

Resurrection of the genus *Licornia* for *Scrupocellaria jolloisii* (Bryozoa) and related species, with documentation of *L. jolloisii* as a non-indigenous species in the western Atlantic

LEANDRO M. VIEIRA¹, MARY E. SPENCER JONES² AND JUDITH E. WINSTON³

¹Departamento de Zoologia, Instituto de Biociências and Centro de Biologia Marinha, Universidade de São Paulo, São Sebastião, SP 11600–000, Brazil, ²Department of Life Sciences, Natural History Museum, Cromwell Road, London, SW7 5BD, UK, ³Virginia Museum of Natural History, 21 Starling Avenue, Martinsville, VA 24112, USA

Recent studies of the large cheilostome bryozoan genus Scrupocellaria have shown a greater degree of taxonomically informative morphological variation in zooids, opesia, and polymorphic structures than previously recognized. Only one subgenus has been named within the genus, Retiscrupocellaria d'Hondt, 1988, erected for Scrupocellaria jolloisii. In this work we further analyse S. jolloisii and its related species, resurrecting an earlier genus name, Licornia van Beneden, 1850 for Licornia jolloisii, and nine relatives, L. annectens, L. cervicornis, L. cyclostoma, L. diadema, L. ferox, L. gaspari, L. longispinosa, L. macropora, and L. prolata. Licornia jolloisii was originally described from the Red Sea, and most species of the genus occur in the Indo-Pacific region. The species, however, has now been found in the Western Atlantic, in the Florida Keys, US, and in Bahia de Todos Santos, Brazil.

Keywords: Bryozoa, Candidae, exotic species, first record, new combination, *Retiscrupocellaria*

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INTRODUCTION

The genus *Scrupocellaria* van Beneden, 1845 comprises about 80 extant species of Candidae (Bock, 2012) characterized by bifurcation type 8 (acc. Harmer, 1923) and zooids with a basal vibracular chamber. Despite the morphological variations found among species assigned to *Scrupocellaria* (e.g. shape of zooids, opesia and polymorph structures; see Harmer, 1926), only one species has been reassigned to a distinct subgenus. The subgenus *Retiscrupocellaria* d'Hondt, 1988, erected for *Acamarchis jolloisii* Audouin, 1826, is distinguished by branches joined by transversal tubes and basal vibracular chambers with an oblique groove to the axis. No additional records or taxonomic information have been published on this subgenus since its description, and a thorough search of the bryozoan taxonomic literature revealed that van Beneden (1850) had already introduced a new genus *Licornia* for *Acamarchis jolloisii*, giving that name priority.

Acamarchis jolloisii was described from Egypt (Audouin, 1826), and later recorded in the Red Sea by Waters (1909) under two different names, *Scrupocellaria jolloisii*, for specimens with spines, and a new species *Scrupocellaria mansueta* Waters, characterized by unarmed zooids. Both were

synonymized by d'Hondt (1988) under *S. jolloisii* (incorrect subsequent spelling). Waters (1909) noted the absence of *Scrupocellaria jolloisii* in the Suez Canal, but Hastings (1927) later reported its occurrence from the Suez Canal (Port Said area, Egypt). D'Hondt (1988) reported the species from the Mediterranean coast of Israel.

The present study includes a description of the genus *Licornia* and the type species, *Licornia jolloisii*. Additional information on the genus *Licornia* is provided, and new combinations for nine species previously assigned to *Scrupocellaria* are established. We also report *Licornia jolloisii* for the first time outside the Red Sea and Mediterranean waters; newly invasive for the south-eastern Atlantic coast of the United States of America and the north-eastern coast of Brazil.

MATERIALS AND METHODS

Western Atlantic material of *Licornia jolloisii* was obtained from 1–2 m of water under overhangs in the limestone walls of a man-made canal at Big Torch Key, one of the Florida Keys. It was collected in December, 2005 by Don De Maria of Sea Samples, Summerland Key, Florida. North-eastern Brazilian specimens were obtained from 1 m depth on artificial substratum at Itaparica, Todos os Santos Bay, Bahia state. They were collected in January, 2011 by Laura Pioli Kremer and in February, 2012 by Rosana Moreira

Corresponding author:

L.M. Vieira

Email: leandromanazoni@hotmail.com

Rocha from fouling panel samples. Voucher specimens were deposited at the Virginia Museum of Natural History (VMNH, USA) and Museu de Zoologia da Universidade de São Paulo (MZUSP, Brazil). Comparative specimens listed are deposited at the Natural History Museum, London (NHMUK, UK), Museum of Tropical Queensland, Townsville (MTQ, Australia), Museum Victoria (NMV, Australia), Santa Barbara Museum of Natural History (SBMNH, USA) and the Smithsonian Institution, National Museum of Natural History (NMNH, USA). In addition to the comparative material, type and non-type specimens of *Scrupocellaria* deposited in different collections, including those of American Museum of Natural History (AMNH, USA), Museum of Comparative Zoology (MCZ, USA) and Muséum national d'Histoire naturelle (MNHN, France) were also examined.

All colonies were examined under a stereomicroscope and selected specimens were mounted for examination in a scanning electron microscope (SEM), a Zeiss EVO-60 at the VMNH for coated specimens and an SEM with an environmental chamber, a LEO 1455-VP at the NHMUK for uncoated specimens. Measurements were made from digital SEM images using the analysing software ImageJ[®].

SYSTEMATICS

- Class GYMNOLAEMATA Allman, 1856
 Order CHEILOSTOMATA Busk, 1852
 Suborder NEOCHEILOSTOMINA d'Hondt, 1985
 Infraorder FLUSTRINA Smitt, 1868
 Family CANDIDAE d'Orbigny, 1851
 Genus *Licornia* van Beneden, 1850

TYPE SPECIES

Acamarchis jollaisii (sic) Audouin, 1826 (misspelling of *Acamarchis jolloisii* Audouin) by original designation.

SYNONYM

Retiscrupocellaria d'Hondt, 1988 [Type species: *Acamarchis jolloisi* Audouin, 1826 (incorrect subsequent spelling) by original designation, see d'Hondt (1988), p. 198]

DIAGNOSIS

Candidae having almost rectangular zooids with broadly oval opesia occupying most of the frontal surface, and with anastomosing tubes connecting the colony branches. Joints crossing the proximal opesia of outer zooids and below the opesia of the inner zooids at the bifurcation. Cryptocyst vestigial or absent. Frontal scuta and oral spines often present. Frontal avicularia present, triangular to aquiline. Vibracular chamber tapering distally, triangular to drop-shaped, with a proximal rhizoidal foramen; uncurved setal groove directed obliquely to the axis of the internode and occupying about two-thirds of vibracular chamber length; single axial vibraculum. Ooecia with porous ectooecium.

REMARKS

Bryozoan taxonomists have long considered *Scrupocellaria* van Beneden, 1845 to be a well-defined genus. Mixtures of characters, however, are observed among the many species assigned to this genus: viz. ovicells with single fenestra or with many pores, variable shape and size of opesia, basal vibracular chamber, and frontal and lateral avicularia (Tilbrook &

Vieira, 2012). D'Hondt (1988) also recognized the presence of shared characteristics between *Acamarchis jolloisii* and some other species of both *Scrupocellaria* and *Canda*, and designated a new subgenus, *Retiscrupocellaria*. This subgenus was characterized as having anastomosing tubes connecting the colony branches, as in *Canda* Lamouroux, 1816—but having internodes with zooids in a single plane, unlike *Canda* which has zooids in two series with their frontal surfaces facing obliquely outwards from the axis—having a vibracular chamber at the proximal end of the basal zooidal surface (as in *Scrupocellaria*), having colonies with planar branches (as in *Scrupocellaria*), but being distinct from *Canda* and *Scrupocellaria* in having a dagger-shaped scutum. On the basis of these differences in morphological characters between *Acamarchis jolloisii* and some other *Scrupocellaria* we also consider *Retiscrupocellaria* a distinct taxon.

However, Van Beneden (1850) had already erected a new genus, *Licornia*, for *Acamarchis jollaisii* (sic) Audouin, although its morphological features or distinctions were not described in the original publication. This genus name has not been used since its original description, but according to the principle of priority of ICZN (1999, Art. 23), *Retiscrupocellaria* d'Hondt, 1988 must be considered a junior synonym of *Licornia* van Beneden, 1850 and no reversal of precedence can be applied (ICZN, 1999, Art. 23.9).

Despite the absence of morphological unity in the genus *Scrupocellaria* (see Tilbrook & Vieira, 2012), the genus (and those species to be included within the genus) must include most of the diagnostic characteristics observed in the type species *Scrupocellaria scruposa*, viz. (i) joints crossing the proximal opesia of outer zooids and below the opesia of the inner zooids at the bifurcation, (ii) aquiline lateral avicularium, (iii) vibraculum with slightly curved setal groove obliquely directed and occupying two-thirds of vibraculum length, (iv) two axial vibracula, (v) ovicell with single small ectooecial fenestra and with an associated avicularium (Figure 1A, B). We used five morphological characteristics to define *Licornia* and distinguish species belonging to the genus from some of the species previously assigned to *Scrupocellaria*: (i) joints crossing the proximal opesia of outer zooids and below the opesia of the inner zooids at the bifurcation (Figure 1C), (ii) lateral avicularia with straight rostrum (Figure 1C), (iii) vibracular chamber almost triangular with oblique to the axis and uncurved setal groove occupying two-thirds of vibracular chamber length (Figure 1D), (iv) single axial vibraculum (Figure 1D) and (v) ooecia with a porous ectooecium (Figure 1C). The combination of porous ectooecium, uncurved oblique setal groove occupying two-thirds of vibracular chamber length, and single axial vibraculum does not occur in other species of *Canda* and *Scrupocellaria* with the exception of *Licornia jolloisii* and the other nine species assigned to the genus (see below).

Licornia jolloisii (Audouin, 1826)
 (Figures 1C, D, 2A–F, 7A, B; Table 1)

Acamarchis jolloisii Audouin, 1826: [figured by Savigny, 1817].

Scrupocellaria jolloisii: Waters, 1909; Hastings, 1927.

Scrupocellaria mansueta Waters, 1909.

Scrupocellaria (*Retiscrupocellaria*) *jolloisi* (sic): d'Hondt, 1988.
Retiscrupocellaria jolloisii: d'Hondt, 2006.

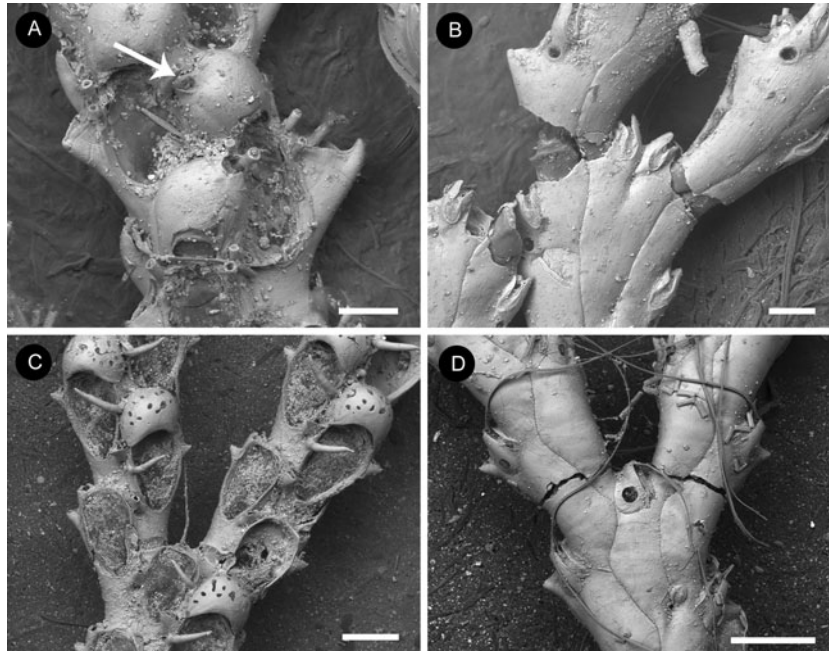


Fig. 1. Morphological differences between the type species of *Scrupocellaria* and *Licornia*: (A, B) *Scrupocellaria scruposa* (Linnaeus, 1758), NHMUK 1847.9.15.28, British waters; see the small avicularium at the distal edge of the oecium (white arrow); (C, D) *Licornia jolloisii* (Audouin, 1826), NHMUK 1926.9.6.84, neotype, Red Sea. Scale bars: A, B: 0.1 mm; C, D: 0.2 mm.

TYPE MATERIAL

Neotype (chosen here): Red Sea [NHMUK 1926.9.6.84, Figures 1C, D, 2A–C].

ADDITIONAL MATERIAL

Licornia jolloisii (Audouin, 1826). *Scrupocellaria jolloisii*, A.B. Hastings det., Red Sea [NHMUK 1926.9.6.85–94]; OM9G-0366-5, 24°25′18.80″S 81°15′23.50″W, Florida, Big Torch Key, #2, collected on 11 December 2005 by Don De Maria, 1–2 m, on limestone [acc. no.2009-015, VMNH 13708.0000, Figure 2D–F]; 12°53′21″S 38°41′03″W, Itaparica, Baía de Todos os Santos, Bahia, Brazil, collected on January 2011 by Laura P. Kremer, 1 m, on panels [MZUSP 1001–1004].

REDESCRIPTION

Colony erect, branched, with branches comprising 5–17 zooids, sometimes joined by anastomosing transversal tubes, pale reddish brown in colour in life. Internode almost straight, with chitinous joints passing across the proximal opesia in both outer zooids at the branch bifurcation. Autozooids

elongate, almost rectangular, slightly wider distally than proximally, with curved distal edges. Oval opesia occupying three-quarters of the zooidal length, broader distally. Cryptocyst absent. Scutum often present, inserted at midline or slightly distal of inner edge of the opesia, spine-like, shaped like a stout, straight elephant tusk, obliquely directed forward and over frontal membrane. One outer and one inner oral spine, vestigial, often absent. Axial zooid without oral spines, or rarely with 1–2 vestigial oral spines. A lateral avicularium present near distal outer edge in each zooid, small, laterally directed; rostrum triangular with hooked mandible. Frontal avicularia (sometimes absent) at inner proximal margin of opesia, monomorphic; rostrum triangular, serrated, angled proximally, triangular mandible hooked distally. A vibracular chamber present on basal surface of each zooid, sometimes inconspicuous in frontal view, tapering distally, almost triangular, small, with oblique setal groove and one proximal rhizoidal foramen; uncurved setal groove occupying two-thirds of the vibracular chamber length; vibracular setae smooth, as long as two zooids. Single axial vibraculum, with proximal rhizoidal foramen. Rhizoids tubular with some retroussé hooks. Ovicells almost globular, with ectoecium perforated by funnel-shaped elongate to circular pores.

Table 1. Measurements (mm) of neotype of *Licornia jolloisii* (Audouin, 1826) from Red Sea (NHMUK 1926.9.6.84).

Structures	N	Min	Max	Mean	± SE
Zooid length	15	0.345	0.497	0.438	0.048
Zooid width	15	0.162	0.225	0.193	0.019
Opesia length	15	0.255	0.342	0.288	0.029
Opesia/autozooid	15	0.56	0.76	0.71	0.08
Scuta length	15	0.115	0.173	0.126	0.022
Frontal avicularia length	15	0.055	0.070	0.060	0.005
Vibracular chamber length	15	0.118	0.136	0.129	0.006
Ooecia length	15	0.145	0.204	0.171	0.016
Ooecia width	15	0.199	0.218	0.208	0.007

Min: minimum; Max: maximum; N: number; SE: standard error.

TAXONOMIC REMARKS

Acamarchis jolloisii was described by Audouin (1826) based on Egyptian specimens figured by Savigny (1817). Audouin (1826) dedicated the species to Mr Jollois, genitive ending *-ii*, the genitive ending for the Latinized version ‘jolloisius’ of that personal name. As was true for other taxonomic authors of the time Audouin did not explain whether species names based on personal names were Latinized or not, and of the names he used, some have *-i* endings and some *-ii*. Since his choice of endings appears to have been deliberate and not a case of lack of knowledge of

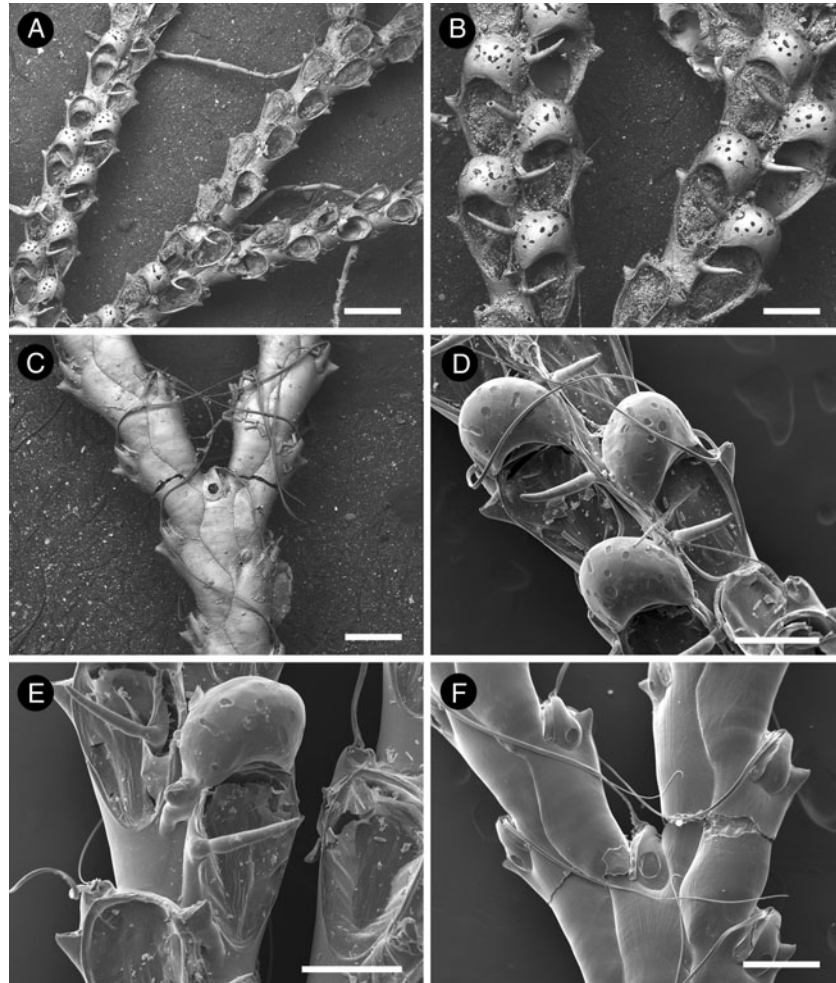


Fig. 2. *Licornia jolloisii* (Audouin, 1826): (A, B, C) NHMUK 1926.9.6.84, neotype, Red Sea; (D, E, F) VMNH 13708.0000, Florida, USA. Scale bars: A: 0.4 mm; B, C, D, E, F: 0.2 mm.

Latinization, it seems preferable to leave his endings as they stand (ICZN, 1999, Art. 3.1.1.3) rather than emend them all to follow one pattern.

No type material exists for *Acamarchis jolloisii*. Therefore, we here designate a neotype from the Red Sea (NHMUK 1926.9.6.84) that is consistent with Savigny's original figures and with the most recent redescription of the species given by d'Hondt (1988).

Waters (1909) described a new species from the Red Sea, *Scrupocellaria mansueta*, distinct from *L. jolloisii* only by the absence of scuta and oral spines in many zooids. We did not have the opportunity to search the remaining original material of the Waters Collection at Manchester Museum to learn if that material still exists (Winston & Woollacott 2008:192, explains some of the history of the Waters Collection). In all examined specimens from the Red Sea, Suez Canal, Florida and Brazil, however, the presence or absence of oral spines, as well as of the stout spiny scuta, changes randomly along the branches of *L. jolloisii* (Figures 1C, 2A). Therefore *S. mansueta* was considered by Hastings (1929) and d'Hondt (1988) to be a junior subjective synonym of *Licornia jolloisii*, a decision with which we agree.

ADDITIONAL SPECIES OF *LICORNIA* EXAMINED

Licornia annectens (MacGillivray, 1887) comb. nov. Syntypes: *Scrupocellaria annectens* MacGillivray, MacGillivray det., 3

microslides, Gaspar Strait, Indonesia, Indian Ocean [NMV F.45606.1–3, the balsam slide specimens could not be examined with SEM, but the light microscopy images of these specimens can be found at the home page of Museum Victoria – <http://collections.museumvictoria.com.au>].

Licornia cervicornis (Busk, 1852) comb. nov. Holotype: *Scrupocellaria cervicornis* Busk, G. Busk det., British Museum Catalogue Collection, Voyage of HMS 'Rattlesnake', off Cumberland Island, 45.7 m (25 fms) [NMHUK 1854.11.15.81]. Paratypes: *Scrupocellaria cervicornis* Busk, G. Busk det., Voyage of HMS 'Rattlesnake', Australia [NMHUK 1899.7.1.4552–3]. Additional specimens: *Scrupocellaria diadema* Busk, S. Harmer det., *Siboga* Expedition, St. 163, specimen 501.G4, Malay Archipelago, Seget, N. end of New Guinea, 29 m [NHMUK 1928.3.6.180, Figure 3A, B].

Licornia cyclostoma (Busk, 1852) comb. nov. Holotype: *Scrupocellaria cyclostoma* Busk, G. Busk det., British Museum Catalogue Collection, Voyage of HMS 'Rattlesnake', Bass Straits, Australia, 82.3 m (45 fms) [NHMUK 1854.11.15.77]. Additional specimen: *Scrupocellaria annectens* MacGillivray, T. Hincks det., Port Phillip Heads, Victoria, Australia (= *Scrupocellaria cyclostoma* Busk, S. Harmer det., 12.7.1922) [NHMUK 1899.6.1.340, Figure 3C, D].

Licornia diadema (Busk, 1852) comb. nov. Holotype: *Scrupocellaria diadema* Busk, G. Busk det., British Museum

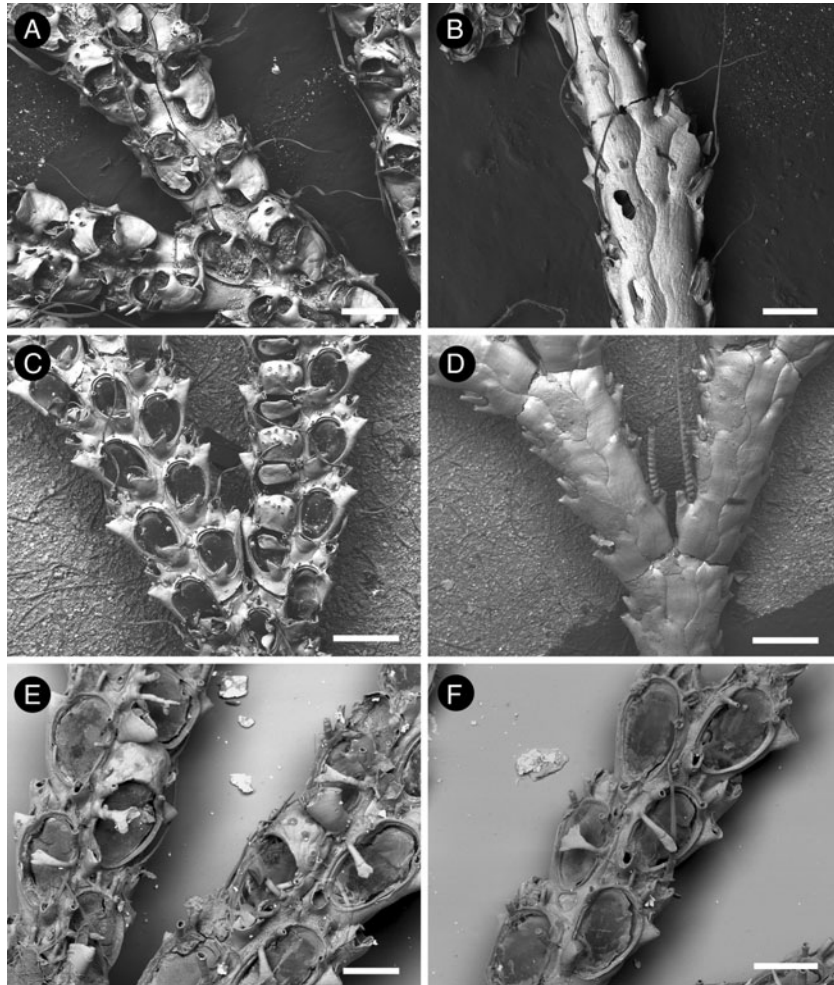


Fig. 3. Species of *Scrupocellaria* herein reassigned to *Licornia*: (A, B) *Licornia cervicornis* (Busk, 1852) comb. nov., NHMUK 1928.3.6.180, north of New Guinea; (C, D) *Licornia cyclostoma* (Busk, 1852) comb. nov., NHMUK 1899.6.1.340, Port Phillip Heads, Australia; (E, F) *Licornia diadema* (Busk, 1852) comb. nov., NHMUK 1854.11.15.80, holotype, Moreton Bay, Australia. Scale bars: A, B, E, FL 0.2 mm; C, D: 0.4 mm.

Catalogue Collection, Voyage of HMS 'Rattlesnake', Moreton Bay [NHMUK 1854.11.15.80, Figure 3E, F]. Additional specimens: *Scrupocellaria diadema* Busk, Canu & Bassler det., US Fish Commission Steamer *Albatross*, St. 5478, off Tacbuc Point, East Leyte, Philippines, 104 m (57 fms) [NMNH 7894]; *Scrupocellaria diadema* Busk, Great Barrier Reef Expedition, St. 12, collected on 24 February 1929 [NMNH 9565].

Licornia gaspari (Thornely, 1907) comb. nov. Syntypes: *Scrupocellaria gaspari* Thornely, L. Thornely det., Gaspar Strait, Indonesia [NHMUK 1936.12.30.146, Figure 4A, B; 1907.8.24.1pt]; *Scrupocellaria gaspari* Thornely, L. Thornely det., Andaman Islands, Indian [NHMUK 1936.12.30.126; NHMUK 1936.12.30.136].

Licornia ferox (Busk, 1852) comb. nov. Holotype: *Scrupocellaria ferox* Busk, G. Busk det., British Museum Catalogue Collection, Voyage of HMS 'Rattlesnake', Louisiade Archipelago [NHMUK 1854.11.15.76]; balsam slide with part of holotype (schizoholotype), mounted by S. Harmer, 28.vi.1922 [NHMUK 1899.7.1.6540]. Additional specimen: *Scrupocellaria ferox* Busk, S. Harmer det., 'Siboga' Expedition, St. 7, specimen 2.A2, Batjulatmat, Java, coral reef [NHMUK 1928.3.6.156, Figure 4C, D].

Licornia longispinosa (Harmer, 1926) comb. nov. Holotype: *Scrupocellaria longispinosa* Harmer, S. Harmer det., 'Siboga' Expedition, St. 144, specimen 108.Ai, Maluku

Islands, Indonesia, anchorage N of Solamakië, 07.viii.1899, 45 m [ZMA 01063au, schizoholotype; RMNH 00054, schizoholotype, NHMUK 1928.3.6.189–90, schizoholotypes, Figure 4E, F; NMNH 9389, schizoholotype].

Licornia macropora (Osburn, 1950) comb. nov. Paratypes: *Scrupocellaria macropora* Osburn, R. Osburn det., AHF 33, Allan Hancock Pacific Expedition, 'Veleo III', St. 1162–40, 33°33'5"N 118°9'45"W, California, Orange County, 11 miles of South of Seal Beach, collected on 23 July 1940 [SBMNH 96151]; *Scrupocellaria macropora* Osburn, R. Osburn det., Allan Hancock Pacific Expedition, St. 1263–41, 1.5 miles off north end of Cedros Island, Mexico, Lower California, 82–100 m (45–55 fms) [NMNH 553519]. Additional specimen: US Fish Commission Steamer 'Albatross', station 2886, off Oregon Coast [NMNH 553520, Figure 5A, B].

Licornia prolata (Tilbrook & Vieira, 2012) comb. nov. Holotype: *Scrupocellaria prolata* Tilbrook & Vieira, Site 813, Sample Id 000125, SBD 001581, Great Barrier Reef, 18.635°S, 147.275°E, 18 September 2003 [MTQ G25341, figured by Tilbrook & Vieira, 2012: fig. 10].

Licornia spp. (two undescribed species). Comparative material: *Scrupocellaria diadema* Harmer, S. Harmer det., Siboga Expedition, St. 99, specimen 68.B2, N. Ubian, Sulu Archipelago, 16–23 m [NHMUK 1928.3.6.178, Figure 5C, D]; *Scrupocellaria diadema* Harmer, P. Hayward det., Coral

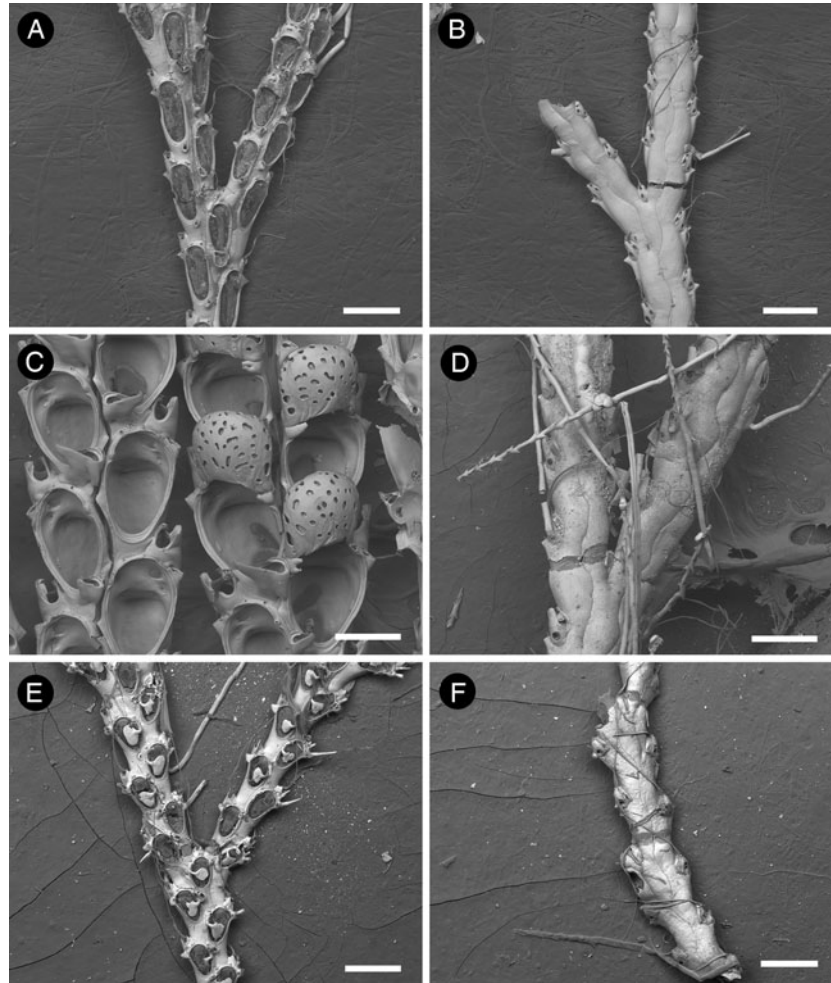


Fig. 4. Species of *Scrupocellaria* herein reassigned to *Licornia*: (A, B) *Licornia gaspari* (Thornely, 1907) comb. nov., NHMUK 1936.12.30.146, Syntype, Gaspar Strait, Indonesia; (C, D) *Licornia ferox* (Busk, 1852) comb. nov., NHMUK 1928.3.6.156, Java; (E, F) *Licornia longispinosa* (Harmer, 1926) comb. nov., Schizoholotype, NHMUK 1928.3.6.189, Maluku Islands, Indonesia. Scale bars: A, B, D, E, F: 0.4 mm; C: 0.2 mm.

Reef Research Foundation, OCDN2370-L, KB CHAN, 07°19.24'N, 134°31.28'E, Palau, Channel between Koror and Babeldaod, 14.v.1994, 20 m [NHMUK 2005.7.27.12, Figure 5E, F].

REMARKS ON SPECIES OF *LICORNIA*

We examined in detail a huge range of material of *Scrupocellaria* deposited in different scientific collections and found some specimens that share the following characters with *Licornia jolloisii*: almost rectangular zooids with opesia occupying more than half of frontal area; joints passing across the proximal opesia in both outer zooids at the bifurcation; cryptocyst vestigial or absent; frontal scuta sometimes absent; small, almost triangular vibracular chamber with oblique and uncurved setal groove, single axial vibraculum, and oecium with many ectoocial pores.

These characteristics are observed in *Scrupocellaria diadema* (see Harmer, 1926; Tilbrook & Vieira, 2012), and this species is reassigned to *Licornia*.

Harmer (1926) noted that many specimens previously assigned to *L. diadema* showed variation in the size of the vibracular chamber, the shape of scuta and the number of oral spines. However, despite the differences among specimens in material from Indo-Pacific waters, Harmer (1926)

synonymized three previously described species under Busk's *L. diadema*: *Scrupocellaria cervicornis* Busk, 1852, *Scrupocellaria annectens* MacGillivray, 1887, and *Scrupocellaria gaspari* Thornely, 1907. Our study shows that the type specimens of these three species belong to *Licornia* and that they are morphologically distinct from each other in autozooid shape, presence and shape of frontal scuta and the number of oral spines. Figure 3A, B shows *L. cervicornis*: with distinct large shield-shaped or heart-shaped scutum, very small lateral avicularium and frontal avicularium with a short base; Figure 4A, B show: *L. gaspari*, without scutum and 2–4 oral spines. *L. annectens* is a balsam slide specimens and no SEM image was possible, but it is distinct in having a small scutum present in ovicelled zooids and large frontal avicularia in axial zooids. All are distinct from Busk's *L. diadema*; e.g. Figure 3E, F which is characterized by possession of a gracile club-shaped scutum and aquiline frontal avicularia with a tubular base (Tilbrook & Vieira, 2012).

Osburn (1950) recorded 18 *Scrupocellaria* species from the Eastern Pacific, seven of them described as new to science. Examination of the Osburn's *Scrupocellaria* specimens deposited at the SBMNH and NMNH revealed one species, *Licornia macropora* (Osburn, 1950) (Figure 5A, B), which shares with *Licornia jolloisii* and *Licornia diadema* the characteristic shape of zooids, position of the joints, frontal avicularia, ovicells and

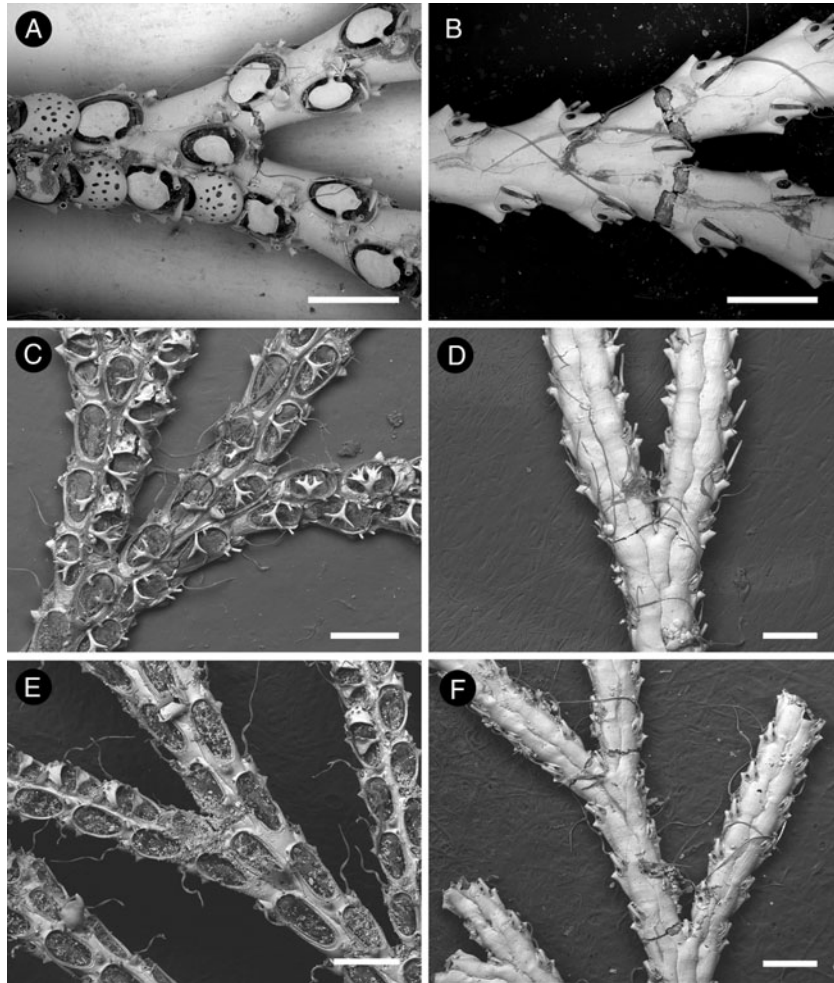


Fig. 5. Species of *Scrupocellaria* herein reassigned to *Licornia*: (A, B) *Licornia macropora* (Osburn, 1950) comb. nov., NMNH 553520, off Oregon, USA; (C–F) two undescribed species of *Licornia*, previously assigned to *Scrupocellaria diadema* Busk, 1852: (C, D) NHMUK 1928.3.6.178, Malay Archipelago; (E, F) NHMUK 2005.7.27.12, Palau. Scale bars: A–F: 0.4 mm.

basal vibracula; *Licornia macropora* is distinct in having a rounded scutum and ooecia with more than 15 pseudopores.

Most characteristics of *L. jolloisii* are also seen in Busk's *Scrupocellaria cyclostoma* (Figure 3C, D) and *Scrupocellaria ferox* (Figure 4C, D), as well as in the *Scrupocellaria longispinosa* Harmer, 1926 (Figure 4E, F); these three species are reassigned to *Licornia*. *Licornia cyclostoma* comb. nov. is distinct by the presence of ringed rhizoids, lateral avicularium with a long base, and the aquiline laterally directed frontal avicularia. *Licornia ferox* comb. nov. has frontal avicularia longer than those of *L. cyclostoma*; they are also distinct by the shape of the lateral avicularium and absence of scutum in *L. cyclostoma*. *Licornia longispinosa* comb. nov. has very long distal spines and zooids with oval scutum in both ovicelled and non-ovicelled zooids.

Tilbrook & Vieira (2012, figure 10) described a new species from the Queensland coast, *Scrupocellaria prolata*, which is here reassigned to *Licornia* because of its morphological similarities with *L. diadema* and *L. cervicornis*. However, *L. prolata* comb. nov. is distinct in producing frontally directed elongate frontal avicularia and in having larger zooids than those of *L. diadema* and *L. cervicornis* (see Tilbrook & Vieira, 2012). In addition, Tilbrook (2006) noted differences between Busk's *S. diadema* and some specimens from Indonesian and Malaysian regions, but the specimens he recorded under the

name *Scrupocellaria diadema* (SBMNH 365098–99; see Tilbrook, 2006: 58, pl. 9, figures A–C) belong to an undescribed species of *Licornia* (see additional comparison in Tilbrook & Vieira, 2012, pp. 33–34).

Among the taxa herein assigned to *Licornia*, two species, *L. annectens* and *L. ferox*, are characterized by the absence of frontal scuta, while in *L. cyclostoma* the scuta are present only in ovicelled zooids. In type specimens of *Licornia diadema* the scutum is often present and dimorphic in ovicelled zooids, but its presence varies in non-ovicelled zooids, as in *L. prolata*. *Licornia jolloisii* is distinguished from other species of *Licornia* by the presence of a stout spine-like scutum with a sharp point.

In summary, in addition to the type species, *L. jolloisii*, another nine species previously assigned to *Scrupocellaria*, including most of those described by Busk (1852), are herein reassigned to the genus *Licornia* van Beneden, 1850: *Licornia annectens* (MacGillivray, 1887) comb. nov., *Licornia cervicornis* (Busk, 1852) comb. nov., *Licornia cyclostoma* (Busk, 1852) comb. nov., *Licornia diadema* (Busk, 1852) comb. nov., *Licornia ferox* (Busk, 1852) comb. nov., *Licornia gaspari* (Thornely, 1907), *Licornia longispinosa* (Harmer, 1926) comb. nov., *Licornia macropora* (Osburn, 1950) comb. nov., and *Licornia prolata* (Tilbrook & Vieira, 2012) comb. nov. Two

undescribed species of *Licornia* were previously assigned to *Scrupocellaria diadema* Busk, 1852 (see Figure 5C–F).

DISCUSSION

The redescription of *L. jolloisii* allows us to reassign 11 additional species to this genus (two of those are undescribed, see Figure 5C–F); thus the formerly a monospecific subgenus, now comprises a genus of 12 species, characterized by (i) fan-shaped colonies with joints crossing the proximal opesia area of outer zooids at the bifurcation, (ii) lateral avicularia with straight rostrum, (iii) small, almost triangular basal vibracular chambers, with oblique and uncurved setal grooves occupying two-thirds of vibracular chamber length, (iv) single axial vibracula and (v) ovicells with many ectoocelial pores.

The jointed transversal tubes on the branches, described for *L. jolloisii* (Figure 1A), were also observed in some colonies of *L. gaspari* and *L. diadema*. The majority of species have rhizoids with hooks, but *L. cyclostoma* has distinctly annulated rhizoids. Hincks (1880) noted smooth and hooked rhizoids in different colonies of *Scrupocellaria reptans* from British waters, while Waters (1909), Tilbrook & Vieira (2012) and Vieira & Spencer Jones (2012) used these characteristics to distinguish different species of *Scrupocellaria*. No variation in the surface of rhizoids was observed in different species of *Licornia*, which suggests that the different morphology in distinct specimens (hooked, smooth or annulated) is not an ecological response and may be useful to distinguish different taxa (cf. *Scrupocellaria hamata* Tilbrook & Vieira, 2012; cf.

Scrupocellaria ellisi Vieira & Spencer Jones, 2012). Further observation using SEM will be important to distinguish additional characteristics (e.g. shape of frontal scuta, shape and position of frontal avicularia) necessary for detection of species complexes (e.g. *Licornia diadema*, see Harmer, 1926), such as have been observed for other bryozoan taxa (Berning *et al.*, 2008; Winston & Woollacott, 2008; Vieira *et al.*, 2010, 2012; Tilbrook, 2012).

The genus *Licornia* is widely distributed in Indian and Pacific waters and more species may exist, but the group does not seem to be as diverse in the Atlantic. Crossland's specimen from Cape Verde Island of *Scrupocellaria cervicornis* Busk was redescribed as *Scrupocellaria tridentata* Waters, 1918, but because of the presence of very large basal vibracula and distinct trifoliate frontal avicularia this species is not reassigned to *Licornia*. Specimens of *L. diadema* were previously collected by Miss Gatty from Cape Verde Island (under the name *Scrupocellaria ciliata* Audouin, 1826; see Busk 1884, p. 23), but reexamination is required to confirm the occurrence of *L. diadema* in this region. Recently *Licornia diadema* has been recorded from the Western Atlantic from Rio de Janeiro, Brazil, by Ramalho *et al.* (2005), making the Florida Keys and Brazilian specimens of *Licornia jolloisii* the second record for the genus in Atlantic waters (Figure 6). Due to the presence of similar species in Australian waters (Tilbrook & Vieira, 2012) and the possibility of cryptic species among colonies from Korea (Lee *et al.*, 2011), however, we suggest detailed morphological studies on specimens reported by Ramalho *et al.* (2005) as *Scrupocellaria diadema* to confirm the identity of Brazilian specimens.

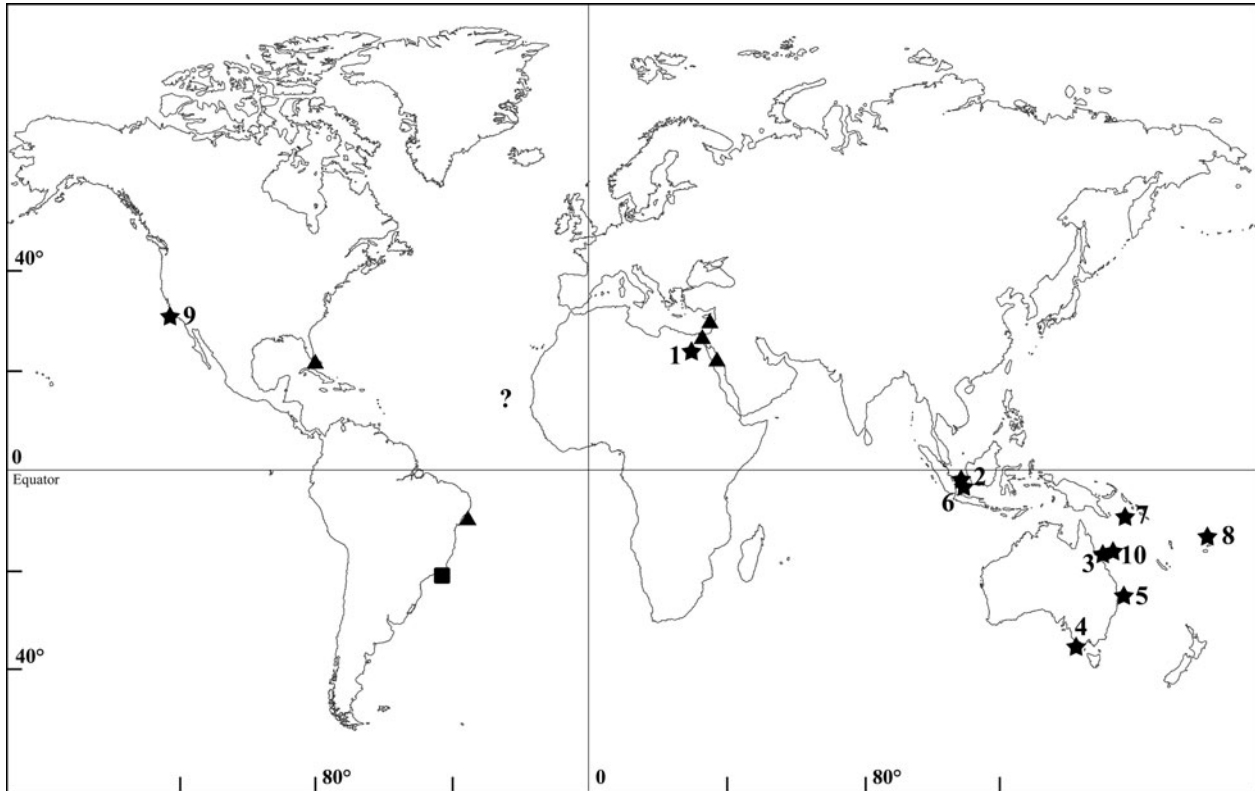


Fig. 6. Type locality of *Licornia* species worldwide [stars; note that the type locality, if Egypt, can be Red Sea coast of Egypt] and new locality records: 1, *Licornia jolloisii* (Audouin, 1826); 2, *Licornia annectens* (MacGillivray, 1887); 3, *Licornia cervicornis* (Busk, 1852); 4, *Licornia cyclostoma* (Busk, 1852); 5, *Licornia diadema* (Busk, 1852); 6, *Licornia gaspari* (Thornely, 1907); 7, *Licornia ferox* (Busk, 1952); 8, *Licornia longispinosa* (Harmer, 1926); 9, *Licornia macropora* (Osburn, 1950); 10, *Licornia prolata* (Tilbrook & Vieira, 2012). Additional records of *Licornia jolloisii* [triangle] and *Licornia diadema* [square] in Atlantic and Mediterranean; Busk's *Scrupocellaria ciliata* Audouin from Cape Verde Island was noted with a question mark in the map, as its placement is still uncertain.

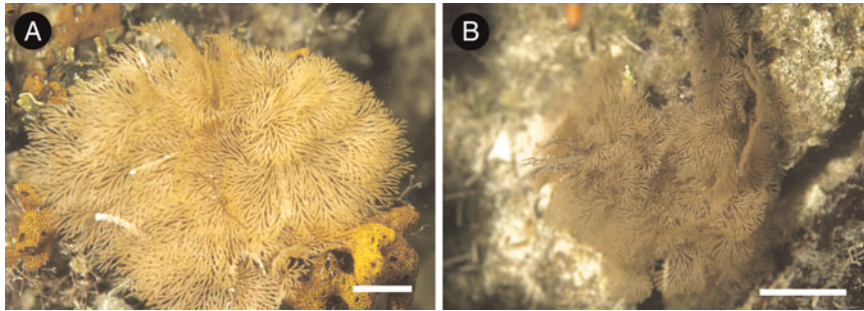


Fig. 7. (A, B) Colonies of *Licornia jolloisii* (Audouin, 1826) on natural substrata found in Florida Keys, USA. Scale bars: 2 cm. Photographs by Don De Maria, Sea Samples, Summerland Key, Florida.

McCann *et al.* (2007) reported 35 species on plates in six different localities of the Southern United States, four of those classified as non-native. Among species classified as cryptogenic (unknown origin), only one member of the family Candidae, *Scrupocellaria bertholletii* Audouin, 1826, was recorded, but examination of the specimens at the VMNH showed that two supposedly endemic species are involved, one of them belonging to *Scrupocellaria curacaoensis* Fransen, 1986. Recently, Johnson *et al.* (2012) reported the first invasive Candidae species on the north-eastern Atlantic coast, *Tricellaria inopinata* d'Hondt & Occhipinti-Ambrogi, 1985. Therefore, *Licornia jolloisii* is the second non-native Candidae species reported from the Atlantic coast of United States, the first on the south-east coast.

Licornia jolloisii was first reported on an artificial substratum (buoy) by Waters (1909) from Suez Bay, while Robertson (1921) noted that this species was very common in the vicinity of the Bay of Bengal, between 70–90 m depth. The species was first reported as invasive at six different points along the Suez Canal, including Port Said, at the Mediterranean entrance of the Suez Canal (Hastings, 1927). The latest record for *L. jolloisii* from the Mediterranean (Israel) was reported by d'Hondt (1988), who found colonies on sandstones and banks of bivalves, an invasion supposedly carried from the North Suez Canal to the coast of Israel, but with an unknown dispersal vector (Galil, 2007). The location of the Florida Keys specimens (Figure 7) in a man-made canal near a major recreational boat route to and from Key West, as well as the volume of commercial shipping traffic through the Straits of Florida, makes it likely that it represents a recent invasion of the area. More collections in this region are needed to determine whether or not the species has persisted or spread since 2005. More recently, some specimens of *L. jolloisii* were also found on artificial panels in Itaparica, Baía de Todos os Santos, NW Brazilian coast. This place is characterized by intense recreational and commercial shipping traffic due to the presence of small boat marinas, the Harbour of Aratu and one oil refinery, with piers for the oil cargo ships and a large shipyard. Further efforts towards extending the understanding of local invasive marine species dynamics are in progress in this area (L.P. Kramer & R.M. Rocha, personal communication).

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Correspondence should be addressed to:

Leandro M. Vieira
Departamento de Zoologia, Instituto de Biociências and

Centro de Biologia Marinha, Universidade de São Paulo, São
Sebastião, SP 11600-000, Brazil
email: leandromanzoni@hotmail.com