-15.46, n=31 2) Small oval isorhizas, 12.31-17.93 x 6.65-7.45, n=14	Not examined	Not examined	Not examined	Herein
Carybdea n. sp. B, paratype, Cape Town	1) Large oval euryteles, 19.33-31.12 x 11.98-16.39, n=33 2) Small oval isorhizas, 13.39-17.62 x 6.06-8.20, n=15	Spherical isorhizas, 15.53-20.64, n=40 Un-id oval ?a-mastigophore, 15.42-16.30 x 9.54-11.05, n=28	Not examined	Not examined	Herein
Tripedalia binata, non-type specimen, Darwin, NT	Moore: 1) Spherical atrichous isorhizas, 12 2) Stenoteles, 18-20 x 10-15 10:1 ratio of stenoteles to isorhizas LG: 1) Microbasic *p*-rhopaloids, 20.13-24.61 x 13.04-15.35, n=25 2) Microbasic euryteles, 14.66-16.55 x 9.94-11.31, n=12 3) Small oval isorhizas, 9.72-11.68 x 5.84-6.86, n=14	Spherical atrichous isorhizas, 12 LG: Spherical isorhizas, 11.67-15.99, n=37	Not reported; LG: Heterotrichous microbasic euryteles, width 6.08-6.66, n=7	Not reported LG: Heterotrichous microbasic euryteles, width 5.58-9.42, n=21	Moore, 1988; Herein

to be continued

TABLE 1 (continued).

	Tentacles	Exumbrellar warts	Gastric cirri	Manubrium	Citations
Tripedalia cystophora, non-type Puerto Rican specimen	Werner: 1) Holotrichous haplonemes, 9-14 x 6-7, 12-15 x 11-14 2) Heterotrichous microbasic euryteles, 16-23 x 12-16 LG: 1) Microbasic euryteles, 14.79-18.07 x 9.35-11.29, n=61 2) Small oval isorhizas, 10.86-12.29 x 5.65 x 6.24, n=6	Holotrichous haplonemes, 11-12 x 6-7, 14-15 x 12-14 LG: Not examined	Heterotrichous microbasic euryteles, 7-9 x 6-7 LG: Tiny microbasic euryteles, 5.44-6.57 x 3.88-4.97, n=14	Heterotrichous microbasic euryteles, 9-11 x 7-9 LG: Nematocysts no found	Werner, 1975; Herein
Carukia barnesi, paratype	Southcott: Egg-shaped tumiteles, 25-26 x 15-18 Hartwick: Microbasic *p*-mastigophores, 25-45 long LG: Lemon-shaped tumiteles, 22.88-26.93 x 14.59-16.46, n=8	Southcott: Spherical anisorhizas, 18-21 LG: Spherical isorhizas, 17.30-19.15, n=21	N/A	Southcott: Not reported LG: Not found	Southcott, 1967; Hartwick (ID poster); Herein
Carukia shinju, holotype	Egg-shaped tumiteles: 18.73-27.78 x 13.21-18.44, n=17	Spherical isorhizas, 17.56-24.27, n=27	N/A	Not examined	Gershwin, 2005b; Herein
Carukia n. sp., holotype (GBR)	Lemon-shaped tumiteles, with distal-facing spines only at distal end, 17.70-24.76 x 12.75-14.70, n=13	Not examined	N/A	Not examined	Herein
Malo maxima, holotype	Club-shaped sub-ovate microbasic *p*-mastigophores (Type 4); spines full length: 34.55-49.32 x 14.59-19.65, n=58	Spherical isorhizas, 23.59-29.82, n=49	N/A	Not examined	Gershwin, 2005b; Herein
Malo n. sp. A "Dampier Irukandji", holotype	Club-shaped sub-ovate microbasic *p*-mastigophores: 31.67-40.47 x 14.01-16.50, n=19	Not examined	N/A	Not examined	Herein
Malo n. sp. B "Halo Irukandji", holotype	Club-shaped sub-ovate microbasic *p*-mastigophores, 32.98-37.56 x 11.65-16.36, n=30	Not examined	N/A	Not examined	Herein
Malo n. sp. C "Pseudo-Irukandji", holotype	Club-shaped sub-ovate microbasic *p*-mastigophores (Type 4); spines terminal: 30.27-36.68 x 13.02-16.04, n=44	Spherical isorhizas, 20.10-24.87, n=45	N/A	Not examined	Herein
Gerongia rifkinae, holotype	O'Reilly: Lemon-shaped LG: Club-shaped sub-ovate microbasic *p*-mastigophores (Type 4); spines full length: 43.32-59.39 x 14.62-17.25, n=27	O'Reilly: Spherical LG: Spherical isorhizas, 21.15-24.77, n=21	N/A	Not examined	O'Reilly et al., 2001; Gershwin & Alderslade, 2005; Herein

to be continued

TABLE 1 (continued).

	Tentacles	Exumbrellar warts	Gastric cirri	Manubrium	Citations
"Morbakka", holotype, Port Douglas	Cleland & Southcott: Holotrichous isorhizas, un-id haplonemes. Hartwick: Microbasic *p*-mastigophores, 45-75; 2 types of football shaped isorhizas, 45 LG: 1) Club-shaped microbasic *p*-mastigophores (Type 4); spines scattered, 60.99-69.97 x 13.72-18.62, n=28 2) Large oval isorhizas of two types, one with loose tubule, one with tight tubule, 49.07-56.61 x 28.31-34.02, n=8	Hartwick: Sub-spherical isorhizas of two types, similar to those on tentacles; LG: 1) Spherical isorhizas, 27.41-30.41, n=28 2) Oval, poorly defined, with papillated outer surface and loosely wound tubule, as wide as type 1, but 1.5x as long	N/A	Not examined	Cleland & Southcott, 1965 (Pl. 2); Hartwick (ID poster); Herein
Tamoya *haplonema*, neotype	Club-shaped macrobasic rhopaloids with distal spines and naked annular swellings on proximal shaft, 30.21-47.17 x 10.85-16.43, n=26	Not examined	Not examined	Not examined	Herein
Chirodropus gorilla (non-type specimen from Ghana)	Similar to *Chironex* but smaller; size difference of nematocysts may be due to specimen size	N/A	Not reported	Not reported	Kingston & Southcott, 1960 [Note: dubious ID]
Chiropsalmus maculatus, holotype	1) Banana-form microbasic mastigophores, 42.68-61.39 x 6.18-12.30, n=27 2) Tiny spherical isorhizas, ca. 12x10, n=1	N/A	Not examined	Not examined	Herein
Chiropsalmus quadrumanus	Marques: Microbasic mastigophores, ellipsoid & ovoid isorhizas, medium & small microbasic euryteles LG: 1) Cigar-shaped microbasic *p*-mastigophores, 44.42-54.01 x 8.50-10.77, n=15 2) Football-shaped *p*-rhopaloids, 27.53-27.95 x 13.73-15.24, n=2 3) Small spherical *p*-rhopaloids, 12.31-13.44 x 11.26-11.81, n=4 4) Rod-shaped isorhizas, 9.09-12.53 x 3.96-4.88, n=11	Marques: Ovoid isorhizas, 5.4-7.8 x 3.0-5.4, n=12	Marques: Microbasic euryteles: Large, 21.0-22.8 x 13.2, n=2; medium, 13.0-16.0 x 8.9-14.4, n=20; and small, 7.8-10.2 x 4.8-7.2, n=20	Marques: Medium microbasic euryteles, 12.6-17.4 x 10.8-11.0, n=13	Calder & Peters (1975); Marques et al. (1997); Herein

to be continued

TABLE 1 (continued).

	Tentacles	Exumbrellar warts	Gastric cirri	Manubrium	Citations
Chiropsalmus n. sp. A (N. QLD), holotype	Kinsey: Identical to *Chironex*, though uniformly smaller Carrette: Same types as *Chironex*, except lacking large class mastigophores; mastigophores 35-55 long; Fewer mastigophores and more isorhizas than *Chironex* LG: 1) Cigar-shaped microbasic *p*-mastigophores, 38.90-45.98 x 9.39-10.26, n=6 2) Large football-shaped isorhizas, 20.77-24.07 x 11.76-13.77, n=7 3) Small oval “beehive” isorhizas, 8.61-9.70 x 6.77-7.89, n=14 4) Small sub-spherical *p*-rhopaloids, 9.20-10.09 x 7.93-8.68, n=3 5) Small rod-shaped isorhizas, 10.97-13.08 x 3.64-4.64, n=16	N/A	Not examined	Not examined	Kinsey, 1986; Carrette et al., 2002; Hartwick (ID poster); Herein
Chiropsalmus n. sp. B (Gove), holotype	Currie et al.: Baseball bat-shaped microbasic mastigophores similar to *Chironex*; trirhopaloids LG: 1) Cigar-shaped microbasic *p*-mastigophores, 39.28-44.84 x 8.79-10.92, n=12 2) Large oval *p*-rhopaloids, 21.27-26.29 x 12.73-14.37, n=10 3) Small oval “beehive” isorhizas, 9.04-9.94 x 6.88-7.71, n=5 4) Small rod-shaped isorhizas, 13.21-14.20 x 6.54-7.27, n=3	N/A	Not examined	Not examined	Currie et al., 2002; Herein
Chiropsoides buitendijki, syntype speicmen	1) Club-shaped microbasic *p*-mastigophores, 85.95-94.14 x 11.14-14.55, n=12 2) Football-shaped microbasic *p*-rhopaloids, 39.71-40.69 x 16.57-17.47, n=2 3) Football-shaped trirhopaloids, 37.31-41.43 x 16.01-17.86, n=14	N/A	Not examined	Not examined	Herein

to be continued

TABLE 1 (continued).

	Tentacles	Exumbrellar warts	Gastric cirri	Manubrium	Citations
Chiropsoides n. sp., holotype, Sri Lanka	1) Hockey-stick-shaped microbasic *p*-mastigophores, 60.79-78.92 x 9.51-11.78, n=11 2) Small oval "beehive" isorhizas, 9.26-11.26 x 7.39-8.30, n=6 3) Small rod-shaped isorhizas, 14.34-15.25 x 3.76-4.22, n=3 4) Small spherical isorhizas, 6.97-9.71, n=11 5) Very small spherical isorhizas, 3.53-4.21, n=8	N/A	Not examined	Not examined	Herein
Chironex fleckeri, non-type juvenile from Townsville	Cleland & Southcott: Elongate microbasic mastigophores, ca 50 long. Rifkin & Endean: Microbasic *p*-mastigophores 22-90 long, large and small heterotrichous microbasic euryteles, holotrichous and atrichous isorhizas. Hartwick: Cigar-shaped microbasic *p*-mastigophores 50-95 long; straight-sided isorhizas 12 long; sub-spherical euryteles 11; football-shaped euryteles 20-35 long. Williamson et al.: At least 6 types, including 2 size classes of mastigophores Carrette: Atrichous and holotrichous isorhizas, large and small trirhopaloids, and two sizes of microbasic mastigophores. LG (6 cm BH): 1) Type 3 banana-form microbasic *p*-mastigophores, 64.90-77.96 x 9.58-12.08, n=25; in 15cm BH: 57.38-92.24 x 9.87-13.83, n=27 2) Large oval *p*-rhopaloids, 31.50-38.77 x 14.53-19.03, n=11 4) Small sub-spherical *p*-rhopaloids, 11.14-17.31 x 8.64-13.26, n=19 5) Small rod-shaped isorhizas, 12.00-19.55 x 4.47-6.55, n=55 6) Ovoid isorhizas with spiraled tubule, 13.19-16.94 x 8.08-9.94, n=4	N/A	Not examined	Not examined	Cleland & Southcott, 1965 (Pl. 2, 3); Rifkin & Endean 1983 (excellent description of types); Hartwick (ID poster); Williamson et al., 1996 (p. 156); Carrette et al., 2002; Herein

to be continued

TABLE 1 (continued).

	Tentacles	Exumbrellar warts	Gastric cirri	Manubrium	Citations
Chironex n. sp. A, Broome WA, holotype	1) Banana-form microbasic *p*-mastigophores with sparsely scattered spines, 48.81-92.26 x 8.34-12.77, n=22 2) Large oval trirhopaloids, 38.94-43.94 x 19.07-19.76, n=6 3) Small sub-spherical *p*-rhopaloids, 9.39-11.94 x 8.69-10.12, n=7 4) Small rod-shaped isorhizas, 12.86-16.61 x 4.03-5.42, n=15	N/A	Not examined	Not examined	Herein
Chironex n. sp. B, Okinawa "volcano", holotype	Oba: 8 types: Microbasic mastigophore; large and small trirhopaloid; holotrichous isorhiza; ellipsoidal isorhiza; ovoid isorhiza; large ovoid isorhiza; microbasic eurytele LG: 1) Banana-form microbasic *p*-mastigophores with sparsely scattered spines, 33.39-69.76 x 6.78-10.44, n=42 2) Large oval *p*-rhopaloids, 31.49-38.77 x 14.53-19.03, n=13 3) Small sub-spherical *p*-rhopaloids, 11.14-17.31 x 8.64-13.26, n=20 4) Oval "beehive" isorhizas, 10.52-12.57 x 7.98-8.30, n=2 5) Small rod-shaped isorhizas, 9.94-19.55 x 4.23-6.55, n=60	N/A	Tiny euryteles, 4.73-5.52 diameter, n=9	Not examined	Oba et al., 2004; Herein

In other taxa (e.g., *Chironex fleckeri* (Plate 31, compare A with C, and compare D upper right and lower left); Okinawan "*Chiropsalmus quadrigatus*" (Oba et al. 2004, fig. 2 ME); *Tripedalia binata* (Plate 13, compare A large and small), the undischarged nematocyst has a v-shaped notch of *p*-mastigophore rhabdoids, whereas the discharged nematocyst has the lobed shaft of rhopaloids. These are herein given the special designation '*p*-rhopaloids' to denote this confusing morphology.

The tentacular nematocysts of *Carukia* have historically been regarded as rhopaloids (Southcott 1967; Rifkin and Endean 1983). However, their shafts are far more cylindrical than those of *Carybdea* or *Alatina*, leading one to wonder whether they might be more appropriately regarded as mastigophores.

Cubozoan cnidomes

A summary of cnidomes of cubomedusae is given in Table 1; an image catalogue of cubozoan cnidae is given in Plates 1–34. The cnidomes of nearly all valid species plus numerous undescribed forms are given; exceptions are:

- *Carybdea marsupialis* Linnaeus: a suitable specimen from near the type locality (Rimini, Italy) could not be obtained
- Most of the species in the genus *Alatina* (i.e., the "*Carybdea alata*" group)
- *Chirodropus gorilla* Haeckel: the taxonomy of this species is problematical, and no specimens are currently available that are indisputably identifiable as this species. The results of Kingston and Southcott (1960) are presented in the table for comparative purposes, but I have examined Southcott's specimens and they are not *C. gorilla* (Gershwin, unpublished notes).
- *Chirodropus palmatus* Haeckel: no extant specimens are known of this species, which has not been seen since the original
- *Chiropsalmus zygonema* Haeckel: no extant specimens are known of this species, which has not been seen since the original
- *Chiropsalmus quadrigatus* Haeckel: nematocysts were not sampled from the holotype, and other specimens were not used because there is doubt as to the true identity of this species (Gershwin, In review).

Remarks for taxonomy

It is with some reluctance that I present this synopsis of cubozoan cnidomes, with concern that it may be used inappropriately; this is a beginning guide based on type material, but only by knowing the full range of variation will we be able to judge the reliability of cnidomes for species diagnosis. First, although I believe that nematocysts are interesting and that it is important to be thorough, they are nonetheless peripheral to current species diagnoses in the Cubozoa, i.e., accurate species identification can be obtained from structural characters alone. While it is theoretically possible that eventually additional cryptic taxa will be distinguished on the basis of their cnidomes, the philosophical issue of cryptic taxa is beyond the scope of this paper. It should be noted, however, that cnidomes are not equally unique among cubozoan taxa; while most genera of Carybdeida can easily be diagnosed with nematocysts, and even some species, the same is not as true for the Chirodropida.

Second, most of the specimens I have had available for examination, and no doubt most of the specimens that others will seek to identify, are preserved. Different preserving methods may have different effects on the shape and size of the nematocysts, potentially leading to inconsistent results; furthermore, many preservation methods inactivate the firing mechanism, resulting in unidentifiable shaft structure, on which proper identification relies. Accurate nematocyst taxonomy is generally based on shaft morphology of discharged capsules, i.e., length of the shaft relative to the capsule, number and position of the shaft swellings, and position of spines (Weill 1934; Halstead 1965; Mariscal 1971; Calder 1974; Williamson et al. 1996; Östman 2000); a notable exception to this is the *p*- and *b*- typing of mastigophores, which is based on the undischarged shaft morphology. While the nematocyst type is determined primarily by the discharged anatomy, the nematocyst size is measured on undischarged capsules for comparison between species. Although clearly different capsule shapes and tubule winding patterns can be found in different taxa, these are often grouped under the same nematocyst category because there is currently no system for recognizing these types of differences. For example, the dominant nematocysts of *Chironex* and *Malo* are both classified as microbasic *p*-mastigophores, but a more sensitive classification system would recognize that their capsule shape and tubule winding patterns are extremely different and diagnostically useful. Therefore, one must be vigilant about describing these features so that they can eventually be incorporated into an accurate and comprehensive system based on discharged and undischarged morphology.

Nonetheless, I think there is value in knowing as much about a species as possible, i.e., having more tools in our proverbial toolbox. The synopsis of nematocyst types and measurements given in Table 1 is only a clumsy first step toward a thorough study, but does serve to illustrate differences consistent with phylogenetic results elsewhere (Gershwin 2005a). A thorough treatment will include parallel measurements of nematocysts from different locations on the tentacles and bell, and from numerous specimens of different sizes and states of maturity; furthermore, it is imperative to sample the missing taxa. Elucidating the range of variability within species, and thus the accuracy of nematocyst diagnosis, should be a top priority of future studies.

Remarks for sting identification

In cases of fatality, syndrome-species linkages, or simple curiosity, it is sometimes desirable to attempt to identify species based on nematocysts left behind during sting events. However, skin scrapings or sticky-tape samples must be interpreted with caution; while the recovered nematocysts may be able to rule in or out certain species, conclusive identification at the species level is often unrealistic. Many closely related species have similar cnidomes, and not all nematocyst types that characterize a species are necessarily left behind in a sting event. Furthermore, cnidomes can change through ontogeny (Carrette et al. 2002; Oba et al. 2004), and most species have different ratios and sizes, and often different nematocyst types, on different parts of the body and even at different locations on the tentacles (L. Gershwin, unpublished). Finally, confusing artefacts may be produced in the skin-scraping and preparation process, as elucidated by Rifkin (in Williamson et al., 1996); if forensic identification is going to be attempted, the best chance appears to be from a sticky-tape sample taken as soon after the sting as possible to avoid nematocyst loss, ideally while still at the beach (Currie and Wood 1995; Williamson et al. 1996).

Several recent attempts at forensic identification illustrate this problem. First, Little and Seymour (2003) linked the nematocysts from a severe Irukandji envenomation to a new species of Irukandji originally identified by me and held in the Queensland Museum collection awaiting publication (*Carukia* n. sp. herein, Plate 17). However, the recovered nematocysts could have been left by any of several species in the North QLD region; they are similar to two local species of *Carukia* (one named, and one undescribed; see Plates 15, 17), and two local species of *Alatina* (see Plates 1–3), and at least two local species of *Carybdea* (see Plates 6, 8). *Carybdea* spp. are not known to give Irukandji syndrome. The syndrome characteristics (Mulcahy 1999; Little et al. 2001; Little and Seymour 2003) would seem to preclude this from having been *Carukia*, in which the syndrome is typically slow to onset, typically characterized by nausea and vomiting, and typically does not cause severe hypertension (Gershwin 2005a). Of the two remaining species, *Alatina mordens* has been demonstrated to cause Irukandji syndrome (Campbell 2005; Gershwin 2005c), and *A. rainensis*, when tested, did not (H. Taylor, pers. comm. 2004). Furthermore, I have studied three specimens caught at the time of the sting in question, and they are all *Alatina mordens* Gershwin. Thus, while we do not have conclusive proof that *Alatina mordens* was the stinger, there is sufficient evidence to question whether the new species of *Carukia* was, as determined by Little and Seymour (2003).

Second, Huynh et al. (2003) provided cnidome evidence that the stinger that killed an American tourist in 2002 could not have been *Carukia barnesi*; however, they did not assign the nematocysts to any particular known or unknown species. The nematocyst figured is unlikely to have come from any species other than those in the 'Pseudo-Irukandji' group (e.g., the undescribed 'Pseudo-Irukandji' or 'Halo Irukandji' from Queensland) (Gershwin 2005a; Gershwin 2005b), which has a tentacular monocnidome of extremely characteristic nematocysts, namely club-shaped Type 4 microbasic *p*-mastigophores (Plates 18A, B, 19, 20, 21A–C). Species in the 'mild Irukandji' group (i.e., 'Morbakka' and *Gerongia rifkinae* Gershwin and Alderslade) have similar nematocysts, but have been experimentally and clinically demonstrated to give only mild Irukandji syndrome (Fenner et al. 1985; Williamson et al. 1996; O'Reilly et al. 2001; Gershwin and Alderslade 2005), and are thus unlikely to have been the cause of a fatal sting; furthermore, neither are known from offshore. Unfortunately, the recovered nematocyst is incompletely discharged, and thus cannot be identified to species.

Third, Wiltshire and her colleagues (2000) identified their subject as *Carukia barnesi*, but even a casual perusal of its original description would have indicated otherwise. The nematocysts they presented were elongate and club-shaped, as in the 'Pseudo-Irukandji' group, rather than short and lemon-shaped, as in *Carukia*. Furthermore, the specimen in their photographs is far too large and robust to be *Carukia*, the tentacles are too thick, and the bell is too evenly rounded; these characters are all consistent with species in the

'Pseudo-Irukandji' group. Hartwick (unpublished ID poster) made the same mistake, identifying his material as *Carukia barnesi*, when in fact, it is more likely to have been the local *Carybdea xaymacana* or 'Pseudo-Irukandji' based on his nematocyst measurements.

Phylogenetic comments

Several interesting phylogenetic patterns are suggested by this study. First, there is a reliable difference in cnidomes between the Chirodropida and Carybdeida, both in the number of nematocyst types and in the categories present. Interestingly, in the Chirodropida, two members of the Chiropsalmidae have short, stubby mastigophores (see Plates 27, 28), whereas the corresponding cnidae in other chiropsalmids more resemble the chirodropids. In the Carybdeida, the Carybdeidae and Tamoyidae cnidomes are each distinctive, but the primary nematocysts of the Alatinidae and Tripedaliidae are similar. Furthermore, many members of the Carybdeidae have both rhopaloids and isorhizas present on the tentacles, but this appears to be less consistent in the Alatinidae and Tripedaliidae, and almost non-existent in the Tamoyidae. It is not clear at this time what these patterns mean in terms of phylogenetic interpretation, but future studies should seek to include nematocysts to address these questions.

Cautionary notes

Safety. Many species of cubozoans can produce severe medical complications. Chemical preservation typically inactivates nematocysts; however, handling unpreserved cubozoan specimens or their nematocysts must be done with great care.

Reliability. The species represented herein are just a sample of the total (largely undescribed) cubozoan species diversity. Furthermore, I have targeted type specimens for taxonomic reasons, but the degree to which these may represent the range of species variation is beyond the scope of this paper. Therefore, users of these data are cautioned to consider variation within species, position on the body, and stage of development.

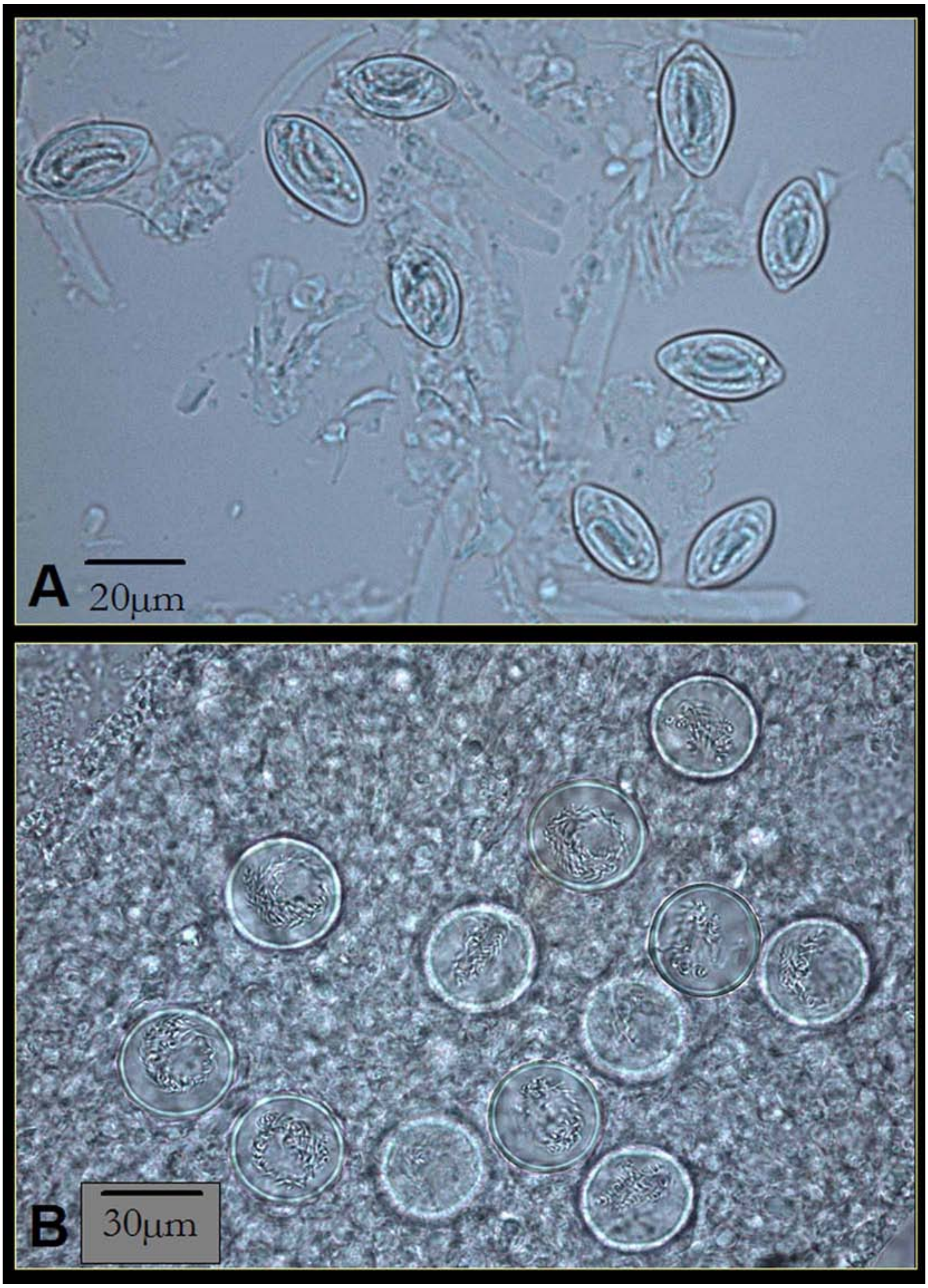

PLATE 1. *Alatina mordens* Gershwin (holotype), tentacular and bell nematocysts. A. Lemon-shaped euryteles, tentacle. B. Spherical isorhizas, bell.

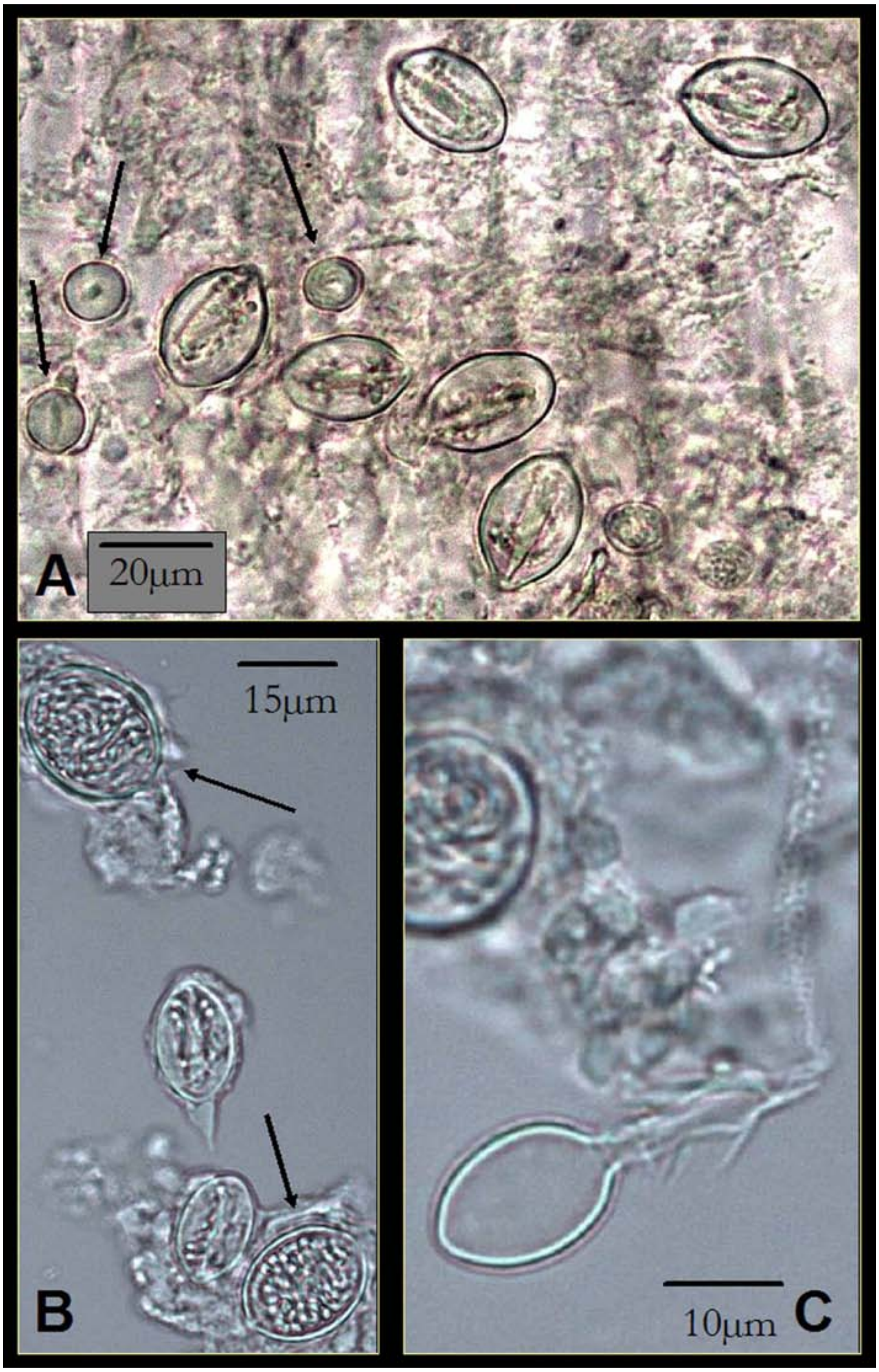

PLATE 2. *Alatina rainensis* Gershwin (holotype), tentacular nematocysts. A, Egg-shaped microbasic euryteles and tiny sub-spherical microbasic ?amastigophores. B, Egg-shaped microbasic euryteles & large oval isorhizas (arrows). C. Microbasic eurytele, discharged, upper right, and two isorhizas, lower left.

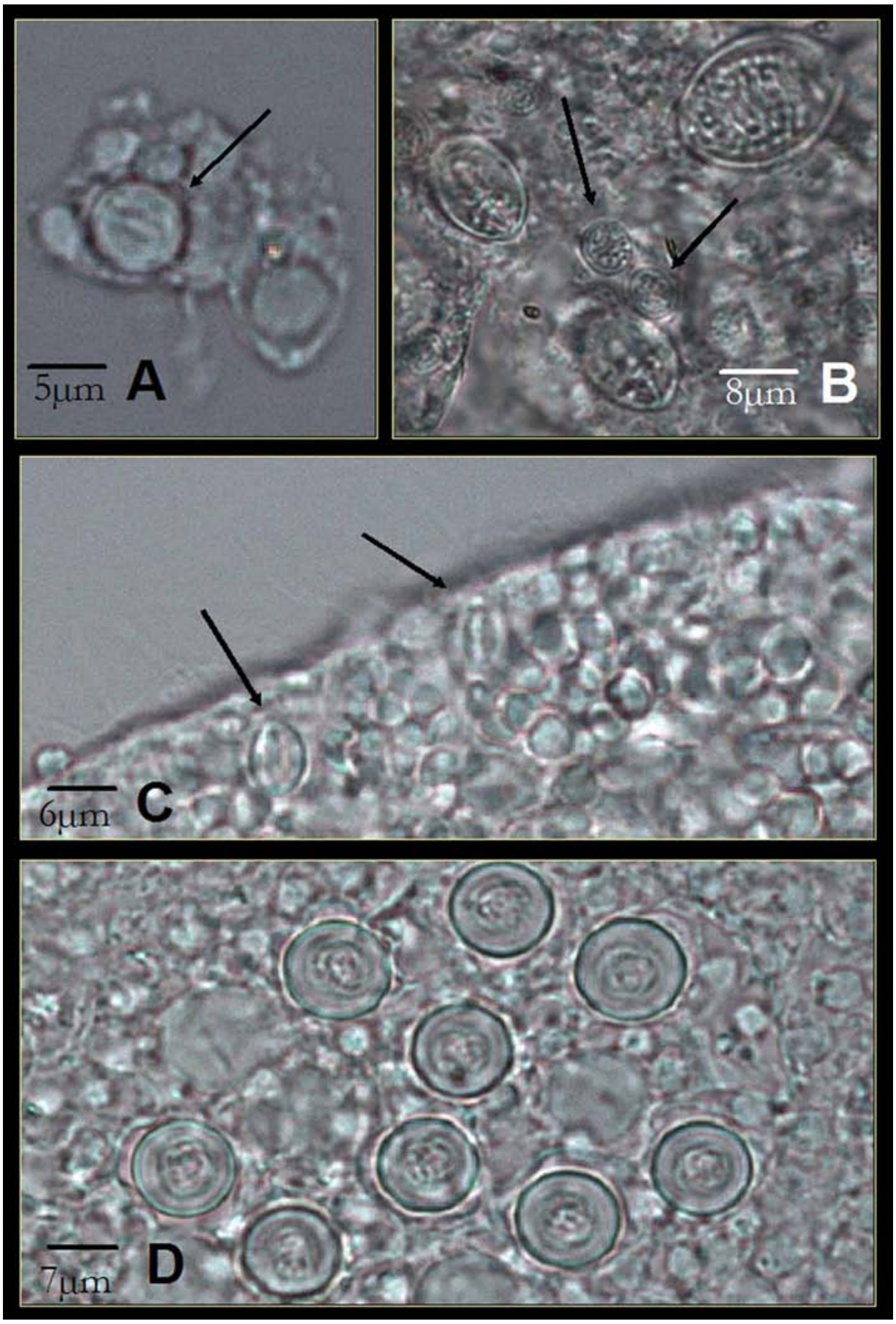

PLATE 3. *Alatina rainensis* Gershwin (holotype), tentacular, phacellar and bell nematocysts. A. Sub-spherical microbasic ?amastigophore (arrow), tentacle. B. Small, ovate isorhizas (arrows) and large oval isorhizas, tentacle. C. Microbasic euryteles (arrows), gastric cirrus. D. Spherical isorhizas, bell.

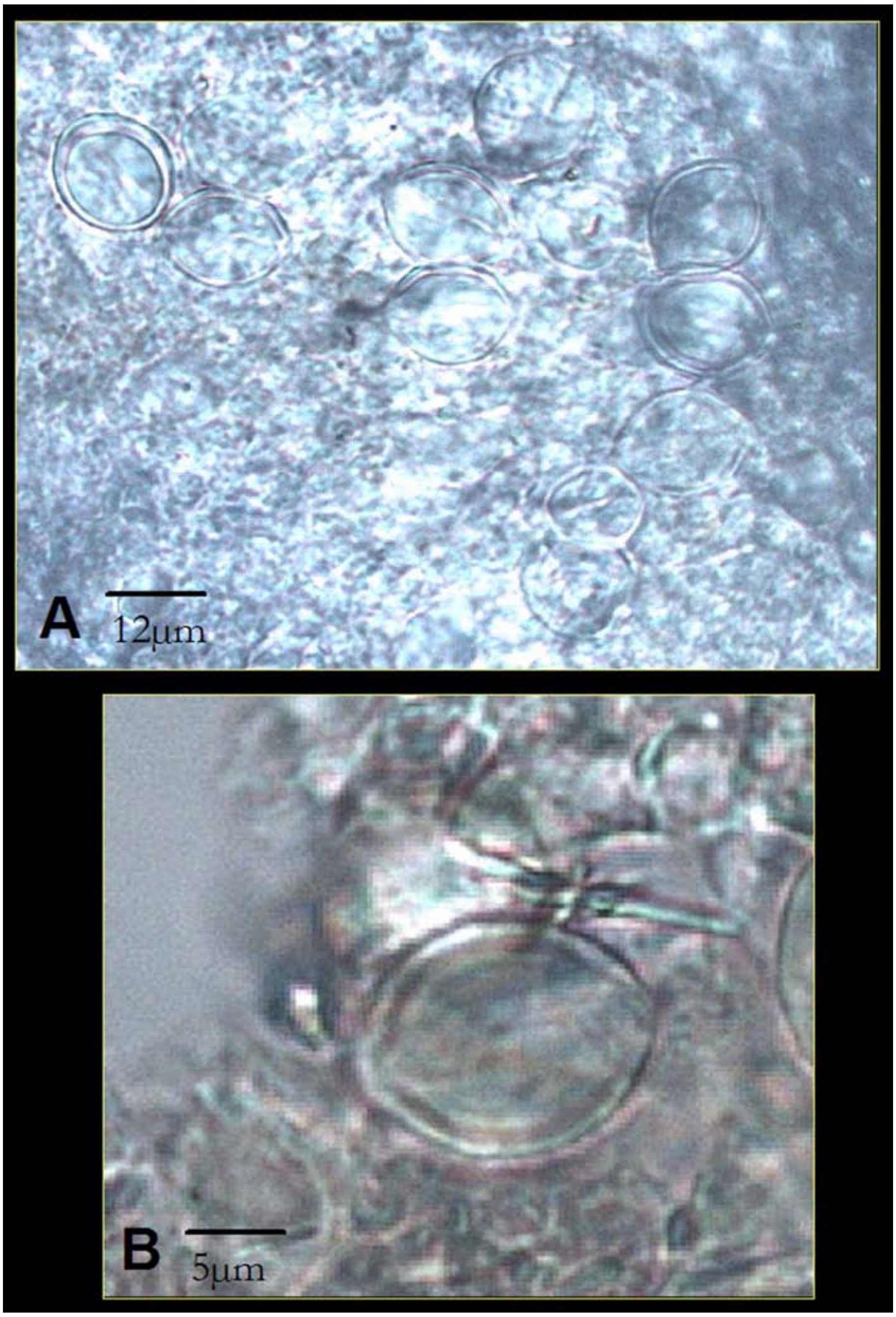

PLATE 4. *Manokia stiasnyi* (Bigelow) (holotype), tentacular nematocysts. A and B. Sub-spherical euryteles with a thickened capsule wall.

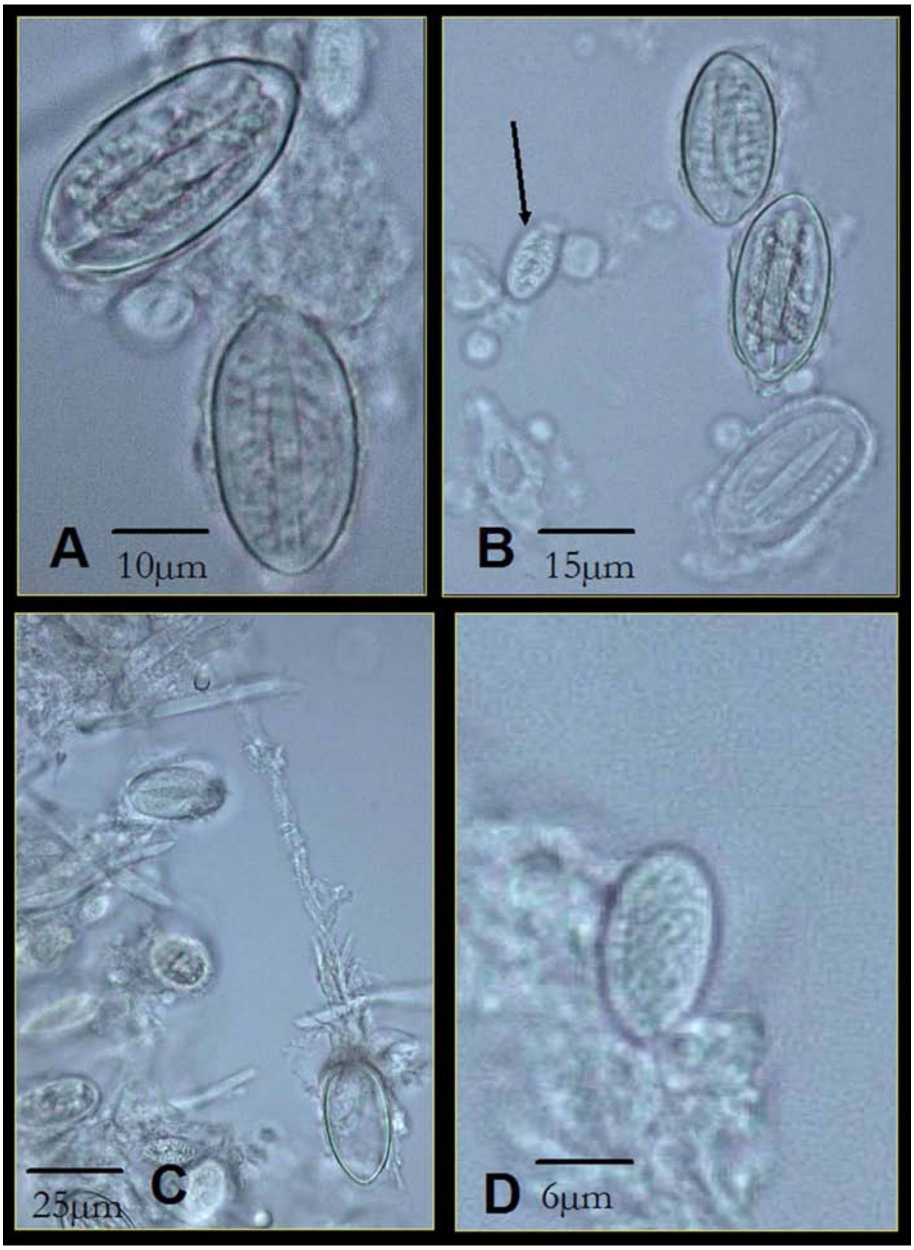

PLATE 5. *Carybdea mora* Kishinouye (neotype), tentacular nematocysts. A and B. Oval microbasic *p*-rhopaloids (left, with v-shaped notch) and elongate oval microbasic euryteles (right, lacking v-shaped notch) and tiny isorhiza (arrow). C. Microbasic *p*-rhopaloid, discharged. D. Tiny isorhiza.

PLATE 6. *Carybdea rastonii* Haacke (neotype), tentacular nematocysts. A. Euryteles and small isorhizas (arrows). B. Egg-shaped microbasic eurytele. C. Small isorhiza.

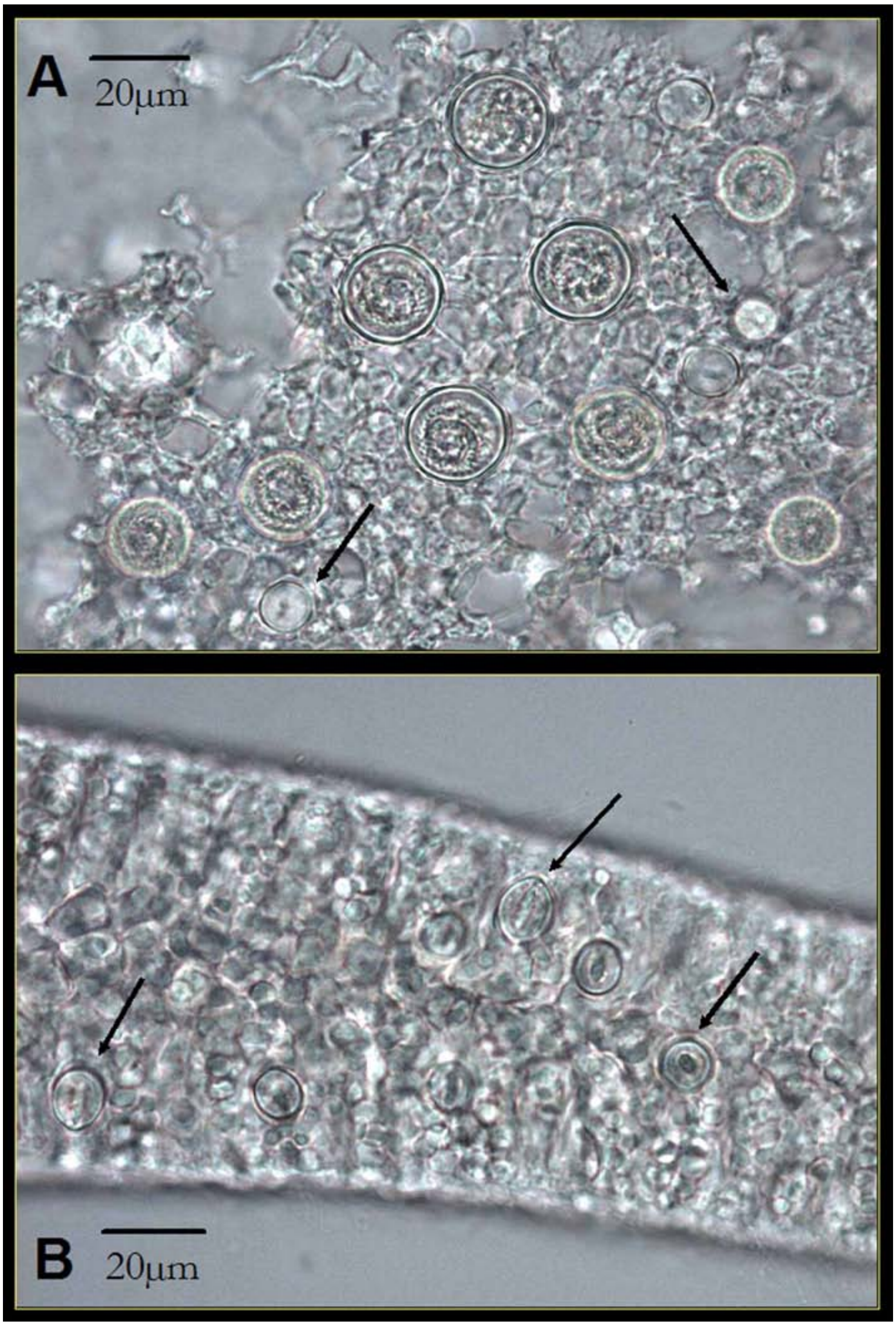

PLATE 7. *Carybdea rastonii* Haacke (neotype), bell and phacellar nematocysts. A. Spherical isorhizas and tiny euryteles (arrows), bell. B. Tiny euryteles (arrows), gastric cirrus.

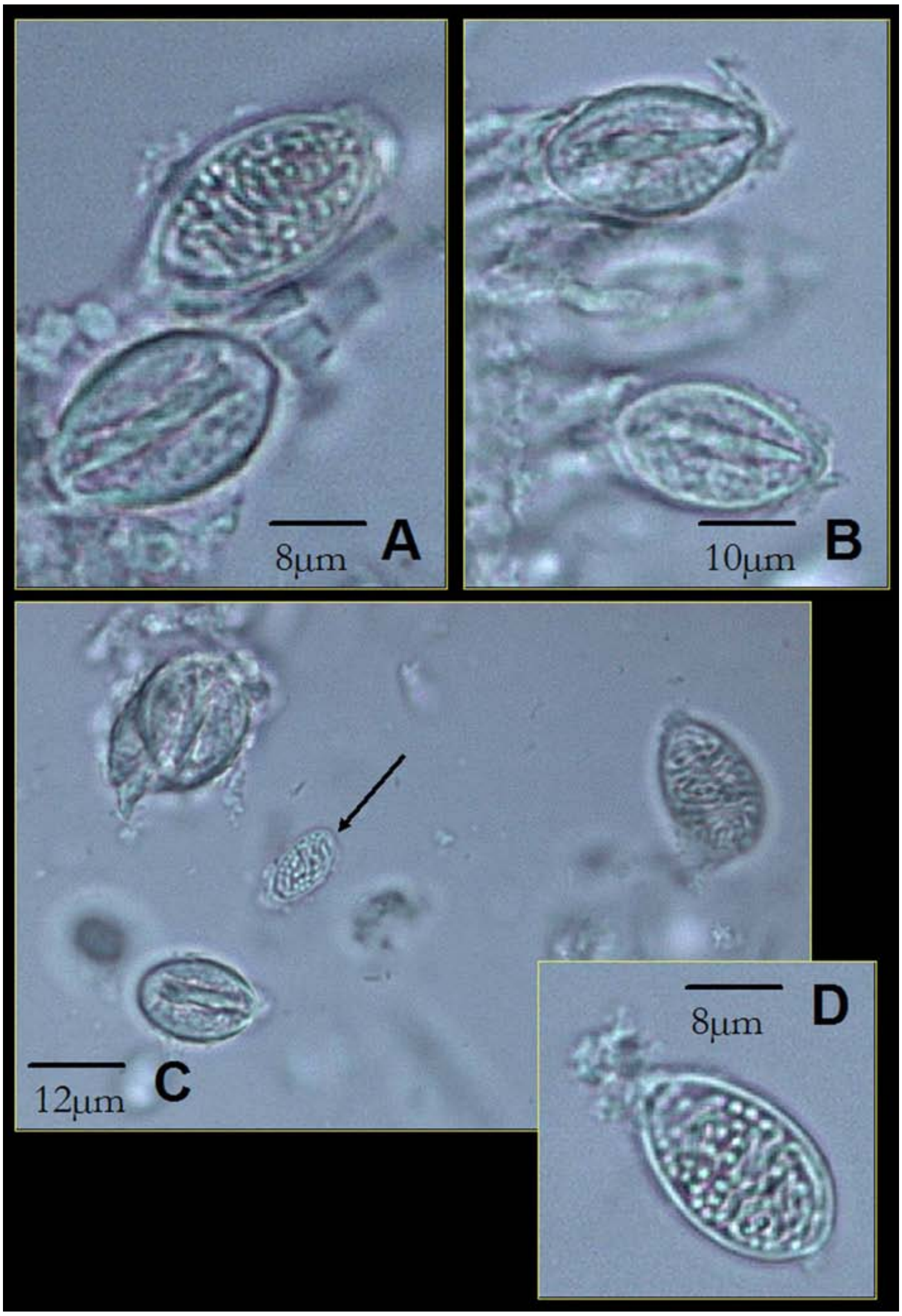

PLATE 8. *Carybdea sivickisi* Stiasny (non-type specimen from Townsville), tentacular nematocysts. A. Egg-shaped microbasic euryteles (lower) and isorhiza (upper). B. Microbasic euryteles. C. Sub-spherical p-mastigophore (lower left) and tiny isorhiza (arrow), plus eurytele (upper left) and isorhiza (right). D. Isorhiza.

PLATE 9. *Carybdea xaymacana* Conant (non-type specimen, Puerto Rico), tentacular nematocysts. A and B. Elongate lemon-shaped euryteles.

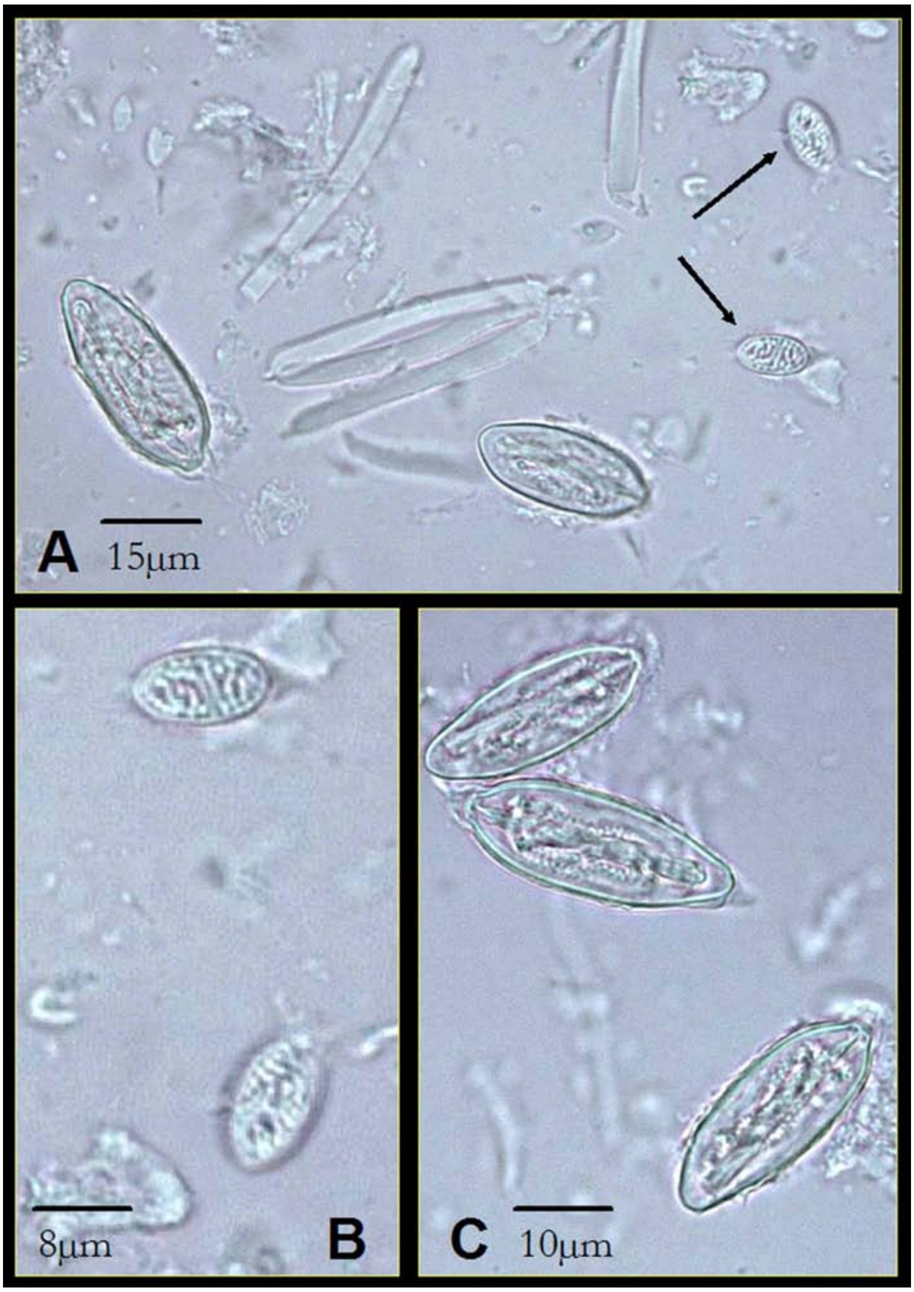

PLATE 10. *Carybdea* cf. *xaymacana* Conant (non-type specimen, Busselton, Western Australia), tentacular nematocysts. A. Elongate lemon-shaped euryteles and small isorhizas (arrows). B. Small isorhizas (from A, enlarged). C. Euryteles.

PLATE 11. *Carybdea* n. sp. (holotype, California), tentacular nematocysts. A and B. Large oval euryteles and small oval isorhizas (arrows).

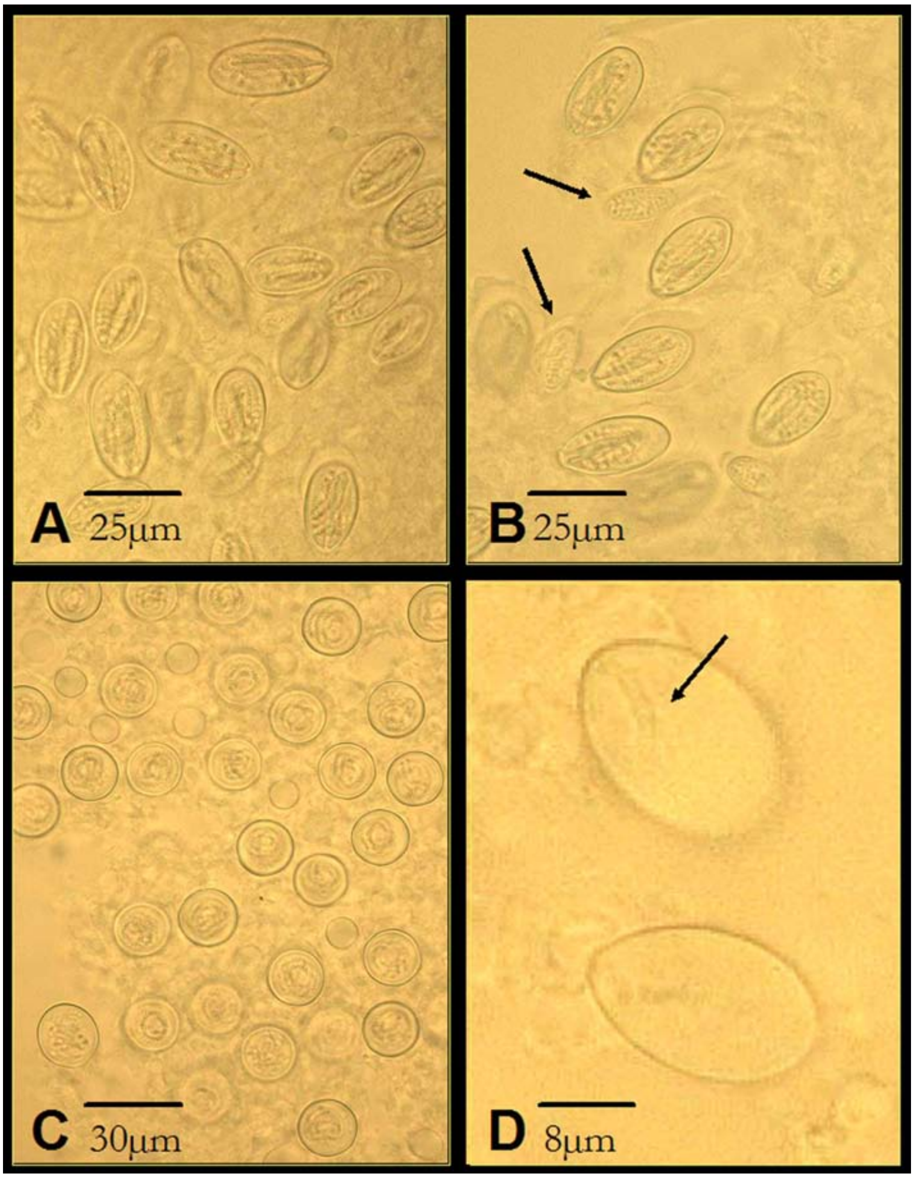

PLATE 12. *Carybdea* n. sp. (paratype, Cape Town), tentacular and bell nematocysts. A. Large oval euryteles, tentacle. B. Small oval isorhizas (arrows) and euryteles, tentacle. C. Spherical isorhizas (large) and un-identified nematocysts (small, polar view), bell. D. Un-identified nematocysts (lateral view), with short flexible shaft but lacking tubule (shaft indicated with arrow), bell.

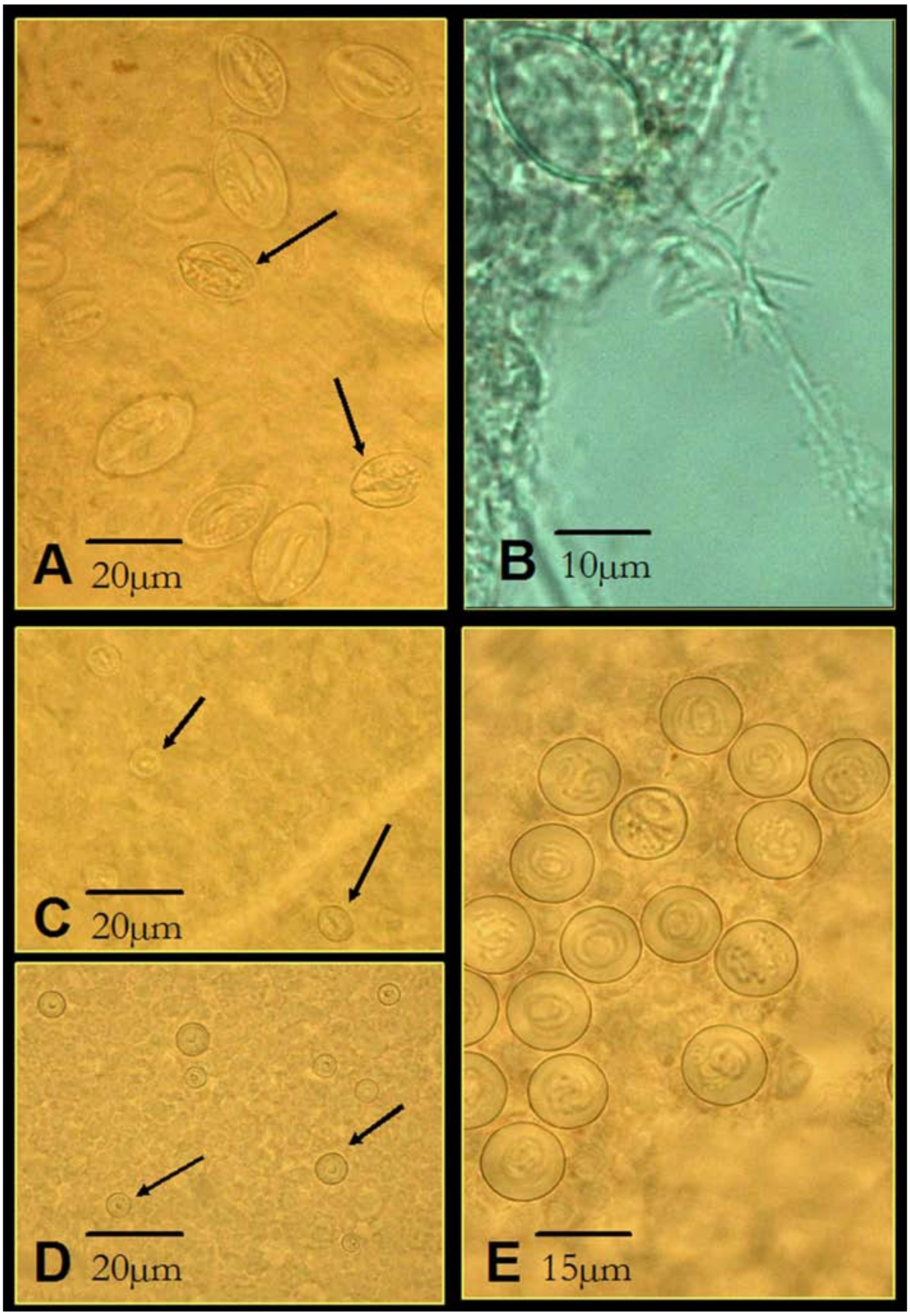

PLATE 13. *Tripedalia binata* Moore (non-type specimen, Northern Territory), tentacular, bell, phacellar, and manubrial nematocysts. A. Large microbasic *p*-rhopaloids and small microbasic euryteles (arrows), tentacle. B. Microbasic *p*-rhopaloid, discharged. C. Tiny microbasic euryteles (arrows), gastric cirrus. D. Tiny microbasic euryteles (arrows), polar view, lip. E. Spherical isorhizas, bell.

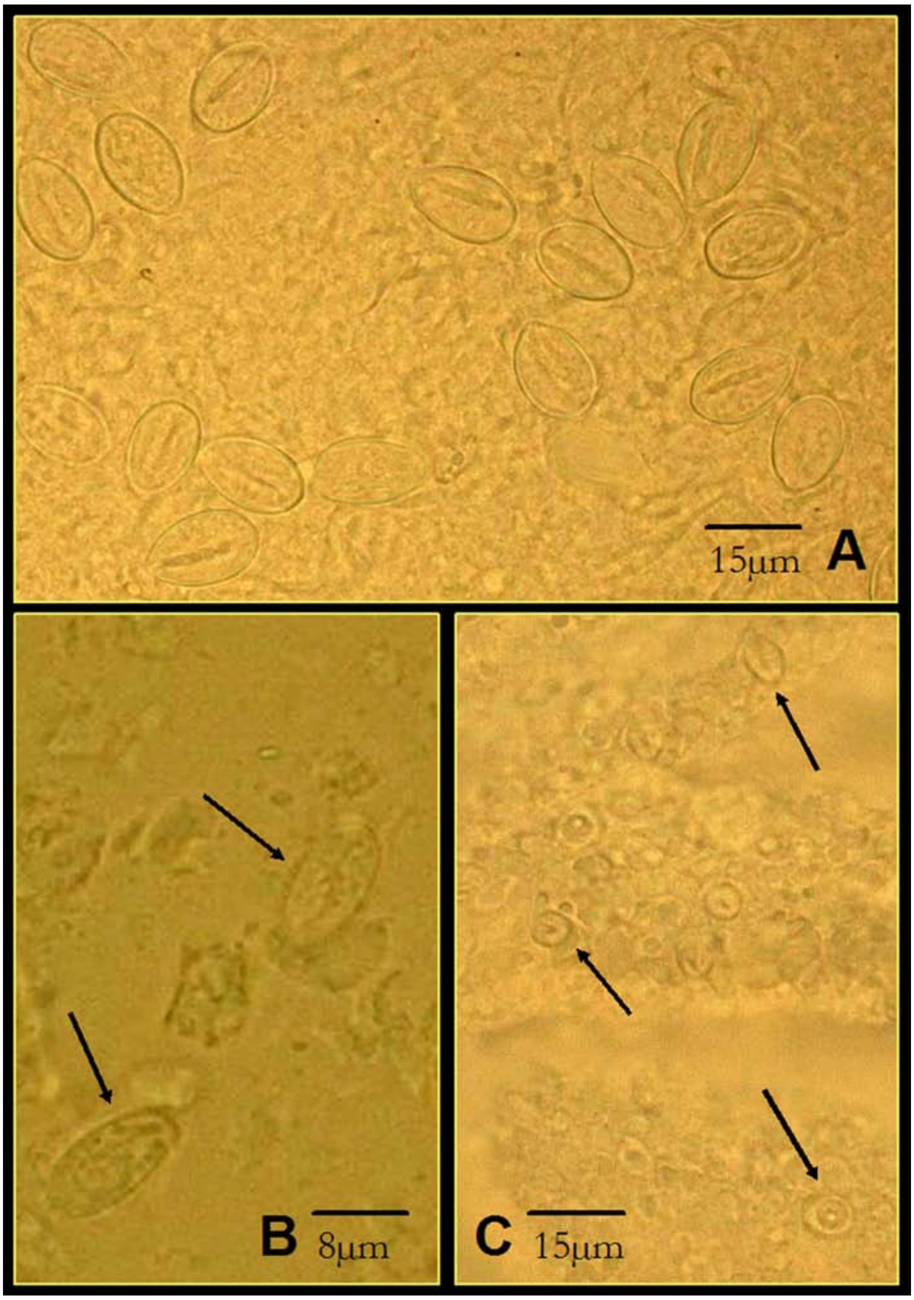

PLATE 14. *Tripedalia cystophora* Conant (non-type specimen, Puerto Rico), tentacular and phacellar nematocysts. A. Microbasic euryteles, tentacle. B. Small oval isorhizas (arrows), tentacle. C. Tiny microbasic euryteles (arrows), polar view, gastric cirrus.

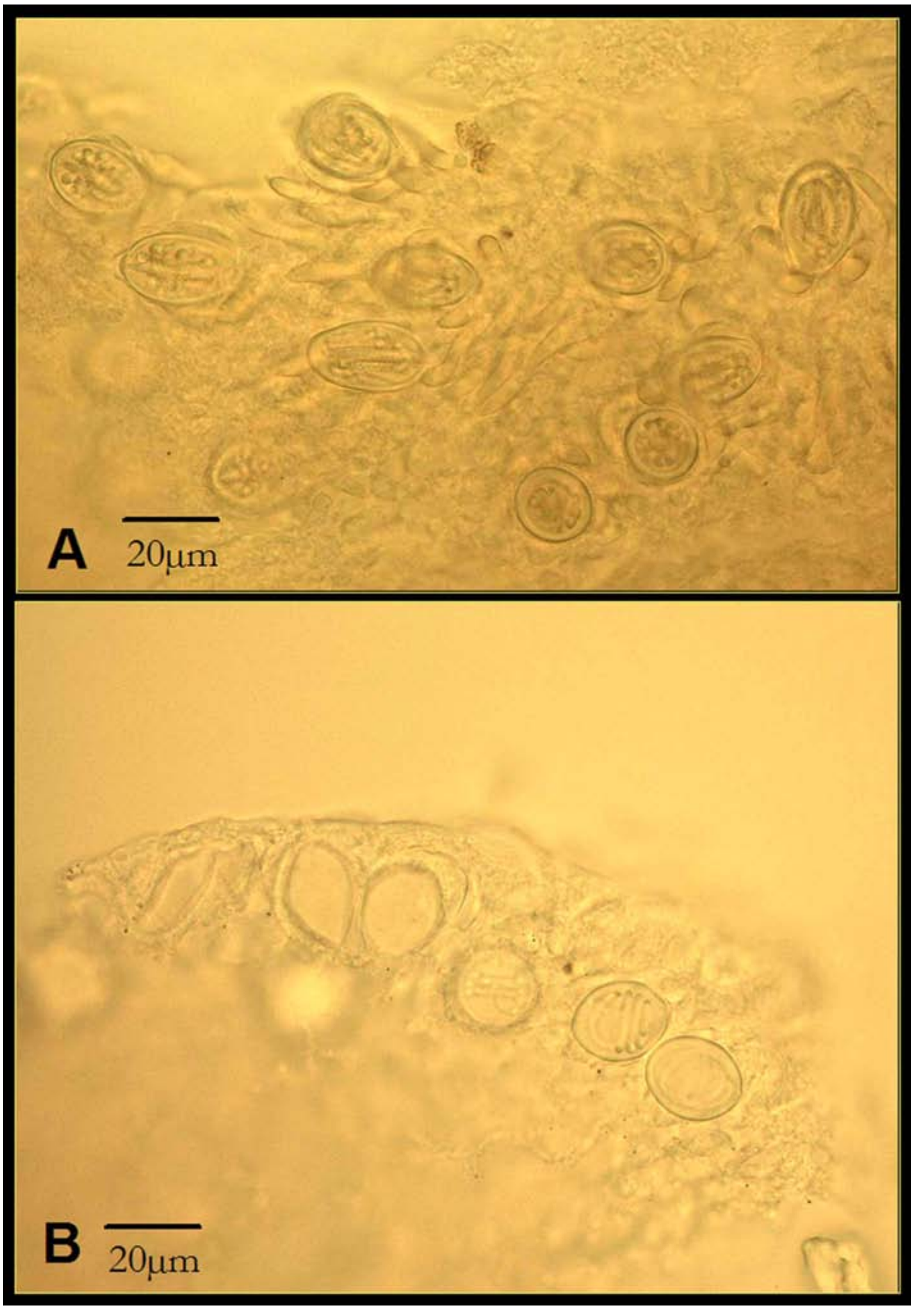

PLATE 15. *Carukia barnesi* Southcott (paratype SAM H346), tentacular and bell nematocysts. A. Lemon-shaped tumiteles, tentacle. B. Spherical isorhizas, bell.

PLATE 16. *Carukia shinju* Gershwin (holotype), tentacular and bell nematocysts. A. Egg-shaped tumiteles. B. Spherical isorhizas, bell. C. Tumitele, discharged.

PLATE 17. *Carukia* n. sp. (holotype, Great Barrier Reef), tentacular nematocysts. A. Lemon-shaped tumiteles. B. Tumitele, discharged.

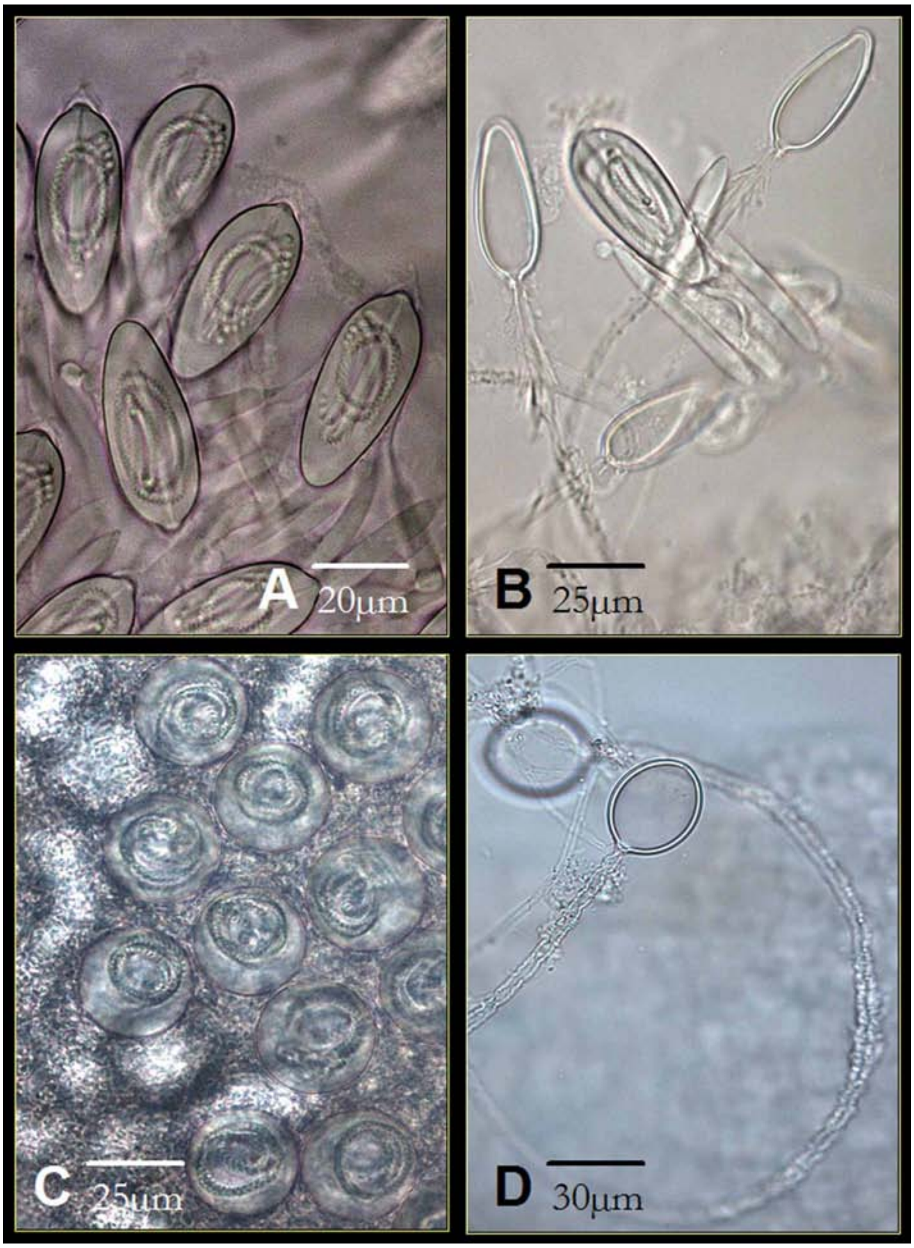

PLATE 18. *Malo maxima* Gershwin (holotype), tentacular and bell nematocysts. A and B. Club-shaped Type 4 microbasic *p*-mastigophores, undischarged and discharged, tentacle. C. Spherical isorhizas, bell. D. Bell isorhizas, discharged.

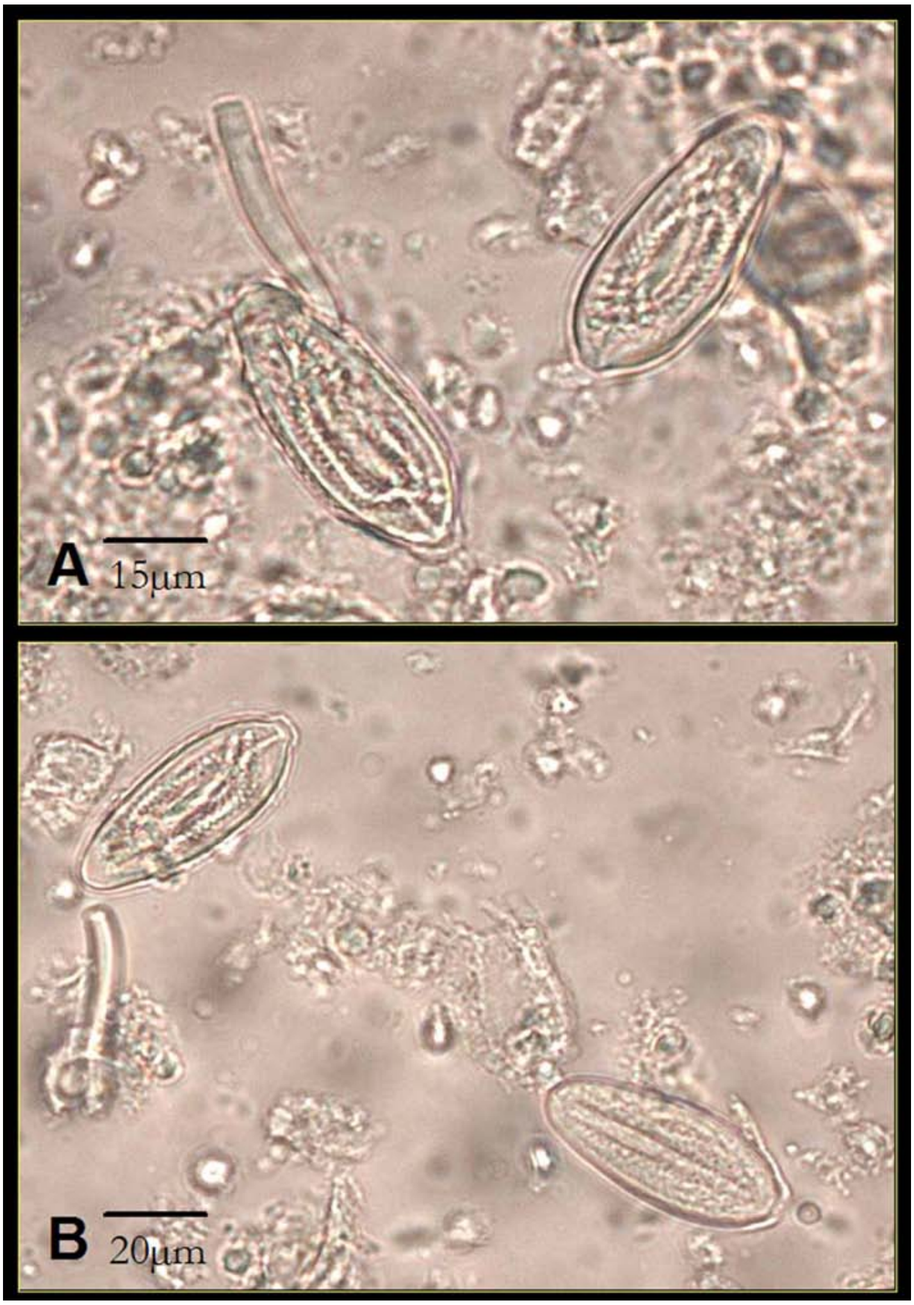

PLATE 19. *Malo* n. sp. A. “Dampier Irukandji” (holotype), tentacular nematocysts. A and B. Club-shaped microbasic *p*-mastigophores.

PLATE 20. *Malo* n. sp. B. "Halo Irukandji" (holotype), tentacular nematocysts. A and B. Club-shaped microbasic *p*-mastigophore, tentacle (B, with spines broken off).

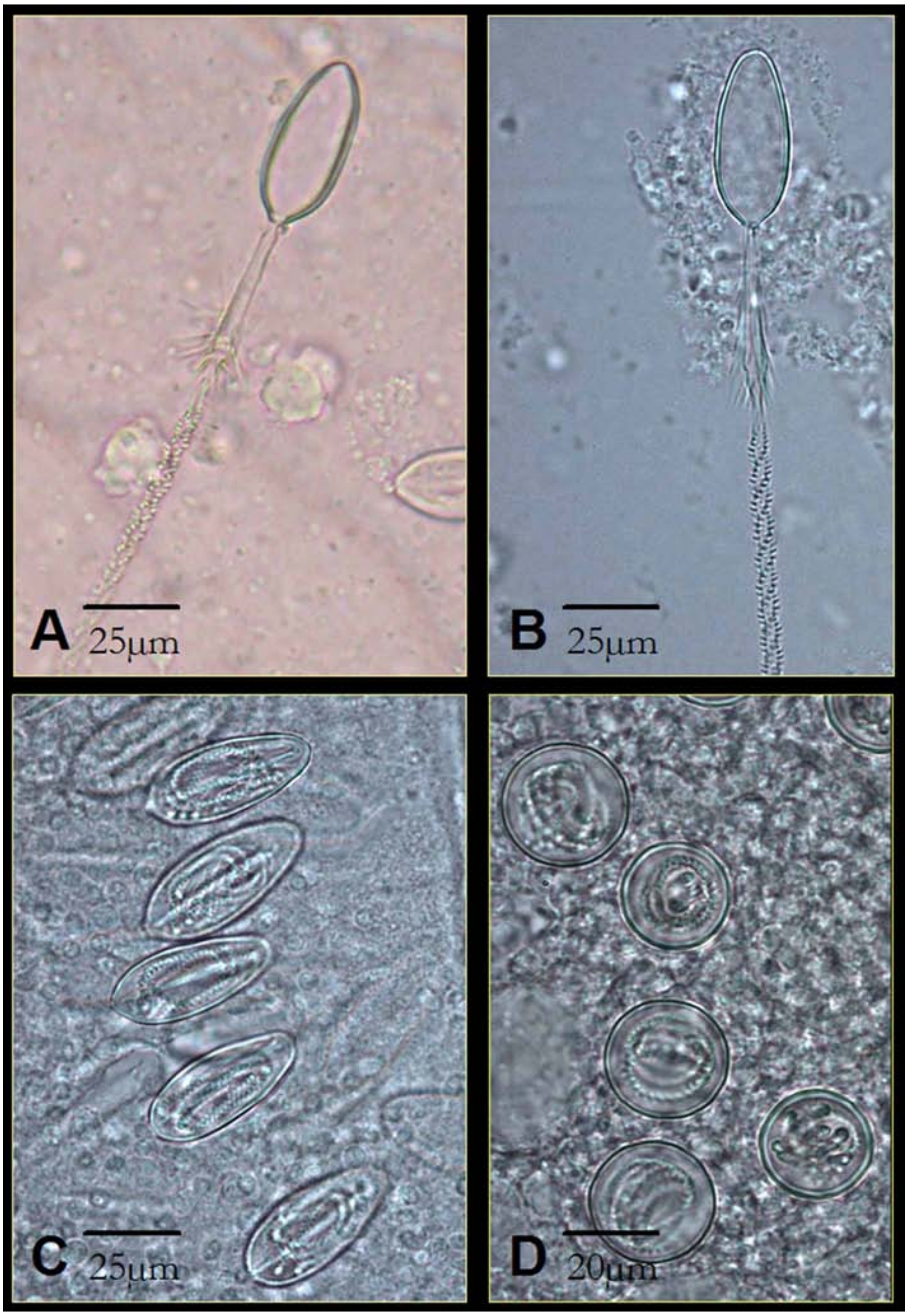

PLATE 21. *Malo* n. sp. C. “Pseudo-Irukandji” (holotype), tentacular and bell nematocysts. A and B. Type 4 microbasic *p*-mastigophores, discharged, tentacles. C. Club-shaped microbasic *p*-mastigophores, tentacle**.** D. Spherical isorhizas, bell.

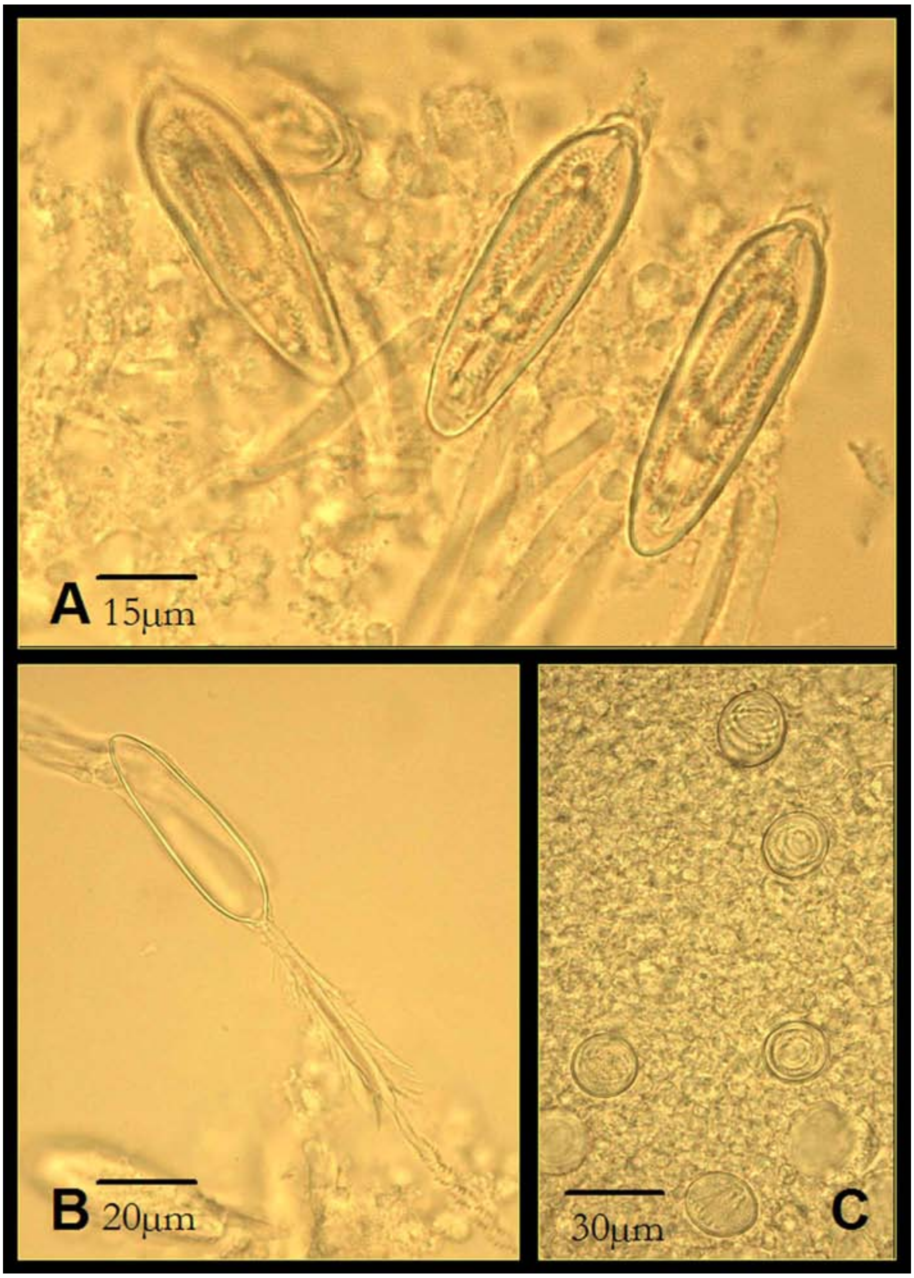

PLATE 22. *Gerongia rifkinae* Gershwin and Alderslade (holotype), tentacular and bell nematocysts. A and B. Club-shaped Type 4 microbasic *p*-mastigophores, undischarged and discharged, tentacle. C. "Spherical" isorhizas, bell.

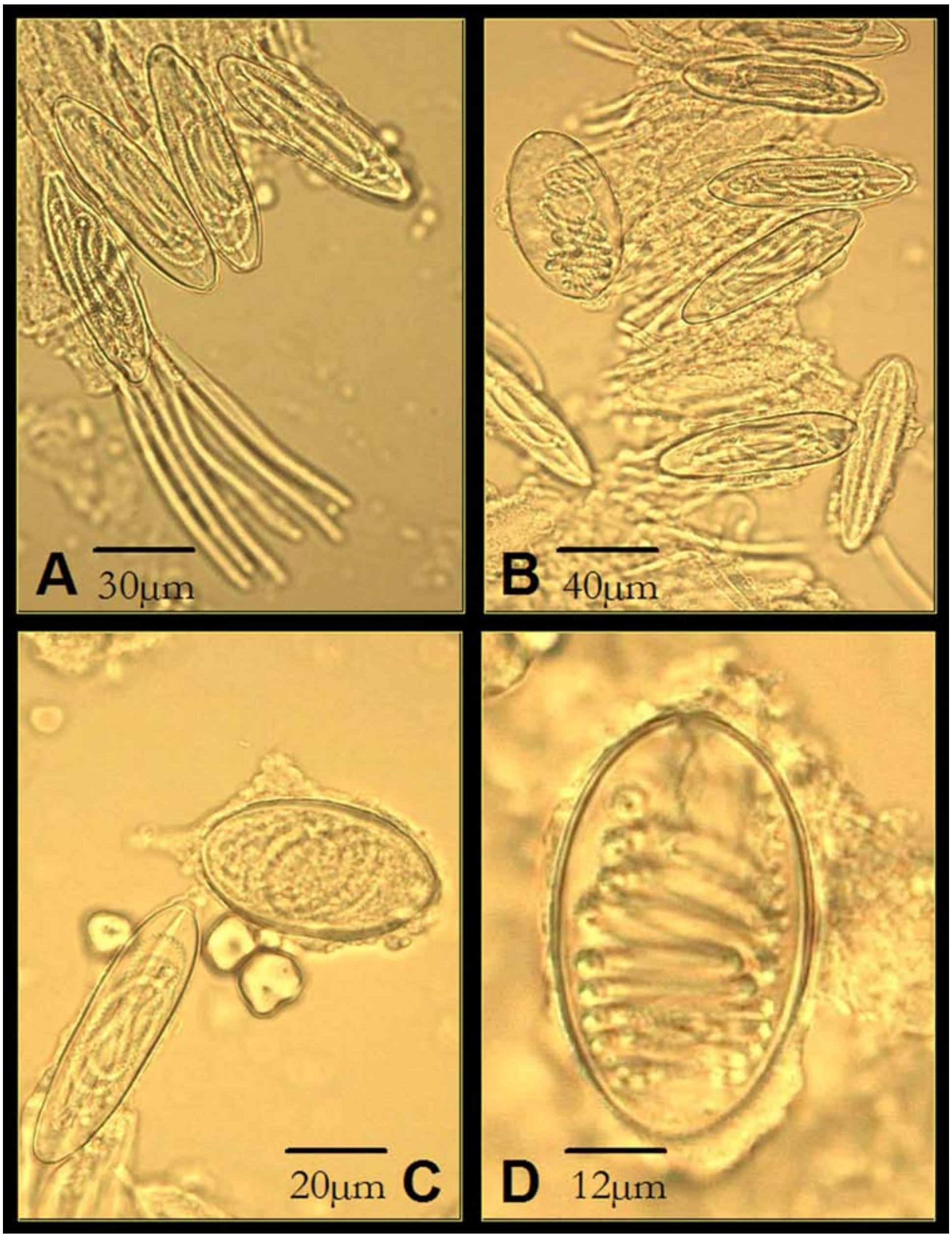

PLATE 23. "Morbakka", Port Douglas, Queensland (holotype), tentacular nematocysts. A. Club-shaped microbasic *p*-mastigophores (with fibrils still connected to the nematocyst in the lower right). B and C. Club-shaped microbasic *p*-mastigophores and large oval isorhiza. D. Large oval isorhiza.

PLATE 24. *Tamoya haplonema* Müller (neotype), tentacular nematocysts. A. Club-shaped macrobasic unidentified rhopaloid. B. Same, partially discharged. C. Same, fully discharged.

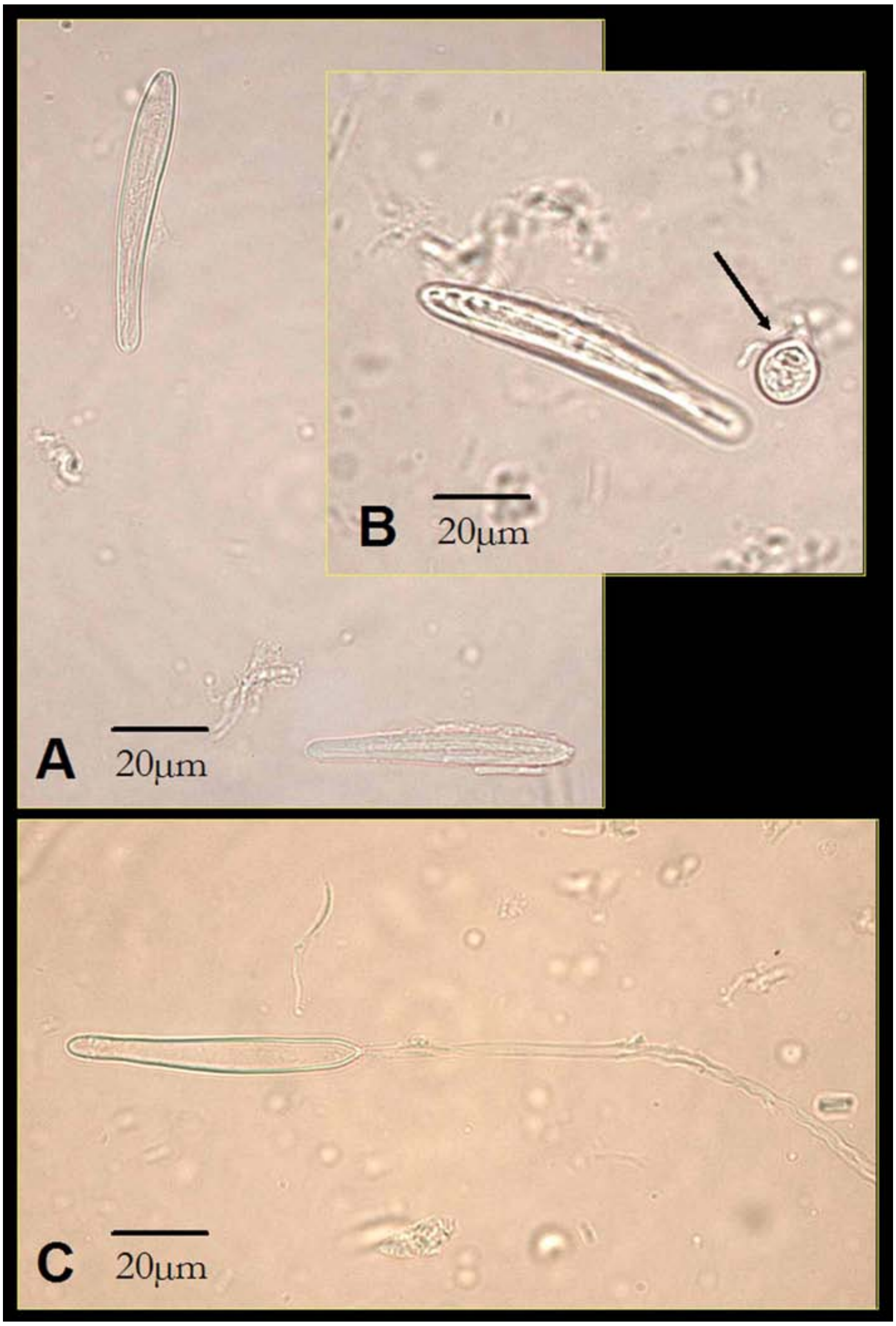

PLATE 25. *Chiropsalmus maculatus* Cornelius et al. (holotype), tentacular nematocysts. A. Banana-form microbasic *p*-mastigophores. B. Microbasic *p*-mastigophore and tiny spherical isorhiza (arrow). C. Microbasic *p*-mastigophore, discharged.

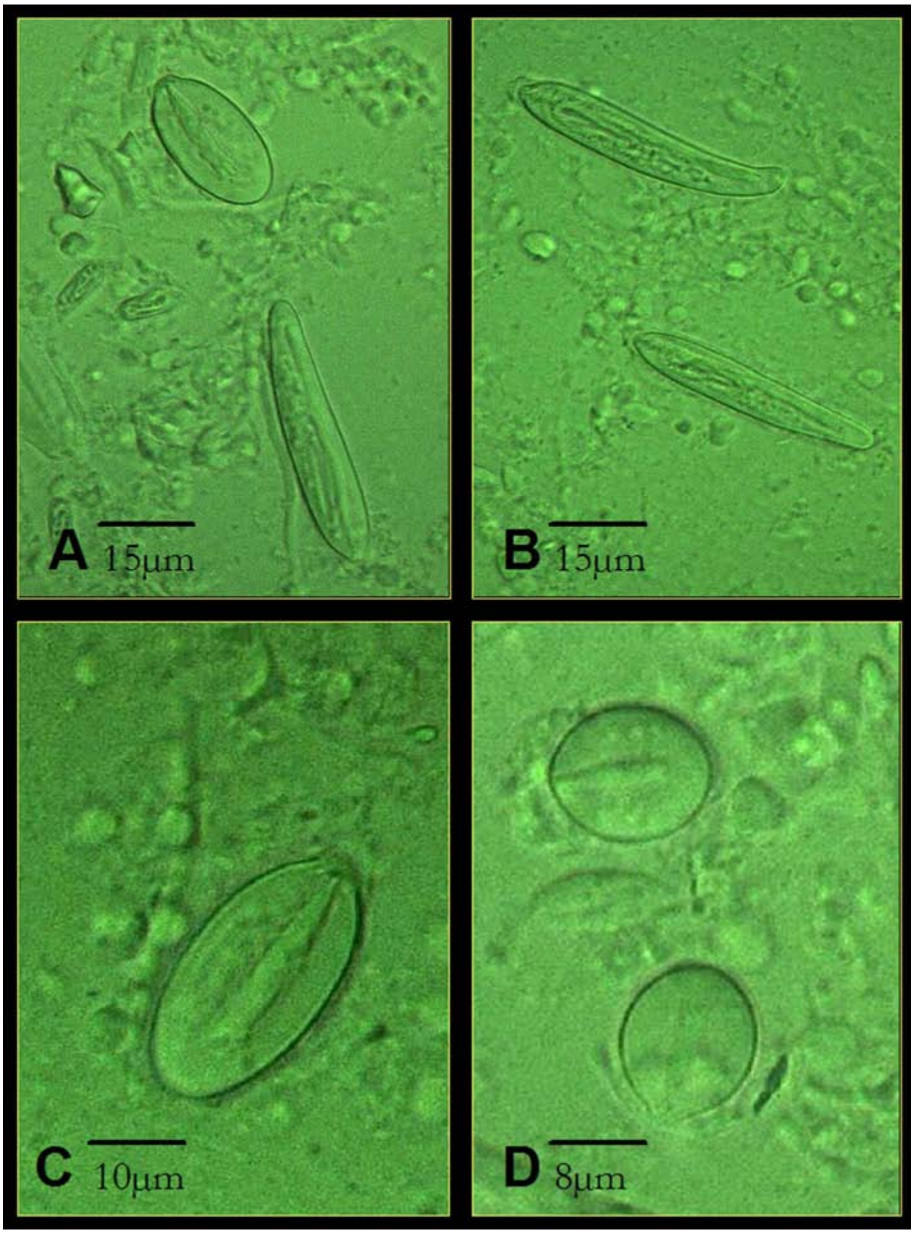

PLATE 26. *Chiropsalmus quadrumanus* (Müller) (neotype), tentacular nematocysts. A. Cigar-shaped microbasic *p*-mastigophore, football-shaped microbasic *p*-rhopaloid, and rod-shaped isorhizas (arrows). B. Cigar-shaped microbasic *p*-mastigophores. C. Football-shaped microbasic *p*-rhopaloid. D. Small spherical microbasic *p*-rhopaloid.

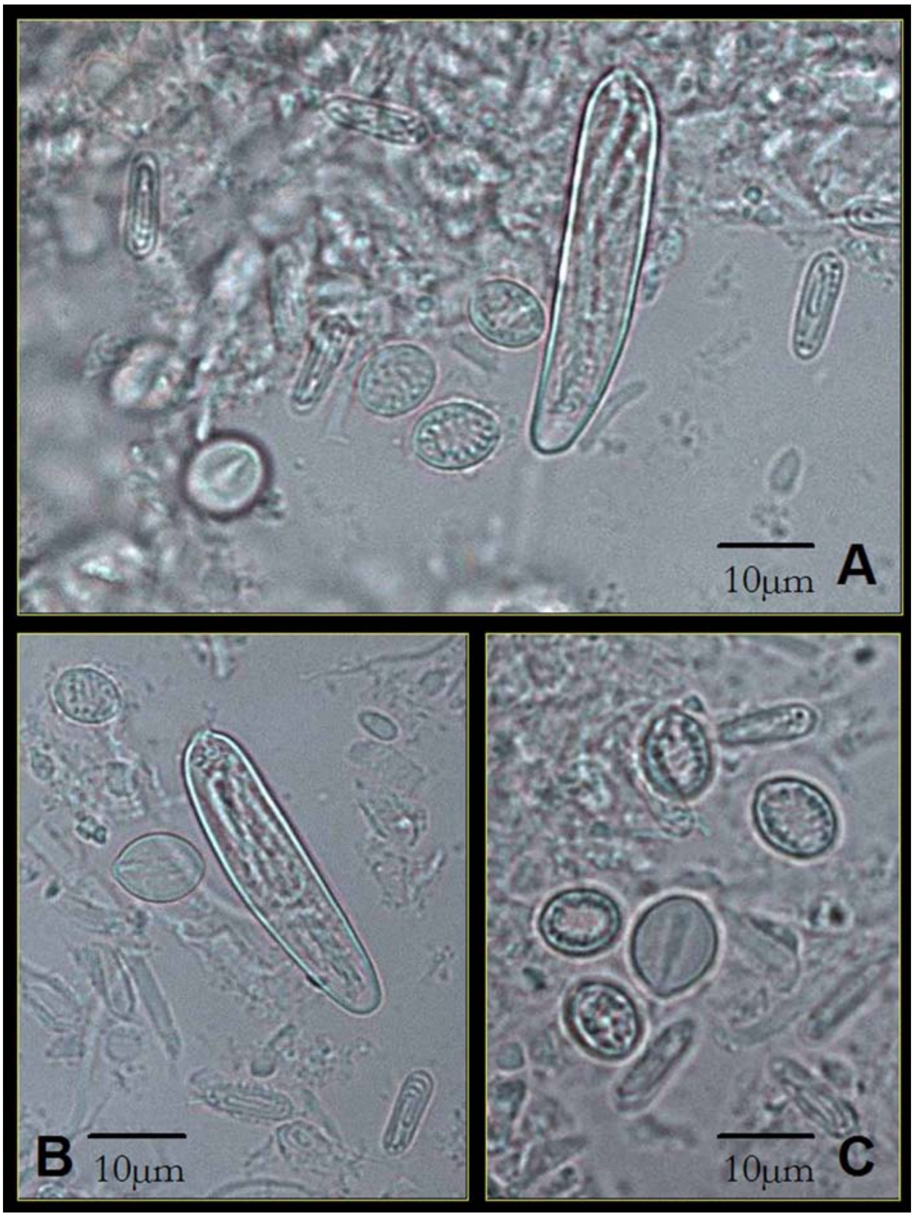

PLATE 27. *Chiropsalmus* n. sp. A (holotype, North Queensland), tentacular nematocysts. A. Cigar-shaped microbasic *p*-mastigophore, small oval “beehive” isorhizas, and rod-shaped isorhizas, plus one sub-spherical *p*-rhopaloid (polar view, lower right). B. Cigar-shaped microbasic *p*-mastigophore, small sub-spherical *p*-rhopaloid, and small rod-shaped isorhizas. C. Small sub-spherical *p*-rhopaloid, small oval “beehive” isorhizas, and rod-shaped isorhizas.

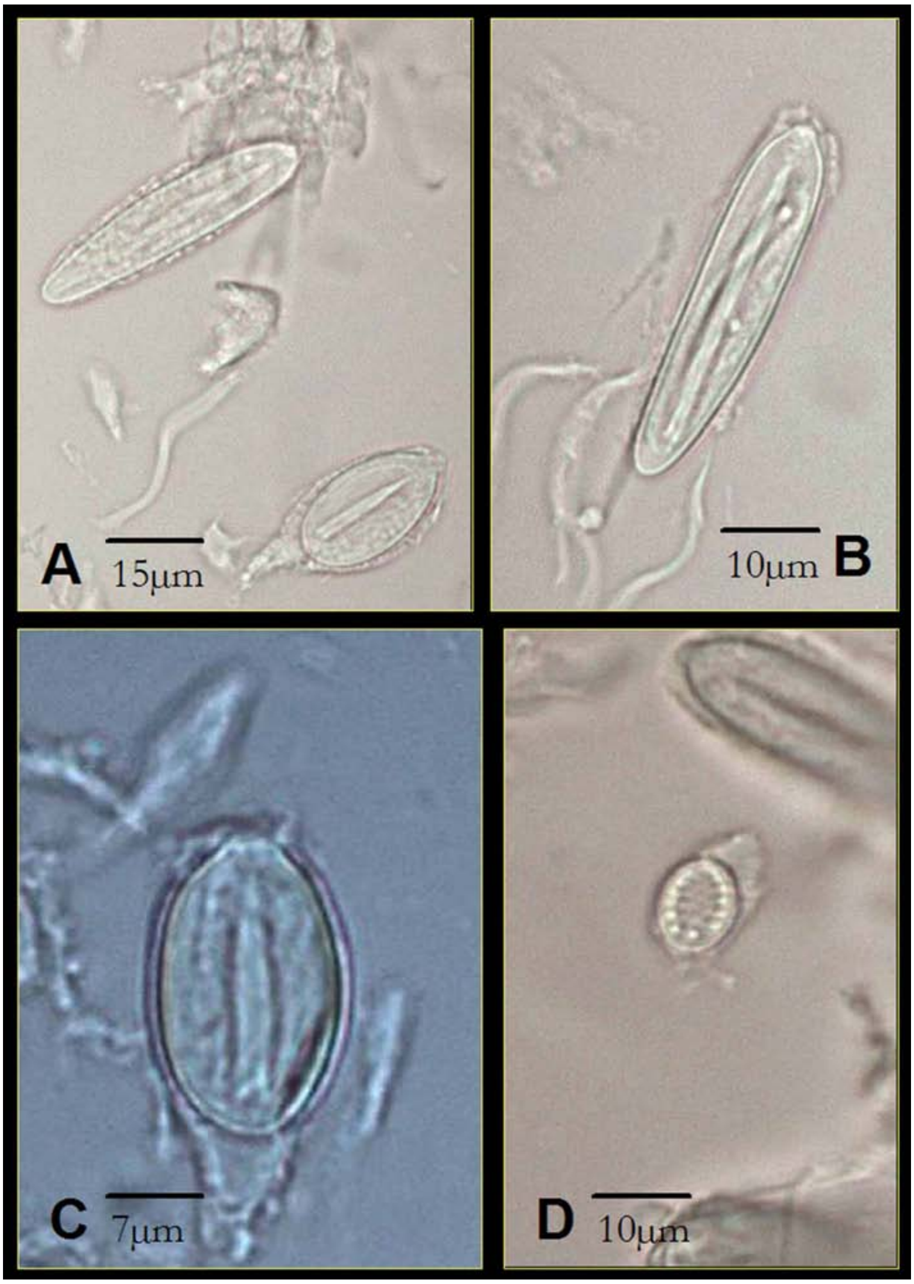

PLATE 28. *Chiropsalmus* n. sp. B (holotype, Gove Peninsula), tentacular nematocysts. A. Cigar-shaped microbasic *p*-mastigophore and large oval *p*-rhopaloid. B. Cigar-shaped microbasic *p*-mastigophore. C. Large oval *p*-rhopaloid. D. Small oval "beehive" isorhiza.

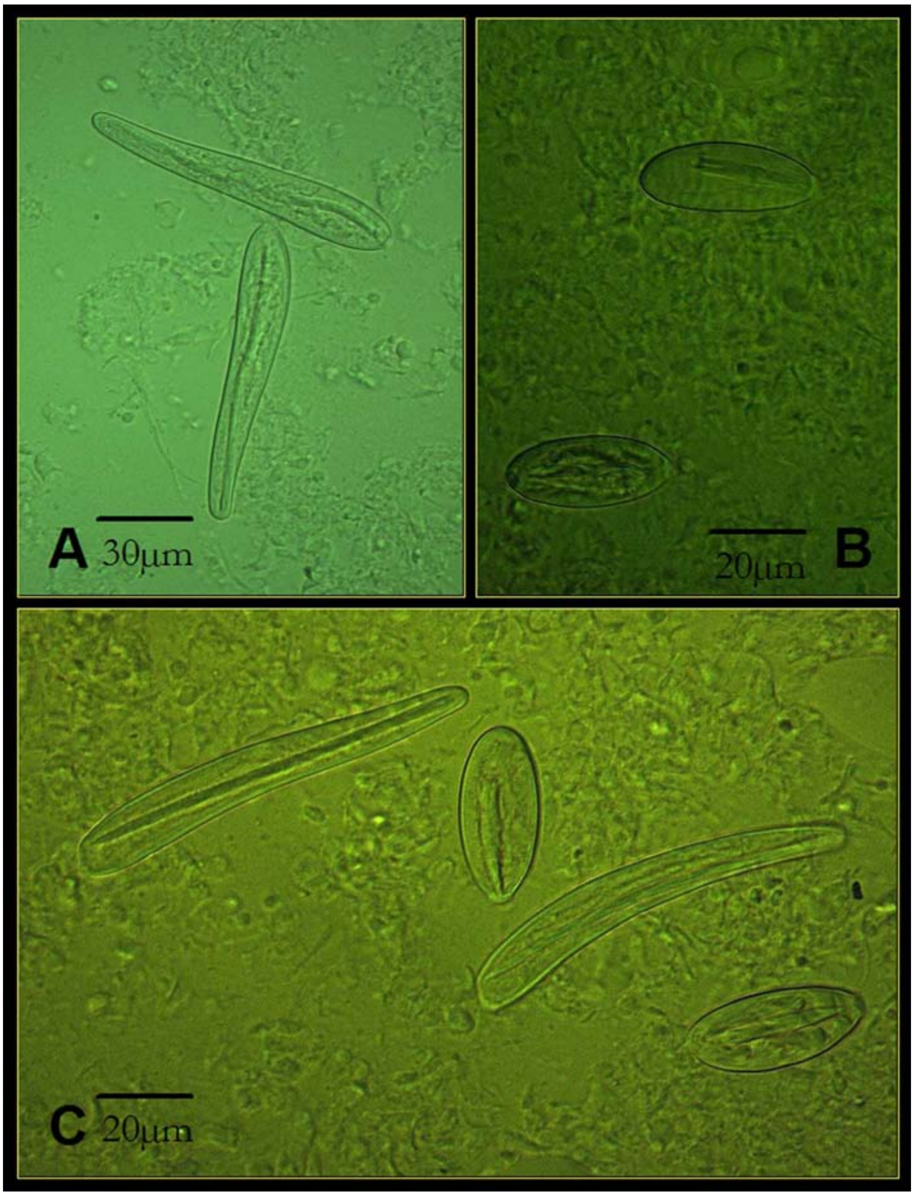

PLATE 29. *Chiropsoides buitendijki* (Horst) (syntype), tentacular nematocysts. A. Club-shaped microbasic *p*-mastigophores. B. Football-shaped microbasic *p*-rhopaloid (left), football-shaped trirhopaloid (right). C. Club-shaped *p*-mastigophores and football-shaped trirhopaloids.

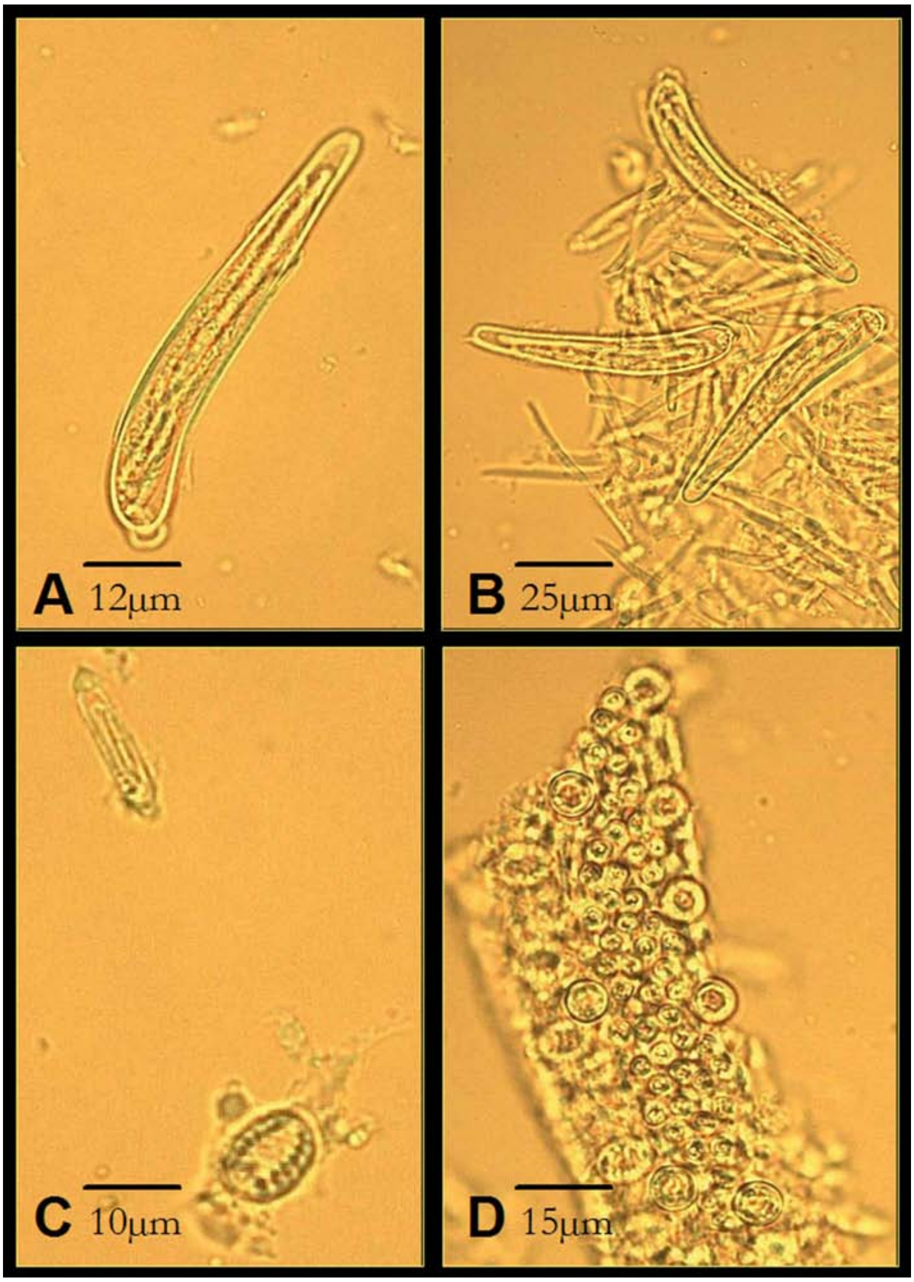

PLATE 30. *Chiropsoides* n. sp. (holotype, Sri Lanka), tentacular nematocysts. A and B. Hockey-stick-shaped microbasic *p*-mastigophores. C. Small rod-shaped isorhiza (upper left) and small oval "beehive" isorhiza (lower right). D. Two size classes of very small spherical isorhizas.

PLATE 31. *Chironex fleckeri* Southcott (non-type juvenile specimen, Townsville), tentacular nematocysts. A. Banana-form microbasic *p*-mastigophore, large oval *p*-rhopaloid, and rod-shaped isorhizas. B. Banana-form microbasic *p*-mastigophore, discharged. C. Banana-form microbasic *p*-mastigophore, discharged large oval *p*-rhopaloid, small sub-spherical *p*-rhopaloid, and rod-shaped isorhizas. D. Small sub-spherical *p*-rhopaloids, discharged (upper right), and undischarged (lower left).

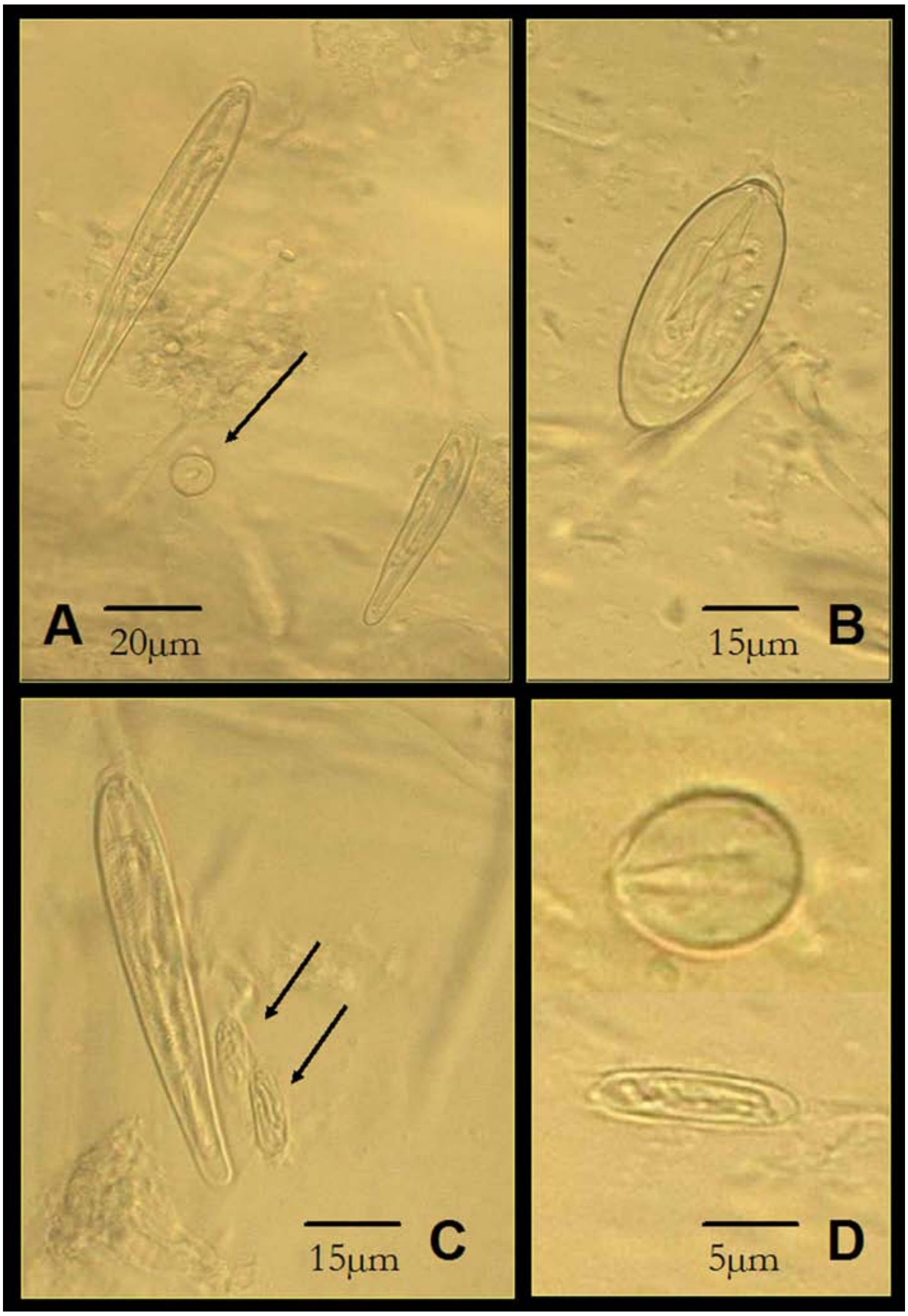

PLATE 32. *Chironex* n. sp. A (holotype, Broome), tentacular nematocysts. A. Banana-form microbasic *p*-mastigophores and sub-spherical *p*-rhopaloid (arrow; polar view). B. Large oval trirhopaloid. C. Banana-form microbasic *p*-mastigophore and rod-shaped isorhizas (arrows). D. Small sub-spherical *p*-rhopaloid (above), and rod-shaped isorhiza (below).

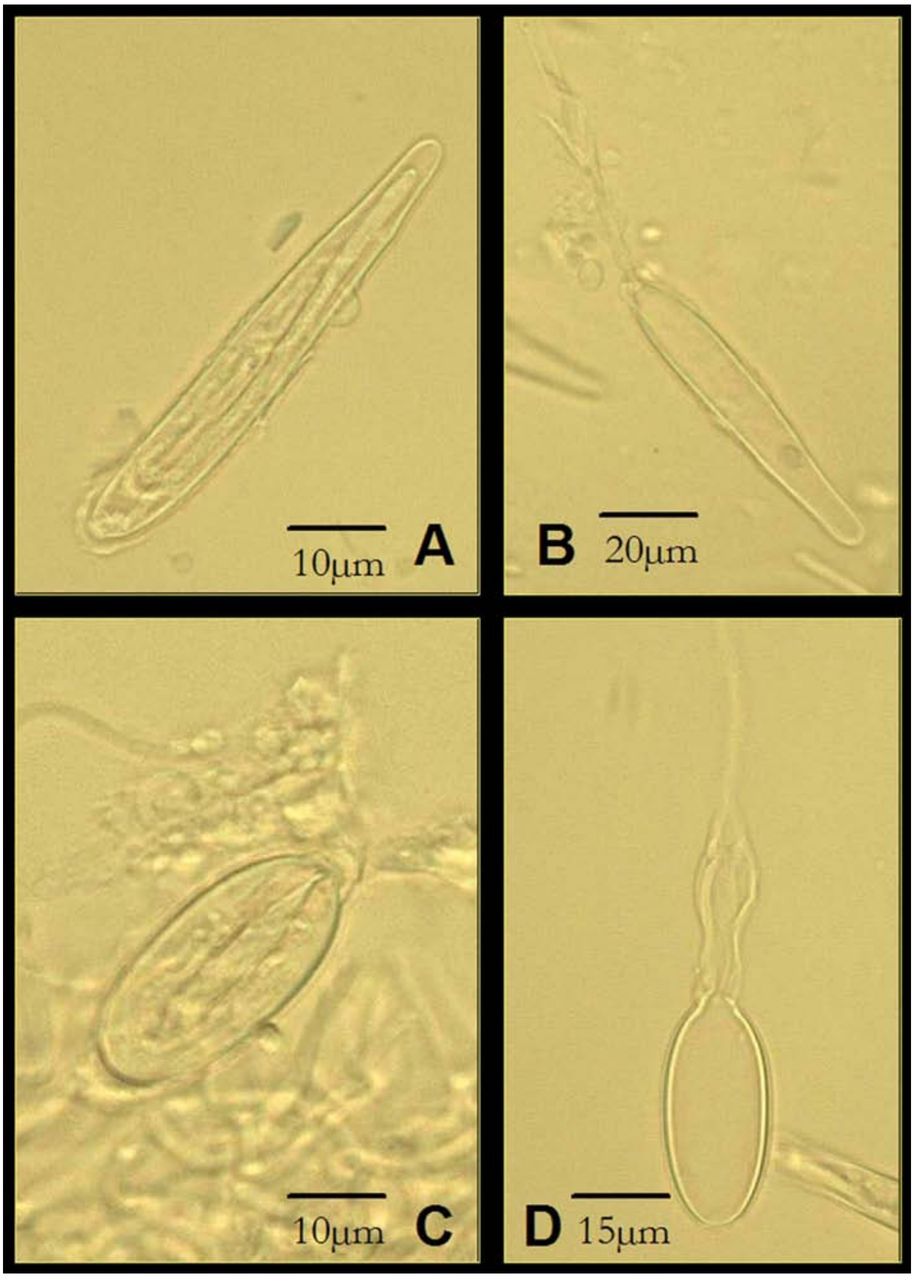

PLATE 33. *Chironex* n. sp. B (holotype, Okinawa "volcano"), tentacular nematocysts. A. Banana-form microbasic *p*-mastigophore. B. Banana-form microbasic *p*-mastigophore, discharged. C. Large oval *p*-rhopaloid. D. Large oval *p*-rhopaloid, discharged.

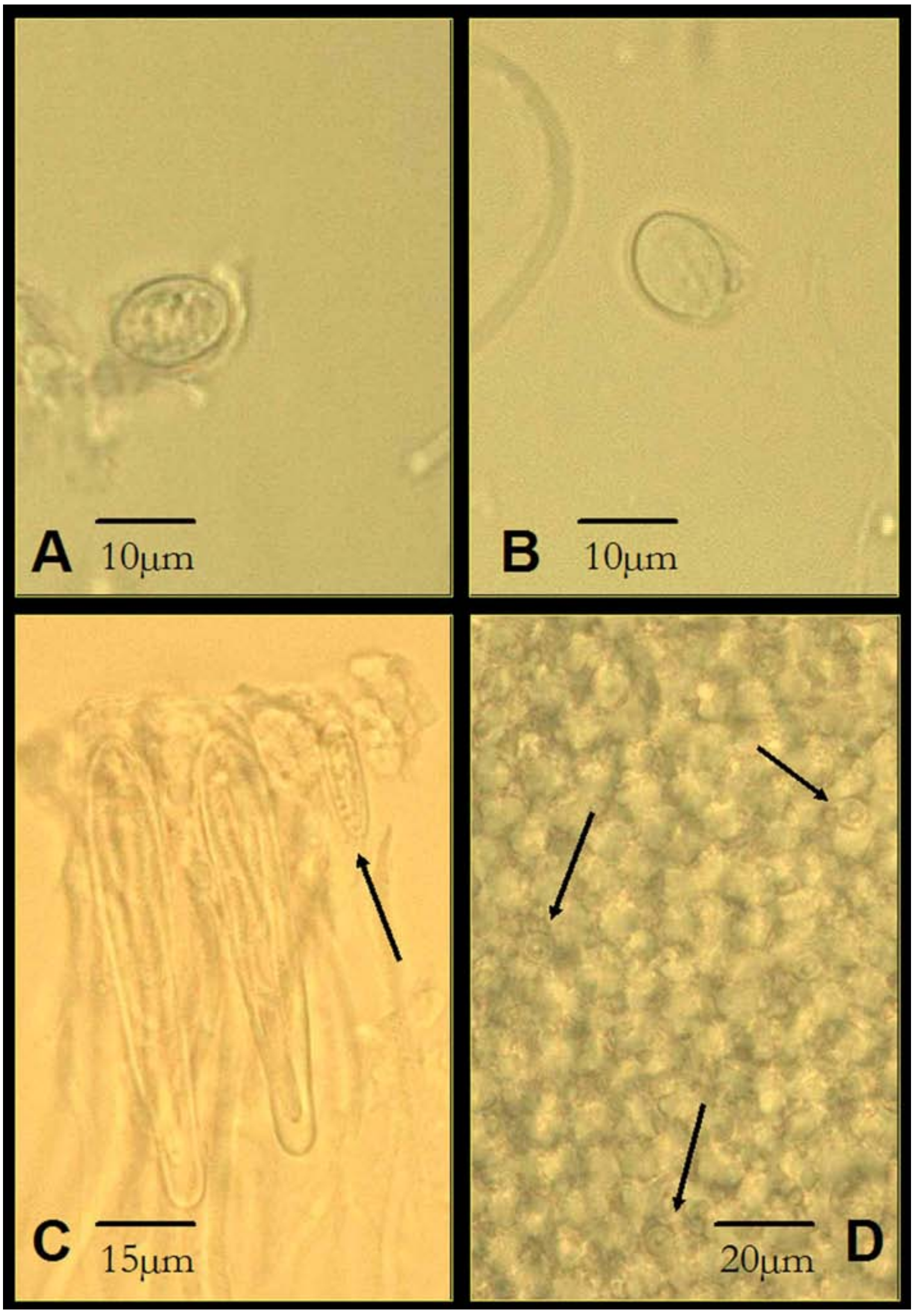

PLATE 34. *Chironex* n. sp. B (holotype, Okinawa "volcano"), tentacular and phacellar nematocysts. A. Small oval "beehive" isorhiza, tentacle. B. Small sub-spherical *p*-rhopaloid, tentacle. C. Banana-form microbasic *p*-mastigophores and rod-shaped isorhiza (arrow), tentacle. D. Microbasic euryteles (arrows), polar view, gastric cirrus.

Key to Nematocysts of the Cubozoa

1A. Undischarged capsule with a well defined shaft, or discharged tubule with a well defined basis.. heteroneme, 2
1B. Undischarged capsule lacking a well defined shaft, or discharged tubule lacking a well defined basis...haploneme, 8
2A. Undischarged shaft slender, with a v-shaped notch in distal end..............................3
2B. Undischarged shaft heavy, without a v-shaped notch in distal end............................5
3A. Discharged shaft cylindrical..*p*-mastigophore, 4
3B. Discharged shaft with prominent swellings.. *p*-rhopaloid, 7
4A. Discharged shaft with short spines pointing outward and long spines pointing away from capsule.. Type 3
4B. Discharged shaft with all spines pointing away from capsule .... Type 4
5A. Discharged shaft with a single swelling at the midpoint or distal end, with all spines confined to the swelling 6
5B. Discharged shaft with three prominent swellings or two prominent and one nearly imperceptible swellings, the centre (largest) swelling bearing spines ..... trirhopaloid
6A. Discharged shaft cylindrical with swelling near the mid-point ....tumitele
6B. Discharged shaft with swelling at the distal end.. eurytele
7A. Capsule large, oval, or football-shaped, with a poorly-defined or loosely-coiled tubule...
.... large oval or football-shaped *p*-rhopaloid
7B. Capsule very small, nearly spherical, without well defined tubule ....
.... small spherical *p*-rhopaloid
8A. Capsule spherical or nearly so ....exumbrellar isorhizas
8B. Capsule oval, ovoid, or rod-shaped...9
9A. Capsule rod-shaped, with straight sides, with loosely coiled tubule; extremely small, common in Chirodropida ....rod-shaped isorhiza
9B. Capsule oval or ovoid 10
10A. Tubule tightly packed, common in Carybdeidae .... oval or ovoid isorhiza
10B. Tubule packed transversely, common in Chirodropida.................. “beehive” isorhiza

For further information on cubozoan nematocysts, the following literature should be consulted: Southcott (1967), Calder and Peters (1975), Endean and Rifkin (1975), Rifkin and Endean (1983), Williamson et al. (1996), Avian et al. (1997), Marques et al. (1997), Yanagihara et al. (2002), and Oba et al. (2004).

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