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Stalked jellyfishes (Cnidaria: Staurozoa) of South Africa, with the description of *Calvadosia lewisi* sp. nov.

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Abstract

Stalked jellyfishes (Cnidaria: Staurozoa) are cryptic, benthic animals, known mainly from polar and temperate waters of the Northern Hemisphere. We describe a new species, *Calvadosia lewisi,* from South Africa and review the staurozoan fauna of the region. Three other species are previously known from South Africa: *Calvadosia capensis* (Carlgren, 1938); *Depastromorpha africana* Carlgren, 1935; and *Lipkea stephensoni* Carlgren, 1933, but all of these are known from very few records and have been poorly illustrated and documented to date. We provide brief descriptions and photographic illustrations for each species and a list of local and global geographical records. Two (*L. stephensoni* and *C. lewisi*), but possibly three (*D. africana*), of the four known South African staurozoan species are endemic from South Africa. The new species, images, and extra distributional records presented here greatly improve knowledge of the staurozoan fauna in South Africa and, consequently, of the Southern Hemisphere.

Key words: Stauromedusae, Amyostaurida, Kishinouyeidae, diversity, taxonomy

Introduction

Staurozoa is a cnidarian class (Marques & Collins 2004) comprising benthic, stalked jellyfishes that live attached to substrata (generally rocks or seaweed), from the intertidal zones to deep hydrothermal vents (Collins & Daly 2005; Mills & Hirano 2007; Zagal *et al*. 2011). Although stauromedusae may be locally abundant (Miranda *et al*. 2012a), they are rarely observed because of their relatively small size and cryptic coloration (Larson 1980; Mills & Hirano 2007). Staurozoan species have a unique life cycle consisting of a non-ciliated planula larva that settles on the substratum and develops into a stauropolyp, which subsequently undergoes apical metamorphosis into a stauromedusa, without strobilation or budding (Wietrzykowski 1912; Kikinger & Salvini-Plawen 1995; Miranda *et al*. 2010). Stauromedusae thus possess characters found both in polyp and medusa stages of other medusozoans (Collins *et al*. 2006; Miranda *et al*. 2013, 2016a).

Stalked jellyfishes have a cosmopolitan distribution, mainly in temperate and polar waters (Larson 1980; Mills & Hirano 2007), but their diversity in the Southern Hemisphere is probably underestimated (Miranda *et al*. 2009; Zagal *et al*. 2011). Currently, there are 49 species described (Miranda *et al*. 2016b), 12 of which occur in the Southern Hemisphere (Table 1) (Grohmann *et al*. 1999; Miranda *et al*. 2009). Specifically for South Africa, there are three species, which were described in the 1930s by O. Carlgren, *viz. Lipkea stephensoni* Carlgren, 1933; *Depastromorpha africana* Carlgren, 1935; and *Calvadosia capensis* (Carlgren, 1938). Since their original descriptions, the only published observation of these species (besides the inclusion of *D. africana* in molecular analyses, e.g. Dawson 2004; Collins & Daly 2005; Miranda *et al.* 2016b) for South Africa is the report of *L.*

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stephensoni and *D. africana* in a regional field guide (Jones 2008). *Lipkea stephensoni* is currently considered to be endemic to South Africa, whereas *D. africana* has also been recorded in both Australia (Zagal *et al*. 2011) and New Zealand (Grohmann *et al*. 1999; Cairns *et al*. 2009; Zagal *et al*. 2011), and *C. capensis* has also been found in Brazil (Miranda *et al*. 2012b).

Recently, a comprehensive molecular phylogenetic analysis of the Staurozoa (using the mitochondrial markers COI and 16S, and the nuclear markers ITS, 18S, and 28S) resulted in the proposal of a new classification for the group (Miranda *et al*. 2016b). Molecular patterns, associated with morphological evidence, demonstrated the existence of a new species from South Africa, identified as *Calvadosia* sp. 4, closely related to *Calvadosia tasmaniensis* (Zagal, Hirano, Mills, Edgar & Barrett, 2011) from Australia and *Calvadosia corbini* (Larson, 1980) from Brazil (but also recorded in Puerto Rico and Mexico; Capriles & Martínez 1970; Larson 1980; Lechuga & Alamo 2005).

In this paper, we formally describe this new species of *Calvadosia* (*Calvadosia* sp. 4, above) and review the South African staurozoan fauna, including images and brief descriptions for all known species, as well as new locality records and details of their local and global distributions.

TABLE 1. Staurozoan species recorded from the Southern Hemisphere, with the addition of the new species *Calvadosia lewisi*, described in this study. *Occurrence of *L. janetae* in the Southern Hemisphere needs confirmation (Lutz *et al*. 2006). The species *Calvadosia corbini*, *Haliclystus inabai*, and *Lucernaria janetae* also occur in the Northern Hemisphere.

Species	Southern Hemisphere localities	References
Calvadosia capensis (Carlgren, 1938)	Brazil, South Africa	Carlgren 1938; Miranda *et al*. 2012b
Calvadosia corbini (Larson, 1980)	Brazil	Grohmann *et al*. 1999
Calvadosia tasmaniensis (Zagal, Hirano, Mills, Edgar & Barrett, 2011)	Australia	Zagal *et al*. 2011
Calvadosia vanhoeffeni (Browne, 1910)	Antarctica	Browne 1910; Carlgren 1930
Calvadosia lewisi sp. nov.	South Africa	This study
Craterolophus macrocystis von Lendenfeld, 1884	New Zealand	von Lendenfeld 1884
Depastromorpha africana Carlgren, 1935	Australia, New Zealand, South Africa	Carlgren 1935; Grohmann *et al*. 1999; Cairns *et al*. 2009; Zagal *et al*. 2011
Haliclystus antarcticus Pfeffer, 1889	Argentina, Antarctica, Chile, South Georgia Island	Pfeffer 1889; Carlgren 1930; Kramp 1952; Amor 1962; Quezada 1969; Mianzan 1989; Davenport 1998; Zagal 2004a, 2004b, 2008; Miranda *et al*. 2009, 2010
Haliclystus inabai (Kishinouye, 1893)	Australia	McInnes 1989; Zagal *et al*. 2011; Falconer 2013
Haliclystus kerguelensis Vanhöffen, 1908	Kerguelen Island	Vanhöffen 1908; Kramp 1957
Lipkea stephensoni Carlgren, 1933	South Africa	Carlgren 1933
Lucernaria australis Vanhöffen, 1908	Antarctica	Vanhöffen 1908; Carlgren 1930
Lucernaria janetae Collins & Daly, 2005*	Southern East Pacific Rise	Lutz *et al*. 2006

Material and methods

Specimens were collected manually during low tide, or by SCUBA diving, in different regions along the South

African coast. Individuals were photographed live, then relaxed by mixing menthol crystals into seawater, and preserved in either 4–5% formaldehyde solution in seawater or in 70–90% ethanol. The taxonomic classification follows Miranda *et al*. (2016b). The species accounts are based on our observations of freshly collected material and on previous literature descriptions, except for *C. capensis*, which we were unable to re-collect, and relied exclusively on published information from both South Africa (Carlgren 1938) and Brazil (Miranda *et al*. 2012b). Specimens of *C. tasmaniensis* and *C. corbini* (Table 2) were also examined for morphological comparison with the South African material.

TABLE 2. Specimens of *Calvadosia corbini* (Larson, 1980) and *Calvadosia tasmaniensis* (Zagal, Hirano, Mills, Edgar & Barrett, 2011) analyzed for morphological comparisons. MZUSP: Museum of Zoology of the University of São Paulo, Brazil; USNM: National Museum of Natural History, Smithsonian, USA.

Species	Catalog number	Locality	Number of specimens	Preservative
Calvadosia corbini	MZUSP 1564	Aracruz, Espírito Santo, Brazil	2	Formaldehyde solution 4%
Calvadosia corbini	MZUSP 1565	Aracruz, Espírito Santo, Brazil	2	Formaldehyde solution 4%
Calvadosia tasmaniensis	USNM 1233739	Fortescue Bay, Tasmania, Australia	2	Formaldehyde solution 4%
Calvadosia tasmaniensis	USNM 1233740	Gerlof Bay, South Australia, Australia	1	Formaldehyde solution 4%

Images of detailed structures were photographed under a Zeiss stereomicroscope SteREO Discovery.V8. Observations and measurements of nematocysts were made on tissues preserved in 4–5% formaldehyde solution, squashed in a drop of fresh water on a microscope slide, covered by a cover slip, and gently compressed to further dissociate the cells (Gwilliam 1956; Mejía-Sanchez & Marques 2013). Ten undischarged capsules of each type of nematocyst were isolated and photographed under a Zeiss microscope AXIO Imager.M2. Measurements were made using the software KLONK Image Measurement 13.2.

Studied materials were deposited in the Iziko South African Museum, Cape Town, South Africa; in the Cnidarian Collection of the Museum of Zoology of the University of São Paulo, Brazil (MZUSP); in the Coastal Branch of Natural History Museum and Institute, Chiba, Japan (CMNH); and in the National Museum of Natural History, Smithsonian Institution, USA (USNM).

Systematic account

Phylum Cnidaria Verrill, 1865

Subphylum Medusozoa Petersen, 1979

Class Staurozoa Marques & Collins, 2004

Order Stauromedusae Haeckel, 1879

Suborder Amyostaurida Miranda, Hirano, Mills, Falconer, Fenwick, Marques & Collins, 2016b

Family Kishinouyeidae Uchida, 1929

Genus *Calvadosia* Clark, 1863

Remarks. *Calvadosia* was originally proposed by Clark (1863) to accommodate a species described by Lamouroux (1815), "*Lucernaire campanulée*" (or *Lucernaria campanulata*), from Calvados, France, therefore

proposing the name *Calvadosia campanulata* (Lamouroux, 1815). Its main difference from other *Lucernaria* is the "four pilasters […] not muscular, as are the pilasters in the pedicel of *Lucernaria quadricornis*" (Clark 1863: 556), i.e., absence of interradial longitudinal muscles associated with the septa of the peduncle.

However, Clark's (1863) proposal was overlooked for many years. Later, Uchida (1929) proposed a new genus, *Lucernariopsis*, for the same "*Lucernaria campanulata*", including species with one-chambered peduncle without muscles, overlooking the availability of the older name *Calvadosia* Clark, 1863. Apparently, Gwilliam (1956: 10) was the only author to notice this nomenclatural issue, concluding that according to the "law of priority, the proper generic name of *Lucernariopsis* Uchida, 1929 is *Calvadosia* Clark, 1863", but he never published his PhD Dissertation on the taxonomy of the Stauromedusae.

More recently, *Lucernariopsis* Uchida, 1929 was officially recognized as a synonym of *Calvadosia* Clark, 1863 (Miranda *et al*. 2016b). In addition, based on molecular and morphological evidence, the former genera *Kishinouyea* Mayer, 1910 and *Sasakiella* Okubo, 1917 were also incorporated into *Calvadosia* (Miranda *et al*. 2016b). Therefore, *Calvadosia* is currently one of the most diverse genera in Staurozoa, with 11 species: *Calvadosia campanulata* (Lamouroux, 1815), *Calvadosia nagatensis* (Oka, 1897), *Calvadosia vanhoeffeni* (Browne, 1910), *Calvadosia cruciformis* (Okubo, 1917), *Calvadosia hawaiiensis* (Edmondson, 1930), *Calvadosia tsingtaoensis* (Ling, 1937), *Calvadosia capensis* (Carlgren, 1938), *Calvadosia cruxmelitensis* (Corbin, 1978), *Calvadosia corbini* (Larson, 1980), *Calvadosia tasmaniensis* (Zagal, Hirano, Mills, Edgar & Barrett, 2011), and *Calvadosia lewisi* **sp. nov.** described in this study.

***Calvadosia lewisi* sp. nov.**
(Figs 1–4)

Kishinouyea sp. South Africa—Miranda *et al*. 2016b: 8, 12–15, figures 3–5.
Calvadosia sp. 4 South Africa—Miranda *et al*. 2016b: 17, 34, 36, figures 7, 16.

Material examined. Holotype: **MZUSP 3415**, 1 specimen, Simon's Town, Cape Town, Western Cape, South Africa (–34.2100, 18.4626), 01 December 2014, depth 3 m, on *Sargassum*, formaldehyde solution 4%, col. C. Foster. Paratype: **MZUSP 3416**, 1 specimen, Simon's Town, Cape Town, Western Cape, South Africa (–34.2100, 18.4626), 01 December 2014, depth 3 m, on *Sargassum*, formaldehyde solution 4%, col. C. Foster. Additional material: **MZUSP 2731**, 1 specimen, Miller's Point, Cape Town, Western Cape, South Africa (–34.2320, 18.4745), February 2013, subtidal, on *Brassicophycus brassicaeformis* and *Anthophycus longifolius*, ethanol 90%, col. D. Robertson-Anderson. **MZUSP 2732**, 1 specimen, Miller's Point, Cape Town, Western Cape, South Africa (–34.2320, 18.4745), February 2013, subtidal, on *Brassicophycus brassicaeformis* and *Anthophycus longifolius*, ethanol 90%, col. D. Robertson-Anderson. **MZUSP 3417**, 1 specimen, Miller's Point, Cape Town, Western Cape, South Africa (–34.2320, 18.4745), February 2013, subtidal, on *Brassicophycus brassicaeformis* and *Anthophycus longifolius*, ethanol 90%, col. D. Robertson-Anderson. **CMNH-ZG7819**, 1 specimen, A-Frame, False Bay, Cape Town, Western Cape, South Africa (–34.2159, 18.4650), 19 January 2003, shallow subtidal (depth 2–3 m), on kelp, formaldehyde solution 5% and transferred to ethanol 70%, col. Y. Hirano. **Iziko South African Museum MB-A083793**, 1 specimen, Miller's Point, Cape Town, Western Cape, South Africa (–34.2320, 18.4745), February 2013, subtidal, on *Brassicophycus brassicaeformis* and *Anthophycus longifolius*, ethanol 80%, col. D. Robertson-Anderson. **Iziko South African Museum MB-A084062**, 1 specimen, Betty's Bay, Overberg, Western Cape, South Africa (–34.3723, 18.8875), May 2013, depth 1 m, on kelp *Ecklonia maxima*, formaldehyde solution 4%, col. E. Firl & C. Pickering. **Not kept**, 1 specimen, Castle Rocks, False Bay, Cape Town, Western Cape, South Africa (–34.2385, 18.4766), February 2010, depth about 5 m; on wrack growing on flat rock, observed by G. Zsilavecz. **Not kept**, 1 specimen, A-Frame, False Bay, Cape Town, Western Cape, South Africa (–34.2159, 18.4650), April 2014, depth 5 m, on *Caulerpa filiformis* growing on sand; observed by G. Zsilavecz.

Diagnosis. Gonadal curved nodular lobes, regular (symmetric) and smooth in shape, facing interradii, arranged in a "zigzag" row on subumbrella.

Description. Body divided into two clearly demarcated regions: calyx and peduncle (Fig. 1D). Calyx wider than high, cruciform (Fig. 1), height 3.11–6.15 mm (mean 4.64 mm, number of individuals measured n = 5), width 5.88–16.48 mm (mean 12.03 mm, n = 5). Peduncle short (Figs 1D, 2C), about 1/4 of the total height, 1.20–1.32 mm tall (mean 1.26 mm, n = 5), width 1.39–2.03 mm (mean 1.85 mm, n = 5). Broad, swollen adhesive circular pedal

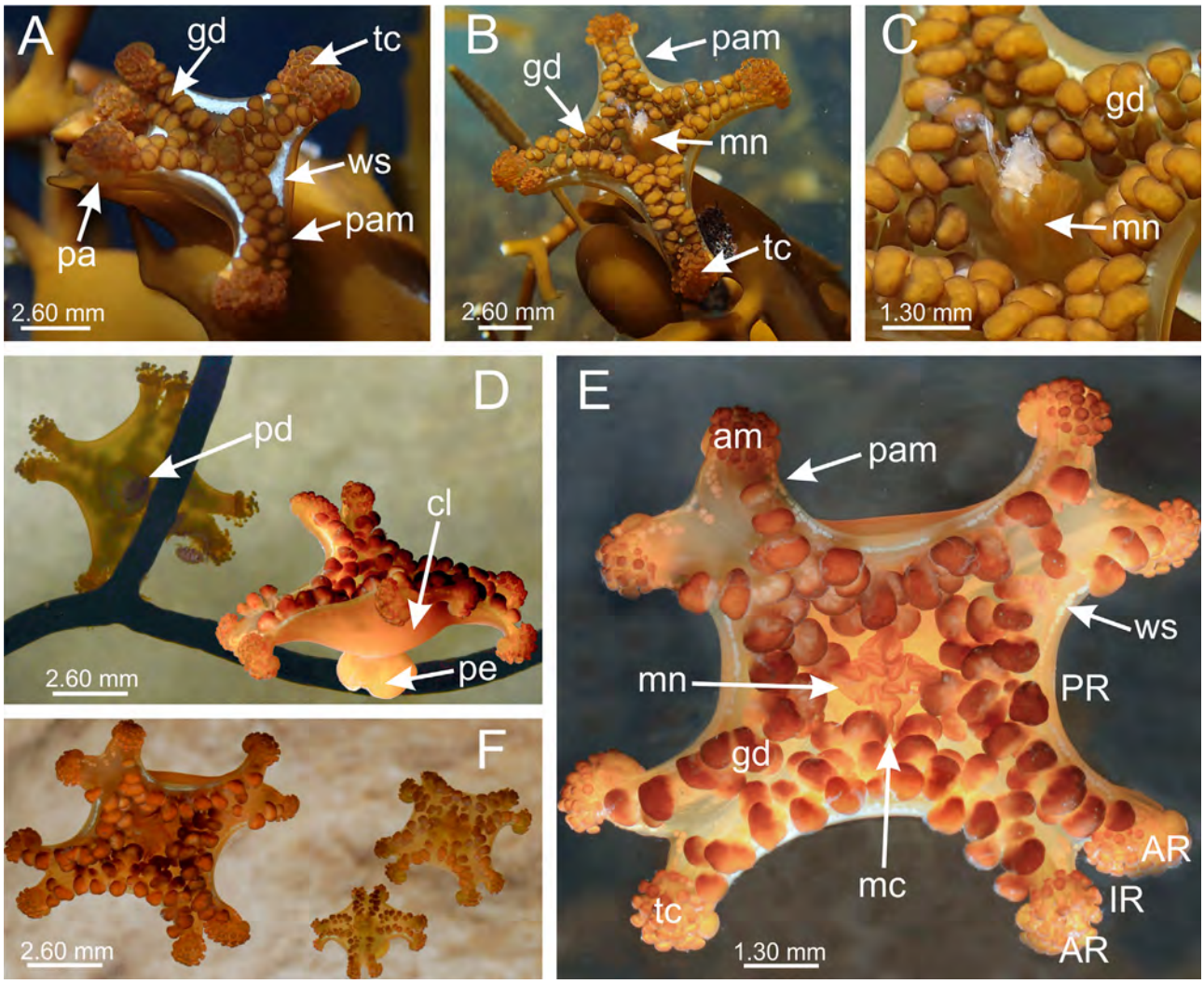

FIGURE 1. *Calvadosia lewisi* **sp. nov.**, living specimens. A, B: Subumbrellar (oral) view of specimens in the field; C: Detail of manubrium, probably discharging undigested material; D: Subumbrellar and exumbrellar (basal) views; E: Subumbrellar (oral) view, indicating the perradial, interradial, and adradial regions; F: Individuals of different sizes. Abbreviations: am, arms; AR, adradial region; cl, calyx; gd, gonad; IR, interradial region; mc, manubrial corner; mn, manubrium; pa, pad-like adhesive structure; pam, paired arms; pd, pedal disk; pe, peduncle; PR, perradial region; tc, secondary tentacles; ws, white spots of nematocysts. Photo credit: Craig Foster (A–C); George Branch (D–F).

disk at base of peduncle (Fig. 2C, E), width 2.48–4.31 mm (mean 3.38 mm, n = 5). Small central pore in the pedal disk of some specimens (Fig. 2E). Peduncle without interradial longitudinal muscle bands, with a single cruciform chamber (in cross-section) that becomes four-chambered basally within the pedal disk (Fig. 2D). Calyx without anchors (rhopalioids) or primary tentacles (Fig. 1). Manubrium with four perradial pleated lips (Figs 1E; 2B, F). Many gastric filaments in gastrovascular cavity. Gastrovascular cavity not divided by vertical tissue composed of double layer of gastrodermis with internal mesoglea, known as claustrum. Eight arms (width 1.00–1.55 mm, mean 1.27 mm, n = 5), organized in four interradial pairs, resembling a cross (Figs 1, 2), hence the common name ‘cross of pearls’. Four U-shaped perradial notches about four times as deep as the U- or V-shaped interradial notches (Fig. 2A). Eight gonads not embedded in gastrovascular cavity, but contained within evaginations from the gastrovascular cavity. Each gonad consisting of several nodular lobes, relatively regular and smooth in shape, and arranged in a single row on subumbrella (Figs 1–3). However, in mature specimens nodules are tightly packed, giving the impression of two rows of nodular lobes (but actually in a “zigzag” row; see Fig. 3D). Regular nodular lobes curved, facing interradii (Fig. 3A, E). Each arm with 8–12 nodular lobes (n = 5). Gonads extending from manubrium to tips of arms (Figs 1, 2B). Each arm with a terminal cluster of secondary tentacles, each cluster with 12–27 (n = 5) hollow, knobbed tentacles, similar in shape (Fig. 2J). Broad pad-like adhesive structures forming a glandular cushion (height 0.46–1.02 mm, mean 0.69 mm, n = 5; width 1.37–3.53 mm, mean 2.39 mm, n = 5) on

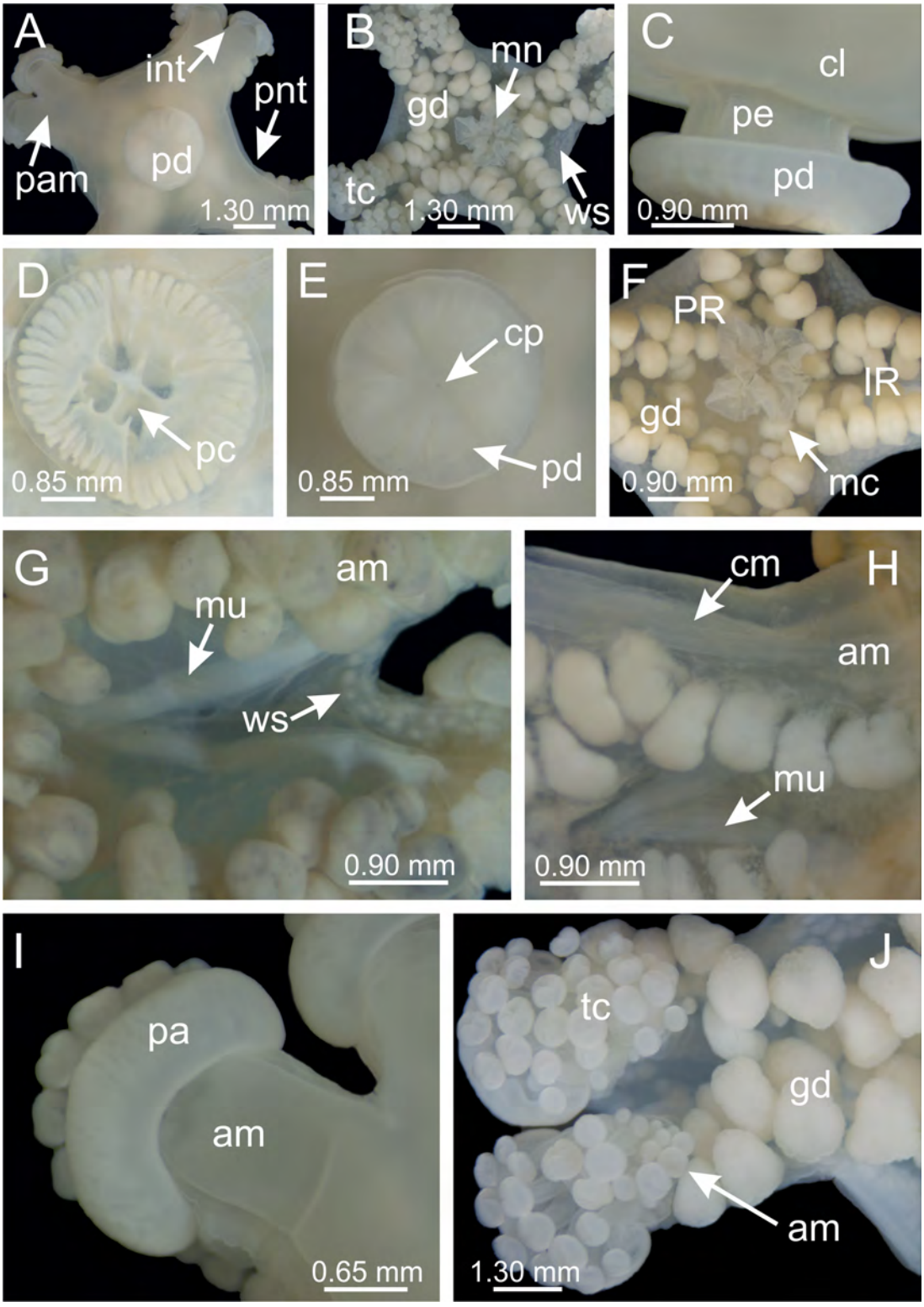

FIGURE 2. *Calvadosia lewisi* **sp. nov.**, preserved specimens (MZUSP 3415, A–C, E–G, I; MZUSP 3416, D, H). A: General view of exumbrella; B: General view of subumbrella; C: Exumbrellar view of the peduncle/calyx connection region; D: Cross section of pedal disk, with four perradial chambers basally; E: Basal view of pedal disk, with a tiny central pore; F: Oral view, indicating manubrium and gonads; G: Interradial longitudinal muscles in calyx, dividing into two bands toward the arms; H: Interradial longitudinal muscles and coronal muscle; I: Detail of pad-like adhesive structures on the exumbrellar tips of arms; J: Subumbrellar tips of arms, with secondary tentacles. Abbreviations: am, arms; cl, calyx; cm, coronal muscle; cp, central pore; gd, gonad; int, interradial notch; IR, interradial region; mn, manubrium; mu, longitudinal muscle; pa, pad-like adhesive structure; pam, paired arms; pc, perradial chambers; pd, pedal disk; pe, peduncle; pnt, perradial notch; PR, perradial region; tc, secondary tentacles; ws, white spots of nematocysts.

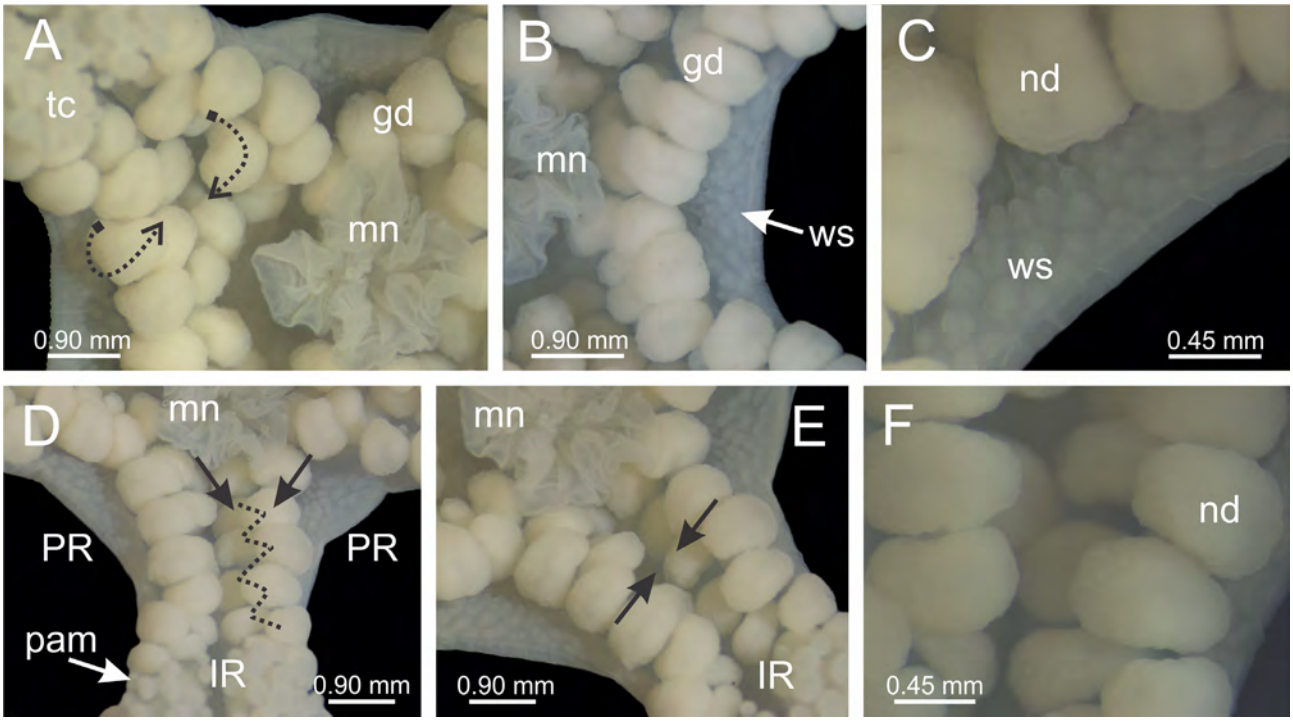

FIGURE 3. Gonads and white spots of nematocysts of *Calvadosia lewisi* **sp. nov.** (MZUSP 3415). A: Nodular curved lobes – curvature of individual lobes shown by dotted arrows; B: Margin of calyx, with white spots of nematocysts; C: Detail of marginal white spots of nematocysts; D: Organization of nodular curved lobes, which are tightly oppressed, giving the impression of two rows of nodular lobes instead of the actual one "zigzag" row; E: Nodular curved lobes facing interradii; F: Detail of nodular curved lobes, with regular shape. Abbreviations: gd, gonad; IR, interradial region; mn, manubrium; nd, nodular lobes; pam, paired arms; PR, perradial region; tc, secondary tentacles; ws, white spots of nematocysts.

tips of arms, on exumbrella, surrounding outermost tentacles near their base (Fig. 2I). Four interradial longitudinal muscles at calyx base, each divided in pyloric region into two bands toward adradial arms (Fig. 2G, H). Coronal muscle divided into eight segments by arms (Fig. 2H). Exumbrella finely granulated with nematocyst (euryteles) warts (Fig. 4D). Conspicuous white nematocyst spots on subumbrella, distributed along calyx margin, at interradii and perradii, to tips of arms (Figs 1A, E; 3B, C). Higher concentration of white spots at perradii, organized in 1–4 rows. White spots also associated with gonads. General color of body reddish to greenish brown (Fig. 1).

Cnidome. Secondary tentacles with two types of nematocysts: isorhiza (abundant), length 18.02–19.65 µm (mean 18.72 µm, number of capsules measured n = 10), diameter 2.12–3.16 µm (mean 2.61 µm, n = 10); and eurytele (scarce), length 14.18–15.96 µm (mean 15.27 µm, n = 10), diameter 5.28–8.04 µm (mean 6.85 µm, n = 10) (Fig. 4A, B). White nematocyst spots with one type of nematocysts: rhopaloids (abundant), length 12.77–15.40 µm (mean 14.29 µm, n = 10), diameter 10.20–11.96 µm (mean 11.34 µm, n = 10) (Fig. 4C).

Etymology. Named after Lewis Jason, a legendary volunteer at the Two Oceans Aquarium (Cape Town, South Africa) who first brought our attention to this animal and made passionate and lengthy notes on the species. Lewis Jason passed away on December 17th, 2014, at the age of 90.

Type locality. Simon's Town, Cape Town, Western Cape, South Africa.

Distribution and habitat. *Calvadosia lewisi* was found at various localities in the Western Cape, South Africa: A-Frame, False Bay, Cape Town; Betty's Bay, Overberg; Castle Rocks, False Bay, Cape Town; Miller's Point, Cape Town; and Simon's Town, Cape Town (Fig. 5C). The species is found from intertidal to shallow subtidal regions, up to 5 m deep, attached to different species of algae.

Remarks. Molecular phylogenetic analyses of Staurozoa (Miranda *et al*. 2016b) revealed a putative new species in South Africa, referred to *Calvadosia* sp. 4 in that study, and herein properly described as *Calvadosia lewisi* **sp. nov.** This species is closely related to *C. tasmaniensis* and *C. corbini*, in a clade whose possible synapomorphy is a broad pad-like adhesive structure on the tip of each arm (Miranda *et al*. 2016b). This feature is also present in *C. hawaiiensis* (Edmondson 1930; Grohmann *et al*. 1999) and in *C. capensis* (Carlgren 1938; Miranda *et al*. 2012b), suggesting that they too may belong to this clade (Miranda *et al*. 2016b). *Calvadosia*

cruxmelitensis has a slightly different pad-like adhesive structure on the tip of the arm, in which the secondary tentacles arise directly from this structure (Corbin 1978; Miranda *et al*. 2016b).

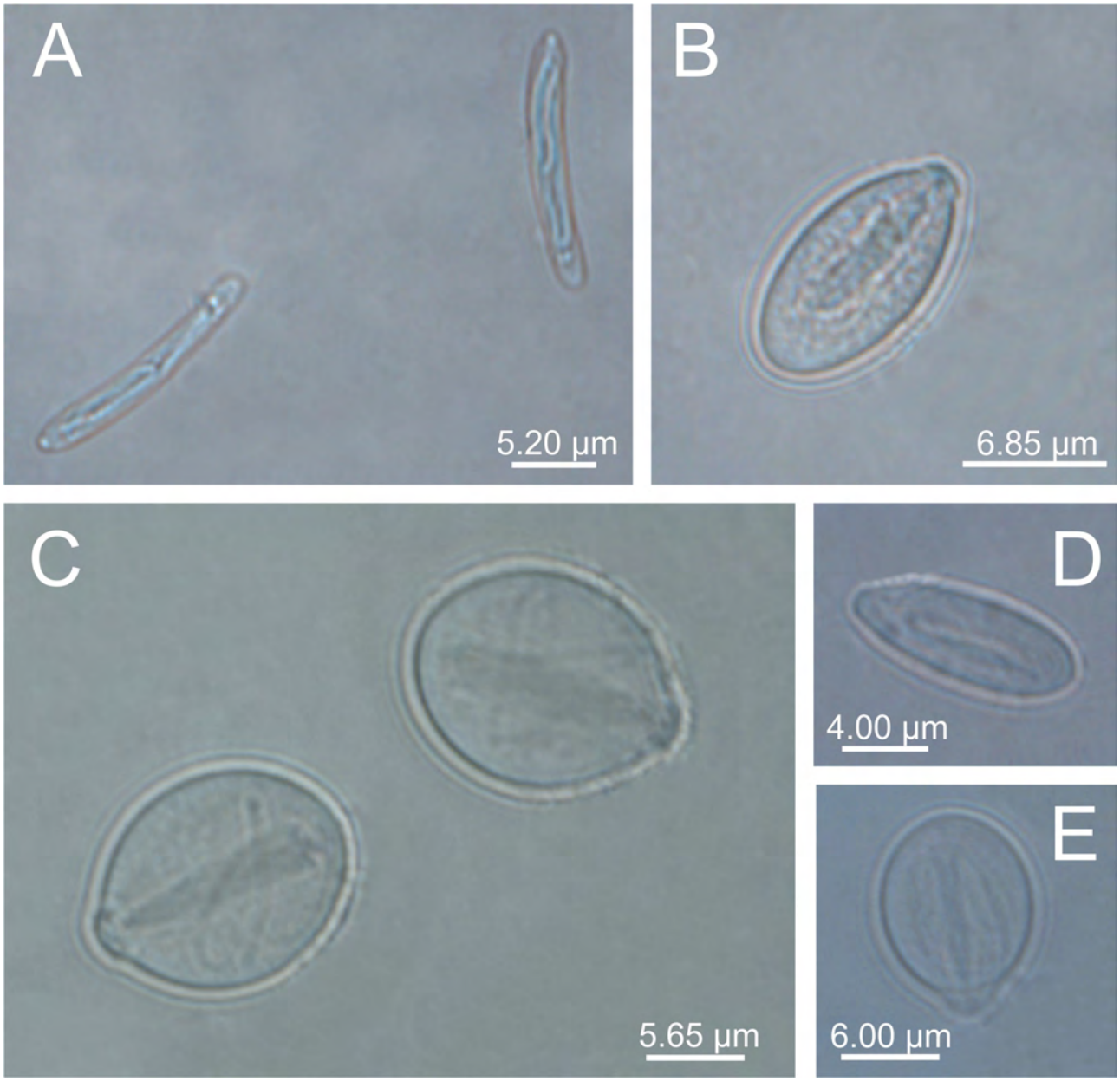

FIGURE 4. Cnidome of *Calvadosia lewisi* **sp. nov.** (MZUSP 3415). A: Isorhiza of secondary tentacles; B: Eurytele of secondary tentacles; C: Rhopaloids of marginal white spots of nematocysts on subumbrella; D: Eurytele of nematocyst warts on exumbrella; E: Rhopaloids of white spots of nematocysts associated with gonads, on subumbrella.

The morphology of *C. lewisi* is similar to *C. tasmaniensis* and *C. corbini*, in accordance with molecular results (Miranda *et al*. 2016b). *Calvadosia tasmaniensis* has been recorded only from Australia (Zagal *et al*. 2011) and *C. corbini* was originally described from Puerto Rico (Larson 1980), subsequently recorded from Brazil (Grohmann *et al*. 1999) and Mexico (Lechuga & Alamo 2005). These species have a wide "open" calyx, cruciform in *C. lewisi* and in *C. corbini* (Figs 1, 6) (Larson 1980; Grohmann *et al*. 1999), with interradial pairing of arms, a feature not evident in *C. tasmaniensis* (Zagal *et al*. 2011). These three species also share a relatively short peduncle (Larson 1980; Grohmann *et al*. 1999; Zagal *et al*. 2011) and broad, pad-like adhesive structures on the tips of the arms (Figs 2I; 6E; 7D). In addition, the gonads of these species are not embedded in the gastrovascular cavity, but are nodular evaginations from the gastrovascular cavity resting on the subumbrella (Figs 1–3, 6, 7) (Larson 1980; Grohmann *et al*. 1999; Zagal *et al*. 2011). The generally smooth shape of the nodular gonads is the hypothetical main distinguishing feature of *C. lewisi*. Analyzed specimens of *C. corbini* and *C. tasmaniensis* (Table 2) have nodular

erect gonads, with irregular shape (described by Larson (1980) for *C. corbini* as looking like "small raisins"), which can have many evaginations, and are distributed in a single, relatively straight row (Figs 6, 7). However, the nodular gonads in *C. lewisi* have a smooth, regular shape, curved toward the interradii, and are tightly arranged in a "zigzag" row (Figs 1–3). Our observations include specimens of different sizes, making it unlikely that there is ontogenetic variation of this feature.

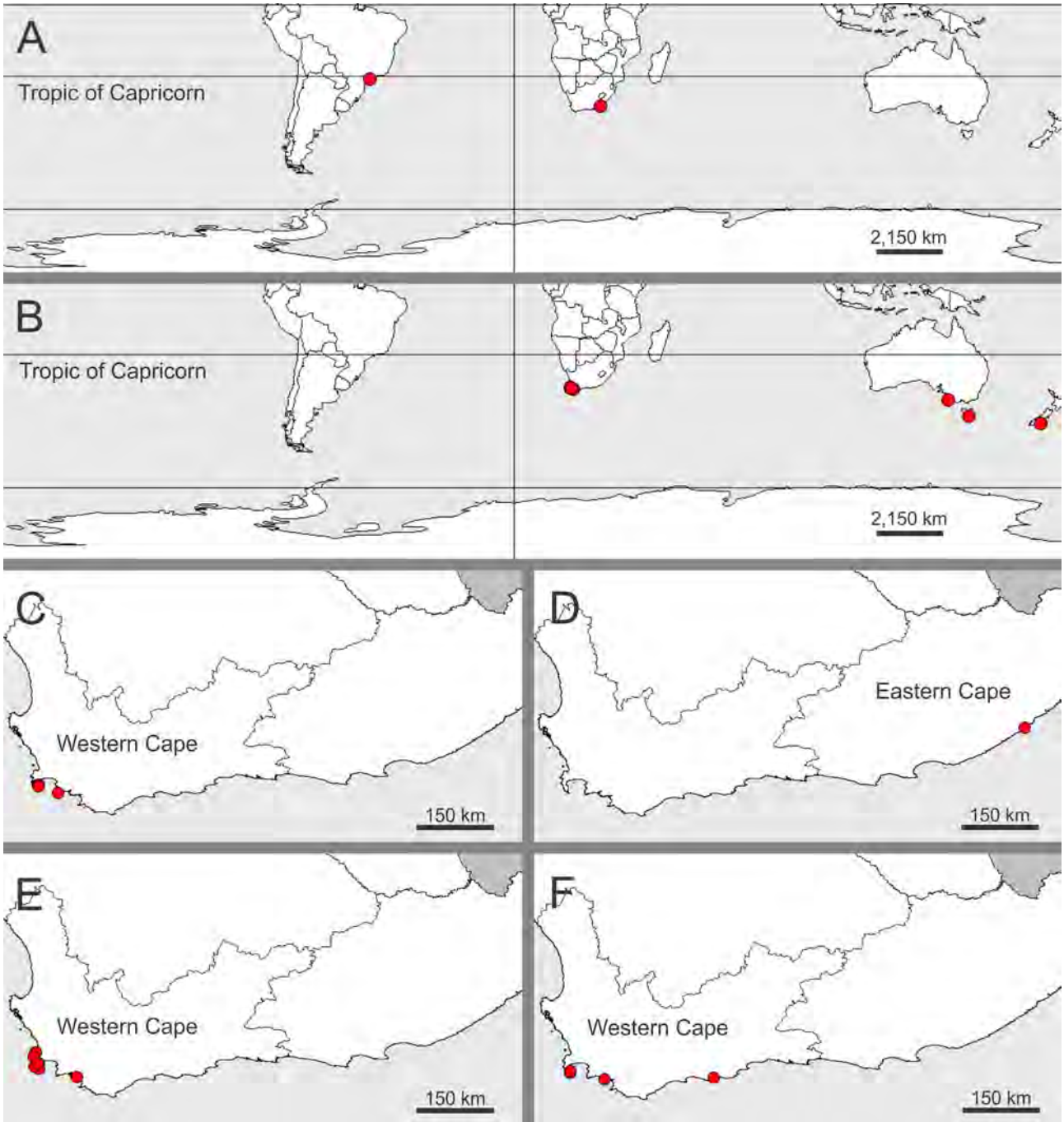

FIGURE 5. Geographic distribution of South African stauromedusae. A: Global distribution of *Calvadosia capensis* (South Africa and Brazil); B: Global distribution of *Depastromorpha africana* (South Africa, Australia, and New Zealand)*; C: Local distribution of *C. lewisi* **sp. nov.** (endemic from South Africa); D: Local distribution of *C. capensis*; E: Local distribution of *D. africana*; F: Local distribution of *L. stephensoni* (endemic from South Africa). Based on Carlgren (1933, 1935, 1938); Zagal *et al*. (2011); Miranda *et al*. (2012b); and new records provided in this study. *Records of *D. africana* outside South Africa need confirmation of their identity (see text and Miranda *et al*. 2016b).

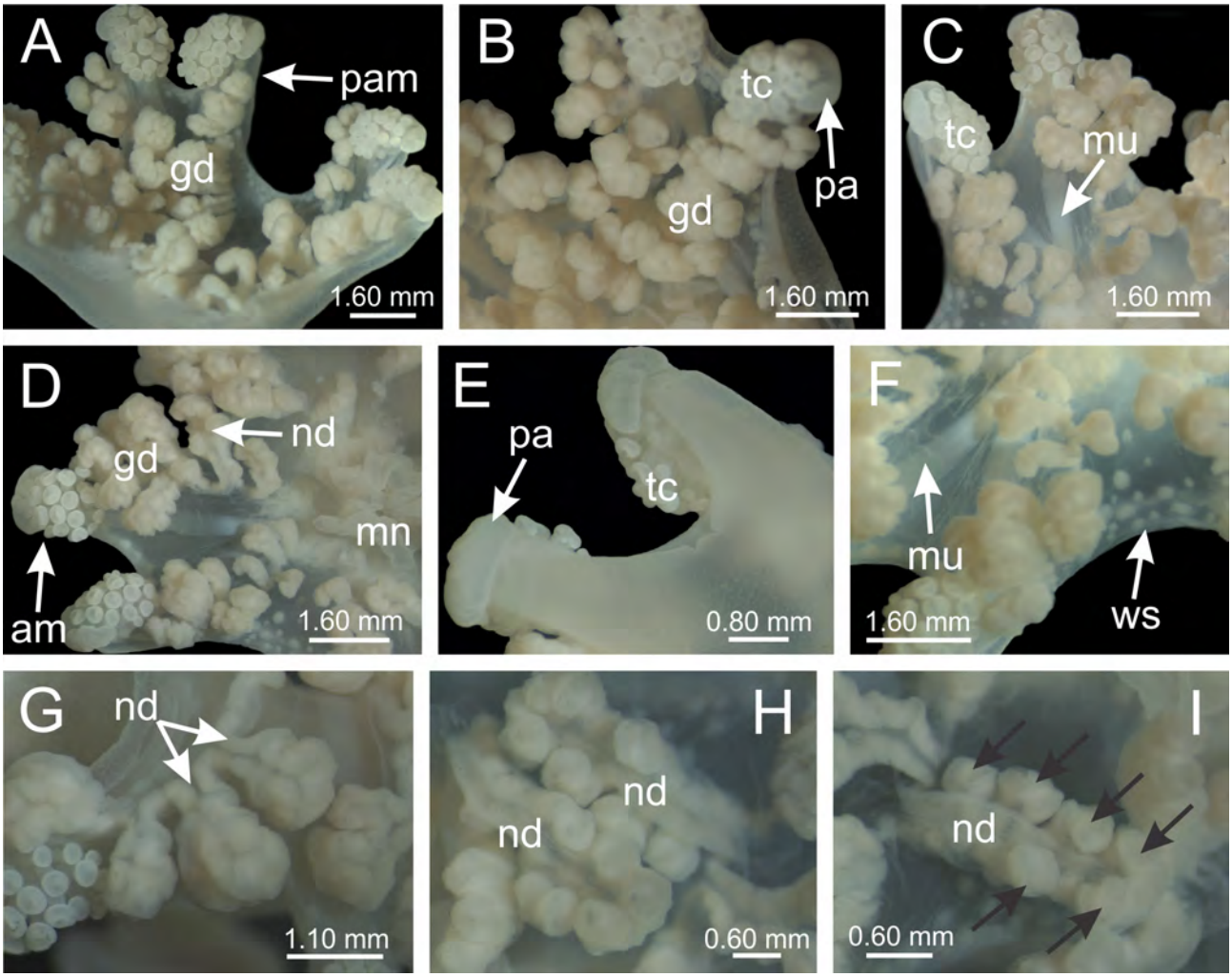

FIGURE 6. *Calvadosia corbini* (Larson, 1980), preserved specimens (MZUSP 1564, A, C–G; MZUSP 1565, B, H, I). A–C: Subumbrellar views, with gonads and paired arms with cluster of secondary tentacle; D: Nodular erect gonads; E: Exumbrellar view, with pad-like adhesive structures on the tips of arms; F: Detail of subumbrellar margin; G–I: Detail of erect nodular lobes of gonads, with irregular shape, sometimes presenting multiple evaginations (indicated by black arrows). Abbreviations: am, arms; gd, gonad; mn, manubrium; mu, longitudinal muscle; nd, nodular lobes; pa, pad-like adhesive structure; pam, paired arms; tc, secondary tentacles; ws, white spots of nematocysts.

Calvadosia capensis (Carlgren, 1938)

(Fig. 8)

Lucernariopsis capensis Carlgren, 1938: 1–6, figures 1–5; Corbin 1978: 285, 289; Grohmann *et al*. 1999: 386; Zagal *et al*. 2011: 652, 660–664; Miranda *et al*. 2012b: 60–64, figures 1, 2; Miranda *et al*. 2016b: 16.
Calvadosia capensis—Miranda *et al*. 2016b: 19, 34, 36.

Source of data. The original description of *C. capensis* (Carlgren, 1938) was based on one specimen collected from intertidal rocks in East London, on the southeast coast of South Africa. The holotype is probably **L393**, from Shelly Beach, East London, Eastern Cape, South Africa (type locality). The material is listed in the "University of Cape Town Ecological Survey" (UCT). In the mid-1980s, UCT donated its museum collections to Iziko South African Museum. However UCT lent samples to specialists without loans being recorded. Iziko South African Museum's curator could not locate the material. In addition, Carlgren (1938) prepared histological sections from this material and one slide is deposited in the Invertebrates Collection of the Swedish Museum of Natural History, catalog number **NRM:EVmain:115053** (GBIF ID 1099397008). A second individual was recorded from Brazil and is deposited in the Museum of Zoology of the University of São Paulo, Brazil, catalog number **MZUSP 1566**

(Miranda *et al*. 2012b). To date the species is known only from these preserved specimens and it has never been seen or photographed alive, despite attempts to collect the species on April 7–8th, 2016, in tidal pools on the rock shore in East London (type locality) and Gunube (about 10km east of East London).

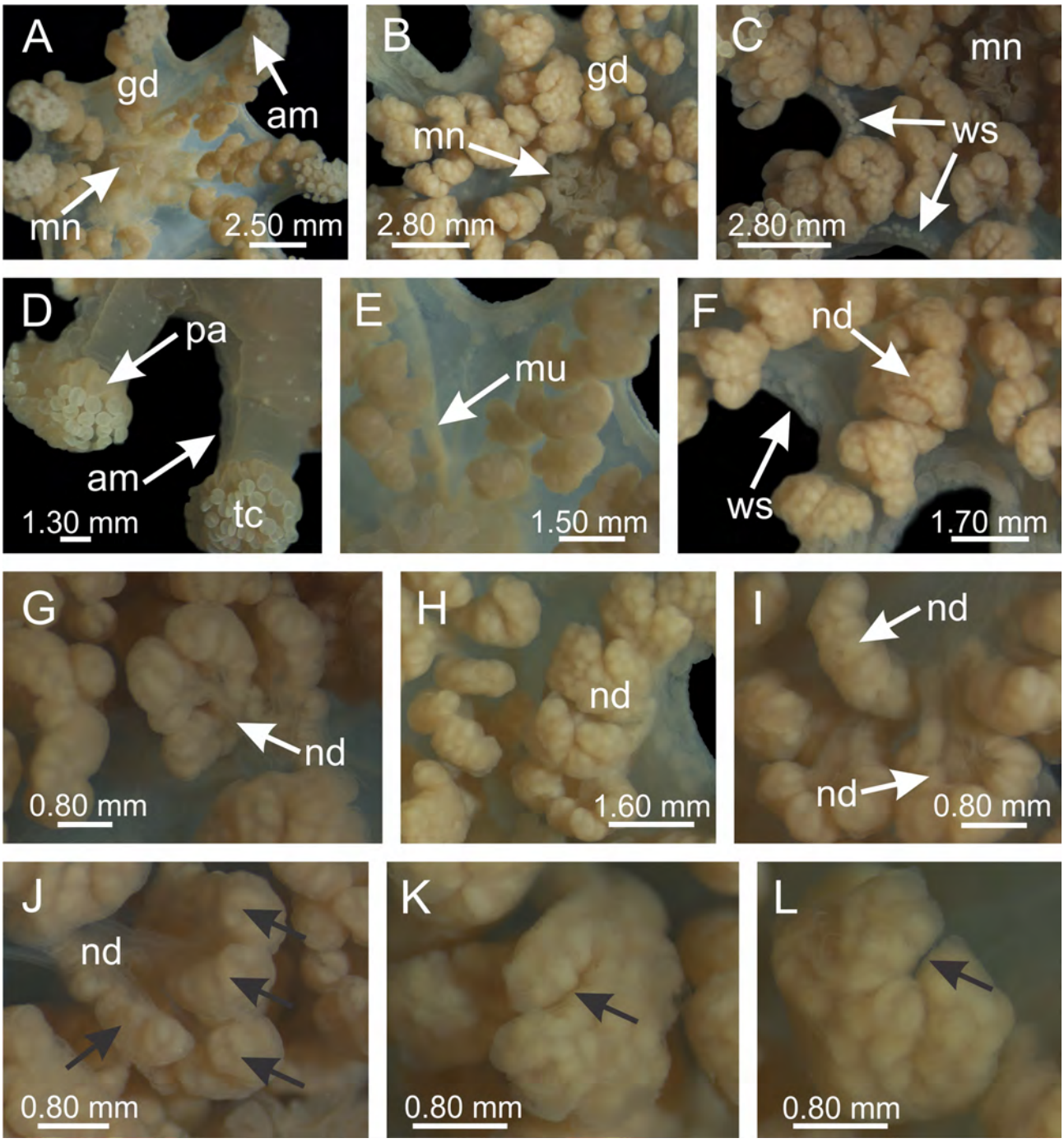

FIGURE 7. *Calvadosia tasmaniensis* (Zagal, Hirano, Mills, Edgar & Barrett, 2011), preserved specimens (USNM 1233739, A, D, E; USNM 1233740, B, C, F–L). A: General oral view; B, C: Detail of subumbrellar oral region with gonads and manubrium; D: Exumbrellar view, with pad-like adhesive structures on the tips of arms; E: Longitudinal muscle toward the arms; F: Detail of subumbrellar margin, with white spots of nematocysts; G–L: Detail of erect nodular lobes of gonads, with irregular shape, sometimes presenting multiple evaginations (indicated by black arrows). Abbreviations: am, arms; gd, gonad; mn, manubrium; mu, longitudinal muscle; nd, nodular lobes; pa, pad-like adhesive structure; tc, secondary tentacles; ws, white spots of nematocysts.

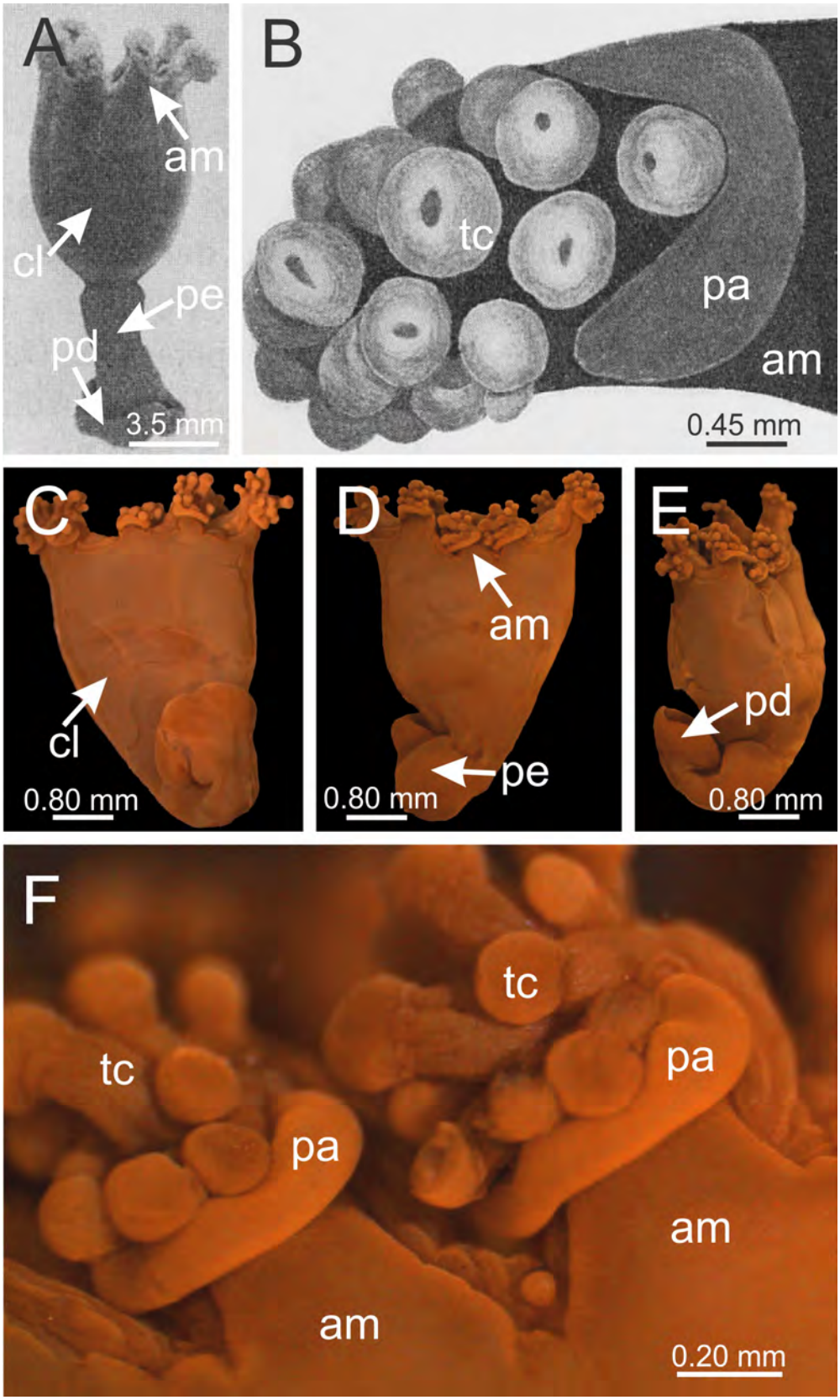

FIGURE 8. *Calvadosia capensis* (Carlgren, 1938), preserved specimens. A: Exumbrellar view (modified from Carlgren 1938); B: Detail of an arm with secondary tentacles and a pad-like adhesive structure (modified from Carlgren 1938); C–E: Exumbrellar view (modified from Miranda *et al*. 2012b); F: Detail of paired arms, with secondary tentacles and pad-like adhesive structures (modified from Miranda *et al*. 2012b). Abbreviations: am, arms; cl, calyx; pa, pad-like adhesive structure; pd, pedal disk; pe, peduncle; tc, secondary tentacles.

Description. (after Carlgren 1938: figures 1–5 and Miranda *et al*. 2012b, figure 1). Body divided into two clearly demarcated regions: calyx and peduncle (Fig. 8A, C–E). Calyx higher than wide, pyramidal, narrowing basally (Fig. 8A, C–E). Peduncle long, about same length as calyx (Fig. 8A, C–E). Peduncle without interradial longitudinal muscle, with single chamber at median region (no histological details at base of peduncle). Broad, swollen adhesive circular pedal disk at base of peduncle (Fig. 8A, E). Calyx without anchors or primary tentacles (Fig. 8A, C–E). Gastrovascular cavity not divided by claustrum. Manubrium with four perradial lips. Numerous gastric filaments in gastrovascular cavity. Eight arms, short, organized in four interradial pairs (Fig. 8A, C–E). Eight gonads not embedded in gastrovascular cavity (but contained within evaginations from the gastrovascular cavity), extending from manubrium to distal end of arms, consisting of several nodular lobes of irregular shape. Each arm with a cluster of secondary hollow knobbed tentacles, similar in shape (Fig. 8B, F). Coronal muscle divided into eight segments by arms. Secondary tentacles with numerous nematocysts of two types: isorhiza and eurytele. Thin, pad-like adhesive structures (abaxial cushion) on tips of arms, on exumbrella, at base of tentacular cluster (Fig. 8B, F). White spots of nematocysts on subumbrella. Preserved specimens green to yellowish brown (only information on preserved specimens available). Total body length about 6.70 to 13.80 mm.

Distribution and habitat. Although known from only two records, this species is widely distributed, having been recorded in Shelly Beach, East London, Eastern Cape, South Africa, in the Indian Ocean (Carlgren 1938); and in Itanhaém, São Paulo, Brazil, in the western Atlantic Ocean (Miranda *et al*. 2012b) (Fig. 5A, D). South African and Brazilian specimens were collected attached to *Sargassum* sp. in the intertidal zone ("University of Cape Town Ecological Survey"; Miranda *et al*. 2012b).

Remarks. *Calvadosia capensis* was described from South Africa based on a single specimen (Carlgren 1938), and its general morphology (Fig. 8) is similar to *C. hawaiiensis*, from Hawaii (Edmondson 1930), with a narrowly-opened (pyramidal) calyx, paired arms, and thin pad-like adhesive structures on the tips of the arms (although overlooked in *C. hawaiiensis* by Larson 1980; see Grohmann *et al*. 1999). However, based on the literature, *C. capensis* has shorter arms and longer peduncle compared to *C. hawaiiensis* (Edmondson 1930, figure 6; Carlgren 1938, figure 1, Miranda *et al*. 2012b, figure 1).

Suborder Myostaurida Miranda, Hirano, Mills, Falconer, Fenwick, Marques & Collins, 2016b

Family Haliclystidae Haeckel, 1879

Genus *Depastromorpha* Carlgren, 1935

Depastromorpha africana Carlgren, 1935

(Figs 9, 10)

Depastromorpha africana Carlgren, 1935: 1–24, figures 1–12; Kramp 1961: 300; Grohmann *et al*. 1999: 386, 387; Dawson 2004: 252, figure 1; Collins & Daly 2005: 222, 226, figures 5–7; Cairns *et al*. 2009: 70; Zagal *et al*. 2011: 651–666, figures 2, 4, 8; Miranda *et al*. 2016b: 2, 6, 12–15, 17, 19, 25, 26, 36, figures 1, 3–5, 7, 12, 13.

Material examined. MZUSP 3418, 8 specimens, Sea Point, Cape Town, Western Cape, South Africa (-33.9130, 18.3874), 22 December 2014, intertidal pools, on *Gigartina polycarpa*, formaldehyde solution 5%, col. & det. C. Griffiths. **MZUSP 3419**, 1 specimen, Kalk Bay, Cape Town, Western Cape, South Africa (-34.1266, 18.4498), 28 March 2013, intertidal pools, on *Caulerpa filiformis*, formaldehyde solution 5%, col. & det. C. Griffiths. **MZUSP 2733**, 1 specimen, Kalk Bay, Cape Town, Western Cape, South Africa (-34.1266, 18.4498), 25 April 2013, intertidal pools, on *Caulerpa filiformis*, ethanol 90%, col. & det. C. Griffiths. **MZUSP 2734**, 1 specimen, Kalk Bay, Cape Town, Western Cape, South Africa (-34.1266, 18.4498), 25 April 2013, intertidal pools, on *Caulerpa filiformis*, ethanol 90%, col. & det. C. Griffiths. **Iziko South African Museum MB-A083795**, 1 specimen, Kalk Bay, Cape Town, Western Cape, South Africa (-34.1266, 18.4498), 28 March 2013, intertidal pools, on *Caulerpa filiformis*, formaldehyde solution 5%, col. & det. C. Griffiths. **Iziko South African Museum MB-A083796**, 1 specimen, Kalk Bay, Cape Town, Western Cape, South Africa (-34.1266, 18.4498), 25 April 2013, intertidal, on *Caulerpa filiformis*, ethanol 80%, col. & det. C. Griffiths. **Iziko South African Museum MB-A083797 (CP 718A)**, 1 specimen, Kalk Bay, Cape Town, Western Cape, South Africa (-34.1266, 18.4498), 9 April 1947,

intertidal, on *Caulerpa filiformis*, ethanol 80%, col. University of Cape Town Ecological Survey, det. C. Griffiths. **Iziko South African Museum MB-A084063**, 5 specimens, Camps Bay, Cape Town, Western Cape, South Africa (-33.9566, 18.3755), 12 January 2016, intertidal, on various large algae in rock pools, ethanol 80%, col. & det. C. Griffiths. **Iziko South African Museum H 5108**, 5 specimens, Castle Rocks, False Bay, Cape Town, Western Cape, South Africa (-34.2385, 18.4766), 19 January 2003, depth 1 m, ethanol 80%, col. Y. Hirano, det. C. Griffiths.

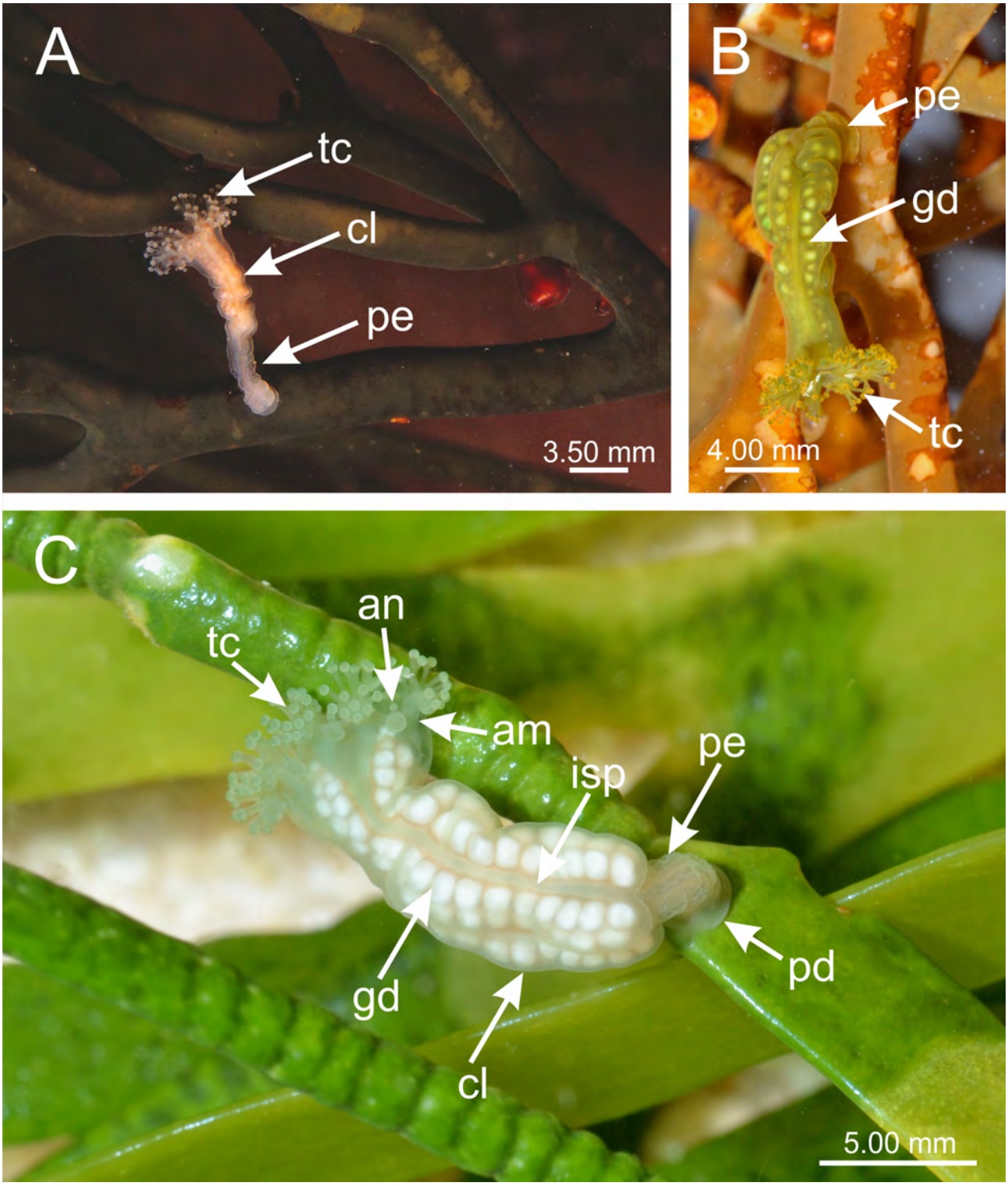

FIGURE 9. *Depastromorpha africana* Carlgren, 1935, living specimens. A–C: Exumbrellar views of specimens attached to *Bicurcariopsis capensis* (A, B) and to *Caulerpa filiformis* (C). Abbreviations: am, arms; an, anchors; cl, calyx; gd, gonad; isp, interradial septum; pd, pedal disk; pe, peduncle; tc, secondary tentacles. Photo credit: Charles Griffiths (A–C).

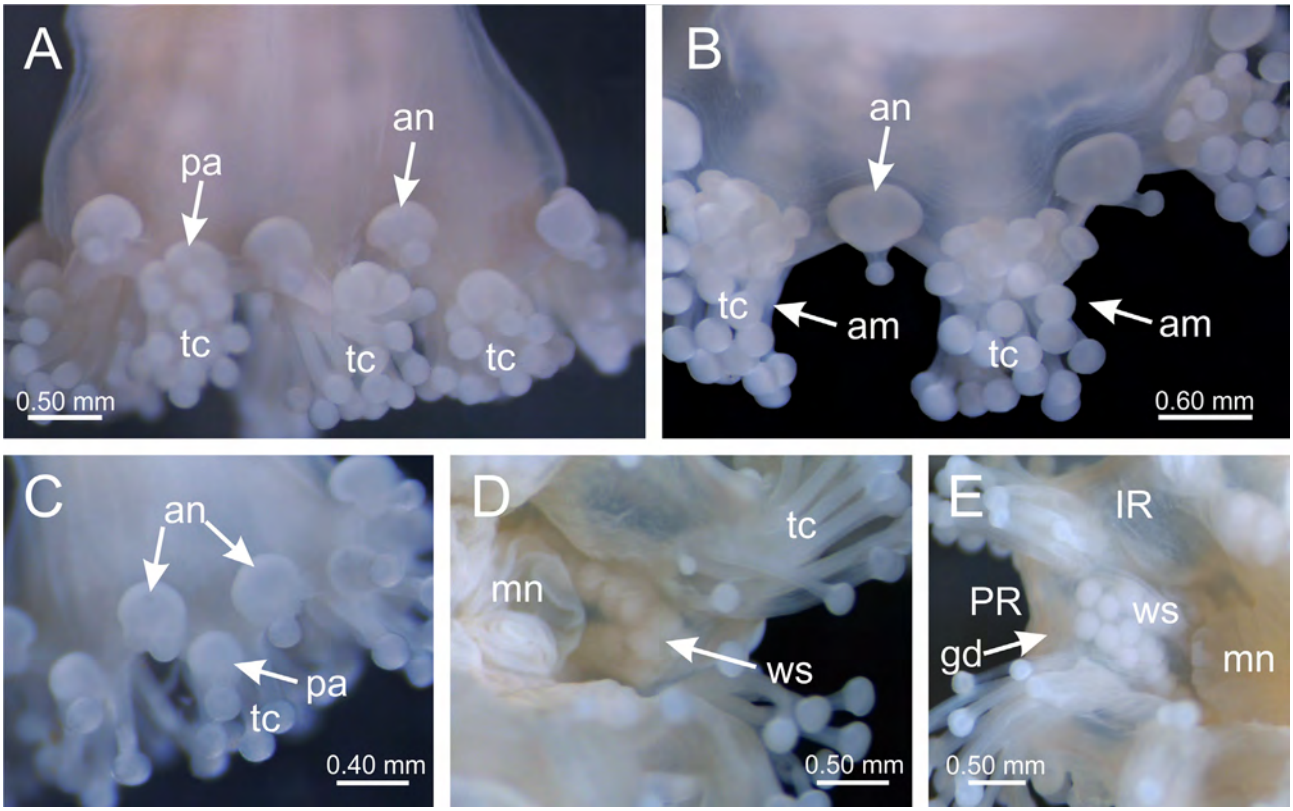

FIGURE 10. *Depastromorpha africana* Carlgren, 1935, preserved specimens (MZUSP 3418, A, B, D, E; MZUSP 3419, C). A: Margin of exumbrella, with arms and anchors; B: Detail of anchors; C: Individual pad-like adhesive structures in the outermost secondary tentacles; D: White spots of nematocysts on subumbrella; E: Perradial gonads associated with white spots of nematocysts on subumbrella. Abbreviations: am, arms; an, anchors; gd, gonad; IR, interradial region; mn, manubrium; pa, pad-like adhesive structure; PR, perradial region; tc, secondary tentacles; ws, white spots of nematocysts.

Not kept, 3 specimens, Scarborough, Cape Town, Western Cape, South Africa (–34.2017, 18.3702), 19 August 2013, from rockpools, on *Sargassum longifolium*, observed by G. Jones. **Not kept**, several specimens, Green Point, Cape Town, Western Cape, South Africa (–33.8990, 18.4078), 17 March 2014, on *Brassicophycus brassicaeformis*, observed by C. Griffiths. **Not kept**, 4 specimens, Moullie Point, Cape Town, Western Cape, South Africa (–33.8996, 18.4046), 22 December 2014, intertidal, on *Champia*, observed by C. Griffiths. **Not kept**; 1 specimen, Hermanus, Overberg, Western Cape, South Africa (–34.4210, 19.2437), March 1991, on *Codium*, observed by C. Griffiths. **Not kept**, 5 specimens; Dalebrook, Cape Town, Western Cape, South Africa (–34.1196, 18.4401), 2 April 1966, shallow subtidal, on *Caulerpa filiformis*, observed by G. Branch. **USNM 1233748**, 5 specimens, Gerloff Bay, Victoria, South Australia, Australia, 13 January 1998, intertidal, formaldehyde solution 5%, col. & det. Y. Hirano

Information on type material. The holotype is probably **A194**, from Oudekraal, Cape Town, Western Cape, South Africa (type locality). As mentioned for *C. capensis*, the material is listed in the "University of Cape Town Ecological Survey" but could not be located in the Iziko South African Museum's collection.

Description. (complemented with Carlgren 1935). Calyx higher than wide, cylindrical (Fig. 9). Peduncle with four perradial chambers and four interradial longitudinal muscles. Gastrovascular cavity divided by claustrum. Manubrium with four perradial lips (Fig. 10D, E). Numerous gastric filaments in gastrovascular cavity. Gonads extending from pyloric region to perradial margin of calyx, embedded in gastrovascular cavity (Figs 9B, C; 10E). Gonadal vesicles organized in rows (Fig. 9B, C). Eight short (rudimentary) adradial arms (Figs 9, 10). Each arm with a cluster of about 25 secondary hollow, knobbed tentacles (Figs 9, 10). Individual, pad-like adhesive structures in outermost secondary tentacles (Fig. 10A–C). Perradial and interradial anchors between arms, with remnant of primary tentacles (Fig. 10A–C). Coronal muscle entire, internal to anchors. White spots of nematocysts associated with perradial gonads (Fig. 10D, E). General color of body very variable: orange, green, yellow, white (Fig. 9). Total body length about 10.0 to 15.0 mm.

Distribution and habitat. The species was recorded for the first time at Oudekraal, Cape Town, Western Cape, South Africa (Carlgren 1935) (Fig. 5B, E). Zagal *et al*. (2011) extended the occurrence of *D. africana* to Victoria and Tasmania, in Australia, and Otago, in New Zealand (Fig. 5B), but molecular data indicated that *Depastromorpha* in Australia might be a distinct species (see *Depastromorpha* sp. AUS in Miranda *et al*. 2016b and remarks below). In this study we provide several new records for the species in the Western Cape, South Africa: Camps Bay, Cape Town; Castle Rocks, False Bay, Cape Town; Dalebrook, Cape Town; Green Point, Cape Town; Hermanus, Overberg; Kalk Bay, Cape Town; Moullie Point, Cape Town; Scarborough, Cape Town; Sea Point, Cape Town (Fig. 5B, E). *Depastromorpha africana* is generally found from the intertidal to shallow subtidal depths, up to 14 m deep (Zagal *et al*. 2011), attached to various species of algae (Zagal *et al*. 2011; this study).

Remarks. *Depastromorpha* was erected by Carlgren (1935) and comprises the single species, *D. africana*, whose original description was based on a single specimen from Oudekraal, Cape Town, South Africa. There are unpublished observations of the species in Australia and New Zealand (Grohmann *et al*. 1999), subsequently confirmed in Victoria and Tasmania (Australia), and Otago (New Zealand) (Zagal *et al*. 2011; specimens deposited in the Tasmanian Museum and Art Gallery, **TMAG K3857–K3862**). According to Zagal *et al*. (2011), individuals from Australia and New Zealand matched Carlgren's (1935) description, although they have slightly smaller dimensions. However, molecular markers from *D. africana* of South Australia differ substantially from those from South African specimens, indicating the existence of a second species of the genus (Miranda *et al*. 2016b). If confirmed, *D. africana* would be endemic to South Africa. Detailed morphological and molecular studies, comparing the populations from South Africa, Australia, and New Zealand are necessary to assess this hypothesis and the possible existence of cryptic species (see examples in Knowlton 2000; Dawson & Jacobs 2001). Whatever the outcome, the South African species will retain its name by priority.

Family Lipkeidae Vogt, 1886

Genus *Lipkea* Vogt, 1886

Lipkea stephensoni Carlgren, 1933

(Fig. 11)

Lipkea stephensoni Carlgren, 1933: 1–15, figures 1–14; Carlgren 1935: 19, 23; Kramp 1961: 299; Grohmann *et al*. 1999: 386; Pisani *et al*. 2007: 7; Zagal *et al*. 2011: 652, 663, 664; Miranda *et al*. 2016b: 20, 26, 32, 38.

Material examined. Iziko South African Museum MB-A083794, 2 specimens, Onrust River, Overberg, Western Cape, South Africa (-34.4196, 19.1801), January 1992, intertidal pools, under rock, ethanol 70%, col. & det. C. Griffiths. **Not kept**, 2 specimens, Smitswinkel Bay, False Bay, Cape Town, Western Cape, South Africa (-34.2743, 18.4728), between 1990–2003, depth 3–4 m, observed by G. Spiby. **Not kept**, 3 specimens, False Bay (between Partridge Point and Castle Rocks), Cape Town, Western Cape, South Africa (-34.2457, 18.4795), April 2012, depth 23 m, observed and photographed by G. Jones.

Information on type material. The holotype is probably **S185**, from Still Bay, Eden, Western Cape, South Africa (type locality), found in pool under stones. The material is listed in the "University of Cape Town Ecological Survey" but could not be located in the Iziko South African Museum's collection.

Description. (complemented with Carlgren 1933). Calyx elongated, funnel-shaped (Fig. 11). Peduncle single-chambered, with four interradial longitudinal muscles. Four interradial septa visible in calyx (Fig. 11D, F, G). Variable number of marginal lappets (arms?), with reduced (rudimentary) tentacles in one row along their margin (Fig. 11A–C), although some specimens with smooth marginal lappets (Fig. 11D–G). Gastrovascular cavity not divided by claustrum. Manubrium with four perradial lips (Fig. 11B, D, G). Numerous gastric filaments in gastrovascular cavity. Gonads embedded in gastrovascular cavity of subumbrella, not extending into marginal lappets (confined to basal part of calyx) (Fig. 11B, D, G). Perradial and interradial anchors absent. Pad-like adhesive structures absent. Coronal muscle entire (Fig. 11D, E). White spots of nematocysts on subumbrellar surface, margin of calyx, and marginal lappets (Fig. 11). General color of body pinkish white (Fig. 11). Total body length about 8.0 to 16.0 mm.

Distribution and habitat. The type locality for *L. stephensoni* is Still Bay, Eden, Western Cape, South Africa

(Carlgren 1933). These new records are also in the Western Cape: Onrust River, Overberg; between Partridge Point and Castle Rocks, False Bay, Cape Town; Smitswinkel Bay, False Bay, Cape Town (Fig. 5F). The species was recorded from intertidal pools to 23 m deep, attached to rocks.

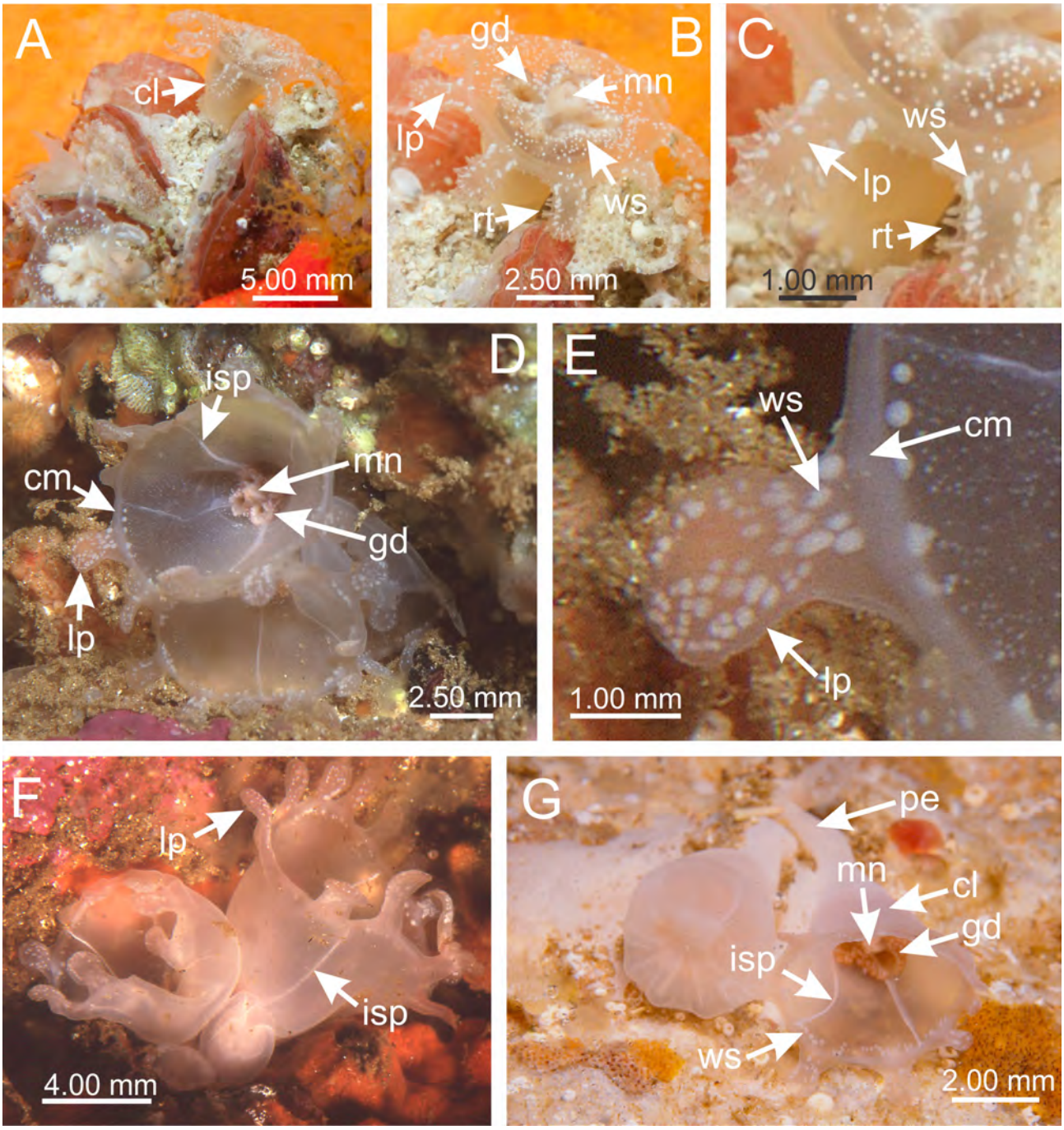

FIGURE 11. *Lipkea stephensoni* Carlgren, 1933, living specimens in the field. A, B, D, F, G: Exumbrellar and subumbrellar views of different specimens; C: Detail of marginal lappet with rudimentary tentacles; E: Detail of marginal lappet without rudimentary tentacles. Abbreviations: cl, calyx; cm, coronal muscle; gd, gonad; isp, interradial septum; lp, marginal lappet; mn, manubrium; pe, peduncle; rt, rudimentary tentacles; ws, white spots of nematocysts. Photo credits: Georgina Jones (A–C); Geoff Spiby (D–F); Charles Griffiths (G; Iziko South African Museum MB-A083794).

Remarks. There are three valid species in the genus *Lipkea*: *Lipkea ruspoliana* Vogt, 1886, *Lipkea sturdzii* (Antipa, 1893), and *Lipkea stephensoni* Carlgren, 1933. *Lipkea ruspoliana* was originally recorded from a single specimen from Alghero, on the Sardinian coast of the Mediterranean Sea (Vogt 1886, 1887). The Sardinian specimen was defined by its peculiar morphology, with eight marginal lappets in the perradii and interradii with

mucous glands, but without tentacles (Vogt 1886, 1887). New specimens recently found in aquaria of the Oceanographic Museum of Monaco have 8–12 adradial lappets (Pisani *et al*. 2007), raising questions about intraspecific variation and the homology of these structures with arms and primary tentacles/anchors (Miranda *et al*. 2016b).

Capria sturdzii Antipa, 1893 was described based on one specimen from Capri Island, Gulf of Naples, Italy, being the only species of the genus *Capria* and the family Capriidae (Antipa 1893). Carlgren (1933) synonymized *Lipkea* and *Capria*, proposing the name *Lipkea sturdzii* (see also Kramp 1961). *Lipkea sturdzii* has not been observed since its original description, but it differs from *L. ruspoliana* by the presence of a row of 16–20 tooth-like or short finger-shaped rudimentary tentacles, which are fused one to another by a web (Antipa 1893; Mayer 1910).

Finally, *Lipkea stephensoni* is the only formally described *Lipkea* species outside of Europe. The species was also described based on a single specimen from Still Bay, Eden, South Africa (Carlgren 1933), characterized by eight adradial short lappets with 30–40 reduced tentacles in one row along their margin (Fig. 11A–C). However, the additional specimens that we observed show that the number of marginal lappets is variable in *L. stephensoni* (Fig. 11; as seems to be common in *Lipkea* species, Pisani *et al*. 2007; Zagal *et al*. 2011), as is the presence of the rudimentary marginal tentacles (Fig 11C, E). The original description of *L. stephensoni* was based on a specimen found in the intertidal zone (Carlgren 1933), but photographs of not-kept *L. stephensoni* stauromedusae revealed that specimens from deeper water (about 23 m deep) have rudimentary tentacles in the lappets (Fig. 11A–C), whereas intertidal and subtidal specimens (Fig. 11D–G) have smooth marginal lappets, similar to those of *L. ruspoliana*, indicating either an intraspecific variation in *L. stephensoni* or the existence of an additional (new) species, a hypothesis that cannot be tested until more specimens become available.

Indeed, the identification of *Lipkea* species is difficult (Zagal *et al*. 2011), based on subtle differences (presence or absence, and number and distribution of reduced tentacle-like structures along the margin of each lappet, Zagal *et al*. 2011) that have never been tested in a phylogenetic context. In addition, there is little information on intraspecific variation (Vogt 1886, 1887; Pisani *et al*. 2007) and no information on morphological changes during development. As a consequence, there are numerous unidentified records around the world, including specimens from Australia (Zagal *et al*. 2011), New Zealand (Cairns *et al*. 2009), and Japan (Miranda *et al*. 2016b). Australian specimens seem to have a similar morphology to *L. stephensoni*, with a single row of 18–27 reduced tentacles along the margin of the lappets (Carlgren 1933; Zagal *et al*. 2011), although, as discussed, it is equivocal whether the presence of rudimentary tentacles should be considered a diagnostic character (Uchida 1929; Zagal *et al*. 2011). Therefore, the validity of described and possibly new *Lipkea* species remains to be vigorously tested in further investigations.

Acknowledgements

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