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**Research Article**

**Taxonomic position of *Lovenella gracilis* (Clarke, 1882)  
(Lovenellidae, Hydrozoa): new evidences of microanatomy justify its  
maintenance in the genus *Lovenella* (Hincks, 1868)**

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**ABSTRACT.** *Lovenella gracilis* Clarke, 1882 is one of the 15 nominal species referred to the genus *Lovenella* Hincks, 1868, characterized by the presence of a basal line demarcating the separation between operculum and hydrotheca. However, *Lovenella gracilis* apparently does not have the demarcating line under light microscopy – therefore, the resurrection of the genus *Dipleuron* Brooks, 1882 was proposed to accommodate this species. The goal of this study is to redescribe the polyp of *L. gracilis* trying to resolve this doubtful taxonomical status. Fertile colonies were collected in the intertidal zone of Rio Grande do Norte and Santa Catarina States, representing the first record of the species for the South Atlantic. Scanning electron microscopy of *L. gracilis* has shown a tenuous demarcation between operculum and hydrotheca, corroborating its position in the genus *Lovenella*. Considering the new evidences presented, we propose the maintenance of the species *L. gracilis* in the genus *Lovenella*, and corroborate the synonymy of *Dipleuron* and *Lovenella*.

**Keywords:** *Lovenella*, *Dipleuron*, operculum, taxonomy, South Atlantic, Brazil.

**Posición taxonómica de *Lovenella gracilis* (Clarke, 1882) (Lovenellidae, Hydrozoa):  
nuevas evidencias de microanatomía justifican su permanencia en el género  
*Lovenella* (Hincks, 1868)**

**RESUMEN.** *Lovenella gracilis* Clarke, 1882 es una de las 15 especies nominales referidas al género *Lovenella* Hincks, 1868, caracterizada por la presencia de una línea basal separando el opérculo de la hidroteca. Sin embargo, la microscopía de luz reveló la ausencia de una demarcación entre el opérculo y la hidroteca de *Lovenella gracilis*, y por eso se propuso su transferencia al género *Dipleuron* Brooks, 1882, que resurgió para acomodar esta única especie. Este trabajo tiene como finalidad la descripción del pólipo de *L. gracilis* con la intención de resolver este status taxonómico dudoso. Las colonias fértiles fueron colectadas en el intermareal de las provincias de Rio Grande do Norte y Santa Catarina y representan el primer registro de la especie para el Atlántico sur. Electromicrografías evidencian una discreta demarcación entre el opérculo y la hidroteca, corroborando la posición de *L. gracilis* en el género *Lovenella*. Con respecto a las nuevas evidencias de la morfología opercular presentadas, se propone la permanencia de *L. gracilis* en el género *Lovenella*, y se corrobora la sinonimia de *Dipleuron* y *Lovenella*.

**Palabras clave:** *Lovenella*, *Dipleuron*, opérculo, taxonomía, Atlántico sur, Brasil.

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**INTRODUCTION**

Leptothecate hydrozoans of the family Lovenellidae Russell, 1953 have a troubled taxonomical history

(Calder, 1991; Bouillon *et al.*, 2004). They have a metagenetic life cycle and, like in many other hydroid taxa, the parallel and independent use of the morphological characters of polyps and medusae

eventually generated a dual classification, with different understandings and diagnoses for the, presumably, same genera.

The genus *Lovenella* was proposed by Hincks (1868), based on the polyp stage, and assigned to the family Campanulariidae. Russell (1953) based on the medusa stage, proposed the family Lovenellidae including the genera *Eucheilota* McCrady, 1859 and *Lovenella* Hincks, 1868. The family Lovenellidae, as described by Russell (1953), includes medusae without marginal cirri, excretory pores or peduncle, with gonads on four simple radial canals, and with lateral cirri. Kramp (1959) proposed the genus *Cirrholovenia* as a third genus for the Lovenellidae, based on the presence of marginal cirri in the medusa, amending the original diagnosis of the family. Other disputable arrangements have also been proposed for the family, even comprising genera traditionally included in the family Haleciidae Hincks, 1868, such as *Campalecium* Torrey, 1902 and *Hydranthea* Hincks, 1868.

The genus *Lovenella* Hincks, 1868, type species *Lovenella clausa* (Löven, 1836), comprises 14 nominal species (Tabla. 1, 2) distributed worldwide (Figs. 1 and 2). Only *L. chiquitita* Millard, 1957 and *L. corrugata* Thornely, 1908 were recorded for the South Atlantic hitherto. The main diagnostic characters of *Lovenella* are the medusae with indefinite number of statocysts and and polyp with hydrotheca well demarcated by a basal line, separating it from the operculum (Fraser, 1944; Kramp, 1959; Bouillon *et al.*, 2004).

Oddly, the polyp of *Lovenella gracilis* Clarke, 1882 is defined by the operculum being a continuation of the hydrothecal wall, therefore lacking a basal line separating operculum and hydrotheca (Calder, 1971, 1975). Based on this unique character, Calder (1991) proposed the resurrection of the genus *Dipleuron* Brooks, 1882 in order to encompass *L. gracilis*. Bouillon & Boero (2000) and Bouillon *et al.* (2004) did not agree with this proposal, arguing that the medusae of *L. gracilis* presents the typical characters of the genus and that the diagnostic characters of the polyps of lovenellid are puzzling, since the opercular structure can be variable within the family, and even within the same genus. No other addition was made to the knowledge of the morphology of *L. gracilis*, and the taxonomical *status* of the species remains doubtful.

The aim of this study is to redescribe in detailed morphology the polyp of *L. gracilis*, based on the first material of the species sampled for the South Atlantic, and reveal new data corroborating its maintenance in the genus *Lovenella*.

## MATERIALS AND METHODS

The material studied was collected in the intertidal zone of Tibau Beach (Tibau, State of Rio Grande do Norte, Brazil) and Bombas Beach (Bombinhas, State of Santa Catarina, Brazil). The colonies were fixed in 92.5% ethanol and 4% formaldehyde solution. We have studied the morphology, morphometry and cnidome of all specimens. Morphological details were studied in scanning electronic microscopy (SEM), following routine protocol (Migotto & Marques, 1999). The cnidome was studied with squashed preparations of the fixed material, in light microscopy. Studied material has been deposited in the Cnidarian Collection of the Museu de Zoologia of the Universidade de São Paulo (MZUSP), São Paulo, Brazil.

## RESULTS

*Lovenella gracilis* Clarke, 1882 (Figs. 3a-3d; 4a-4f).

*Lovenella gracilis* Clarke, 1882, p. 139, pl. 9, fig. 25-39; Fraser, 1944, p. 174, pl. 31, fig. 147; Calder, 1971, p. 61, pl. 4, fig. h, pl. 8, fig. b-c; 1975, p. 298, fig. 3c.

*Dipleuron parvum* Brooks, 1882, p. 135, 139-140.

*Lovenella clausa* Fraser, 1910, p. 364, fig. 26a-d; 1912, p. 45 [non *Lovenella clausa* (Löven, 1836)].

*Dipleuron gracilis*-Huvé, 1952, p. 389, fig. 1a-b, 2a-b; Calder, 1991, p. 3.

**Material examined.** Santa Catarina, Bombinhas, Bombas Beach (27.131°S 48.514°W, 2 m, 3.12.2006)–MZUSP4242, in formaldehyde 4%, without gonophores, on rock and *Sargassum* sp.; MZUSP4260, in ethanol 92.8%, without gonophores, on rock; MZUSP4263, in ethanol 92.8%, with gonophores, on rock; MZUSP4266, in formaldehyde 4%, with gonophores, on rock and *Sargassum* sp. Rio Grande do Norte, Tibau, Tibau Beach (4.835°S, 37.247°W, intertidal zone, on *Donax striatus*, in ethanol 92.8%)–MZUSP5356, with gonophores, 5.6.2004; MZUSP 5357, MZUSP5358, with gonophores, 15.ix.2004; MZUSP5359, with gonophores, 9.3.2004.

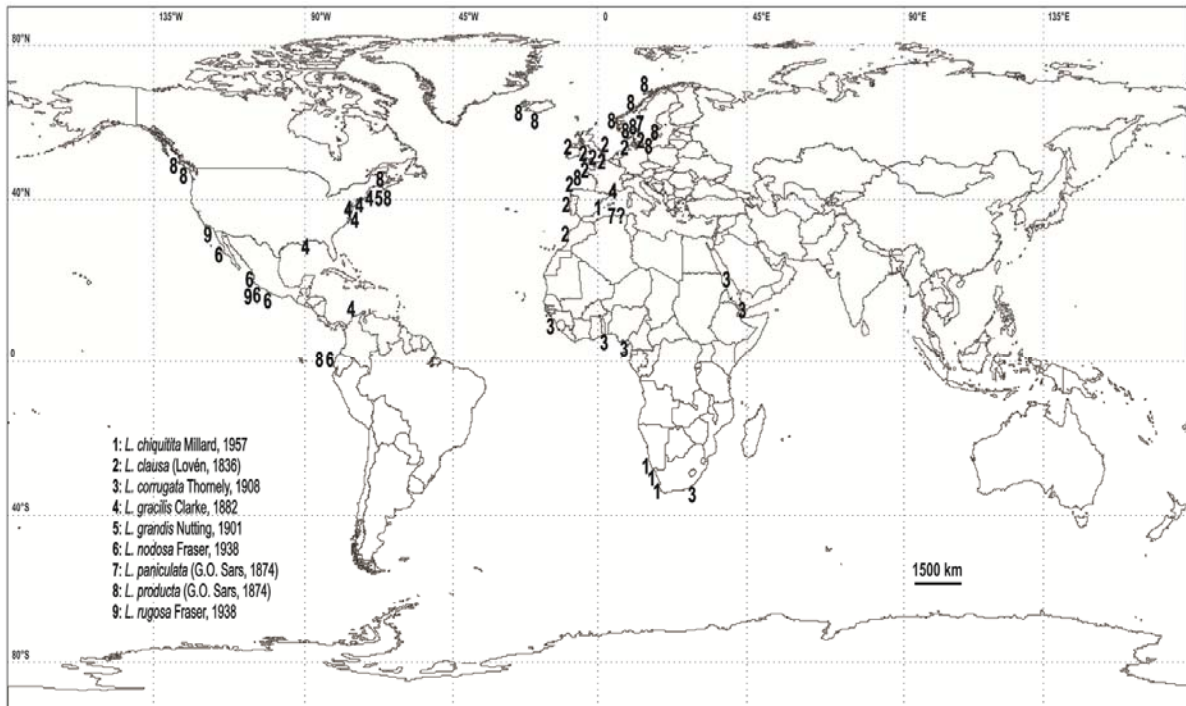
**Description.** Colonies stolonial or erect, up to 19 mm (n = 10) in height, arising directly from creeping hydrorhiza 80-240 µm (n = 10) in diameter. Hydrocaulus monosiphonic, with 0-6 annulations (n = 10) at the proximal region, branched or unbranched, divided into internodes by transverse septa at more or less regular intervals. Perisarc of main stem moderately thick, thinner at secondary branches and pedicels. Internode length 930-6640 µm (n = 10), diameter

**Table 1.** Comparison of the diagnostic characters of *Lovenella* with polyp stage recorded in literature.

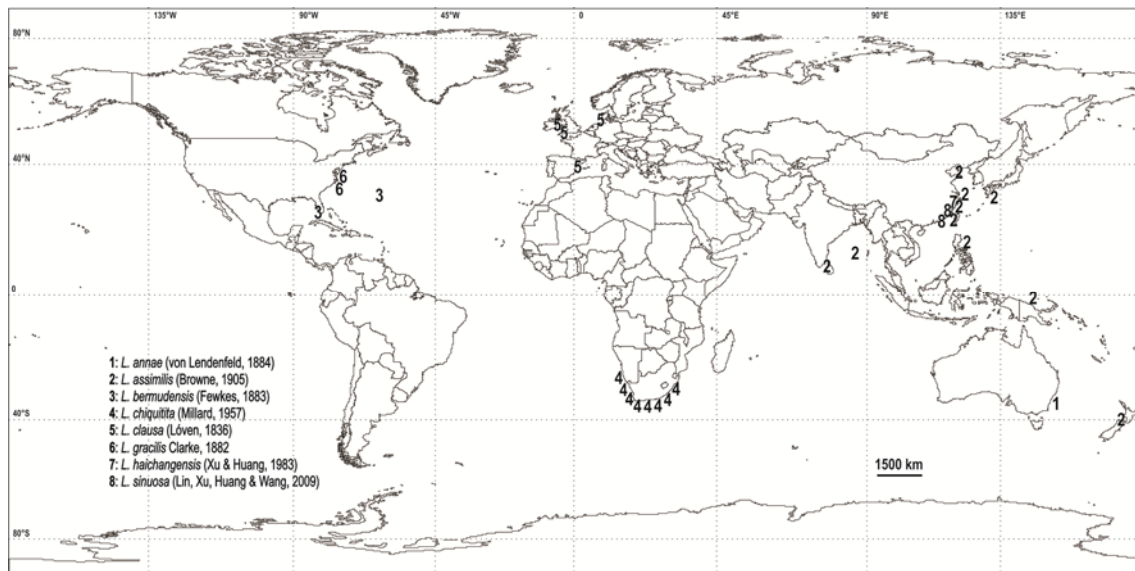
Species	Shape of colony	Growth	Septa per internode	Annulations on pedicel	Hydrothecae	Frequency of hydrothecae regeneration	Shape of operculum valves	Number of operculum valves	Diaphragm	Nematophores	Gonothecae	Arising of gonothecae	References
<i>L. chiquitita</i> Millard, 1957	Stolonial or erect	Sympodial	-	Throughout	Deep-campanulate	Occasionally	Triangular with rounded base	8-10	Oblique	Absent	Smooth, elongated, widening distally	From hydrothiza	Millard (1957, 1975)
<i>L. clausa</i> (Löven, 1836)	Stolonial or erect	Sympodial	-	2-5 on proximal and distal regions	Cylindrical, widening distally	2-3 times	Triangular with rounded base	8-10	Transversal	Absent	Smooth, elongated, widening distally	Axillary from pedicel	García Corrales <i>et al.</i> (1979); Comelius (1995)
<i>L. corrugata</i> Thornely, 1908	Erect	Sympodial	-	3-6 on proximal and distal regions	Deep-campanulate, corrugated proximally	2-4 times	Triangular with rounded base	8-12	Oblique	Absent	Ringed, spindle shaped	Axillary from pedicel	Vervoort (1959); Millard (1980)
<i>L. gracilis</i> Clarke, 1882	Erect	Sympodial	3-4	1-2 on proximal and distal regions	Campanulate	-	Conical	8	Transversal	Absent	Smooth, clavate	Axillary from pedicel	Clarke (1882); Calder (1971, 1975)
<i>L. grandis</i> Nutting, 1901	Erect	Sympodial	-	Not specified	Cylindrical, widening distally	-	Triangular with rounded base	10-12	-	Absent	Smooth, elongated, widening distally	Axillary from pedicel	Nutting (1901); Fraser (1941)
<i>L. nodosa</i> Fraser, 1938	Erect	Sympodial	-	2-3 on distal region	Cylindrical, widening distally	-	Triangular with rounded base	8	-	Absent	Smooth, tubular, widening distally	Axillary from pedicel	Fraser (1938)
<i>L. paniculata</i> (G.O. Sars, 1874)	Erect	Sympodial	-	On proximal region	Cylindrical, widening distally	-	Conical	-	Oblique	Absent	-	-	Sars (1874)
<i>L. producta</i> (G.O. Sars, 1874)	Stolonial	Monopodial	-	3-8 on proximal and distal regions, sometimes, in the middle	Cylindrical, widening distally	-	Conical	Up to 12	Transversal	Present	-	-	Sars (1874); Comelius (1995)
<i>L. rugosa</i> Fraser, 1938	Stolonial or erect	Sympodial	-	Throughout	Deep-campanulate	-	Triangular with rounded base	9-10	Oblique	Absent	Smooth, elongated, widening distally	From hydrothiza	Fraser (1938)

**Table 2.** Comparison of diagnostic characters of species of *Lovenella* with medusa stage recorded in literature.

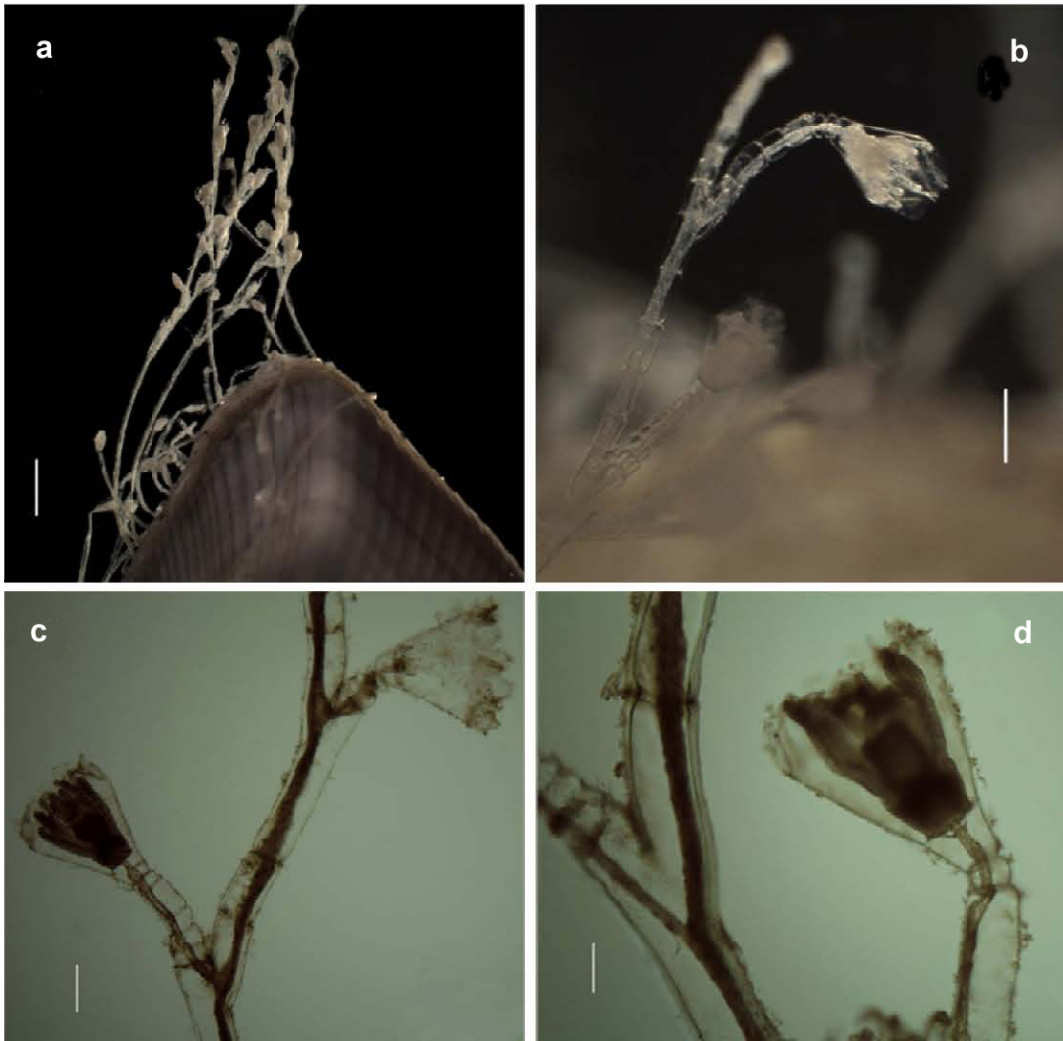
Species	Umbrella	Velum	Manubrium	Number of gonads	Position of gonads	Morphology of gonads	Number of tentacles	Number of statocysts	Number of marginal vesicles	Number of marginal bulbs	Number of cirri	Position of cirri	References
<i>L. annae</i> (von Lendenfeld, 1884)	Broader than high	-	Small, globular, with 4 interradial spots	4	Near radial canals	Oval	8	-	-	8	2 clusters	On each side of tentacles	Kramp (1961)
<i>L. assimilis</i> (Browne, 1905)	Broader than high	Narrow	Short	4	On distal end of radial canals	Oval	4	-	-	5-7	2 clusters	On each side of tentacles	Browne (1905); Hirano & Yamada (1985)
<i>L. bermudensis</i> (Fewkes, 1883)	Wide, low, without raised apex	-	Short and wide	4	On stomach	Spherical	4-8	-	-	4	2	On each side of tentacles	Fewkes (1883); Kramp (1959)
<i>L. chiquitita</i> Millard, 1957	Higher than wide	-	Short	-	-	-	8	-	8	8	-	-	Millard (1975)
<i>L. clausa</i> (Löwen, 1836)	Hemispherical	ca. ¼ of the bell radius	Short and small	4	On distal end of radial canals	Oval and longitudinally divided	16-24	-	16-23	-	1-3	On each side of tentacles	Kramp (1959); Cornelius (1995)
<i>L. gracilis</i> Clarke, 1882	Hemispherical	Wide	Short	4	On midway of 2 radial canals	Spherical	21	-	33	4	-	-	Clarke (1882); Calder (1971)
<i>L. haichangensis</i> Xu & Huang, 1983	Hemispherical	-	Short	4	On 2/3 of the distal portion of radial canals	Slender linear	8	-	16	24	1-2 pairs	On each side of tentacles and marginal bulbs	Xu & Huang (1983)
<i>L. sinuosa</i> Lin, Xu, Huang & Wang, 2009	Flatter than hemispherical	-	-	4	On proximal portion of manubrium	Linear, longitudinally divided	4	7-8	-	4	8-10 pairs	On each side of tentacles	Lin <i>et al.</i> (2009)



**Figure 1.** Distribution of the polyp stage of the species of the genus *Lovenella* Hincks, 1868. 1: Millard. (1957, 1975); García Corrales *et al.* (1979); 2: Hincks (1868); García Corrales *et al.* (1979); Cornelius (1995); 3: Thomeley (1908); Jäderholm (1920); Vervoort (1959); Millard (1980); 4: Clarke (1882); Huvé (1952); Calder (1971, 1975); Bandel & Wedler (1987); Manning & Lindquist (2003); Dougherty & Russell (2005); Calder & Cairns (2009); 5: Nutting (1901); Fraser (1941, 1944); 6: Fraser (1938); Lees (1986); Calder *et al.* (2009); 7: Sars (1874); Picard (1955); 8: Fraser (1937, 1938, 1944); Vervoort (1985); Cornelius (1995); Schuchert (2000); 9: Fraser (1938, 1939, 1948); Calder *et al.* (2009). The symbol “?” refers to the doubtful record of Picard (1955) concerning *L. (?) paniculata*.



**Figure 2.** Distribution of the medusa stage of the species of the genus *Lovenella* Hincks (1868) 1: von Lendenfeld (1887); Kramp (1961); 2: Browne (1905); Kramp (1959, 1961); Bouillon (1984, 1995); Hirano & Yamada (1985); Navas-Pereira & Vannucci (1991); Xu *et al.* (2008); Xu (2009); 3: Fewkes (1883); Kramp (1959); 4: Millard (1975); 5: Hincks (1871); Russell (1936a, 1936b, 1953); Kramp (1959, 1961); 6: Clarke (1882); Brooks (1882); Calder (1971); 7: Xu & Huang, (1983); 8: Lin *et al.* (2009).



**Figure 3.** Light microscopy of *Lovenella gracilis* Clarke, 1882. a) General aspect of the colony from Rio Grande do Norte (Scale: 1 mm), b) detail of the hydrothecae (Scale: 200  $\mu\text{m}$ ), c) general aspect of a portion of the hydrocaulus of the colony of Santa Catarina, with internodes and hydrothecal pedicel arising from distal apophysis (Scale: 200  $\mu\text{m}$ ), d) detail of the hydrothecae and hydrocaulus (Scale: 100  $\mu\text{m}$ ).

87.5-160  $\mu\text{m}$  ( $n = 10$ ), with 1-7 septa ( $n = 10$ ), supporting hydrothecal pedicel arising from distal apophysis. Apophyses alternate; branches or additional pedicels, when present, arising laterally to the apophysis. Pedicels either annulated throughout or with 2-11 ( $n = 10$ ) distal annulations, length 110-820  $\mu\text{m}$  ( $n = 10$ ), diameter 75-120  $\mu\text{m}$  ( $n = 10$ ). Hydrotheca campanulate, 350-740  $\mu\text{m}$  ( $n = 10$ ) deep from rim to base, 215-340  $\mu\text{m}$  ( $n = 10$ ) wide at margin, 100-180  $\mu\text{m}$  ( $n = 10$ ) wide at diaphragm; diaphragm thin, transversal; operculum with 8-11 triangular to pentagonal valves ( $n = 10$ ), apparently as folded continuation of hydrothecal wall, but with discrete line demarcating operculum from hydrotheca (only in SEM). Gonothecae inverted cone-shaped,

length 620-1180  $\mu\text{m}$  ( $n = 10$ ), diameter at margin 150-270  $\mu\text{m}$  ( $n = 10$ ), diameter at base 100-200  $\mu\text{m}$  ( $n = 10$ ); walls smooth, distal region of gonothecae deepened, with a central aperture. Gonothecal pedicels short, length 60-300  $\mu\text{m}$  ( $n = 10$ ), diameter 60-120  $\mu\text{m}$  ( $n = 10$ ), with 2-8 annulations ( $n = 10$ ) throughout, arising near base of hydrothecal pedicels or directly from hydrorhiza; several medusa buds in each gonotheca, but some gonothecae empty. Nematocysts of one type: small microbasic mastigophores, dimensions 6-7  $\mu\text{m}$  X 1.5-2  $\mu\text{m}$  ( $n = 10$ , undischarged capsules).

**Distributional range.** North Atlantic (Clarke, 1882; Brooks, 1882; Fraser, 1910, 1912, 1944; Calder, 1971,

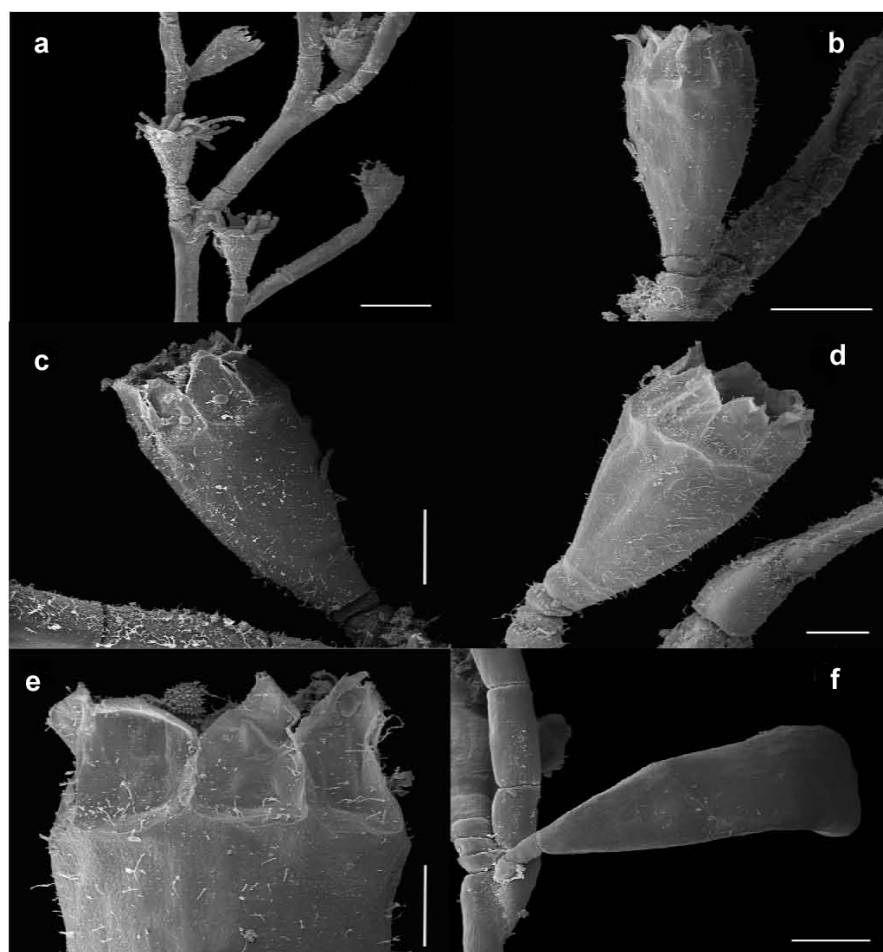
1975; Manning & Lindquist, 2003; Bouillon *et al.*, 2004; Dougherty & Russell, 2005), Gulf of Mexico (Calder & Cairns, 2009), Caribbean Sea (Bandel & Wedler, 1987), Mediterranean Sea (Huvé, 1952; Picard, 1958; Bouillon *et al.*, 2004).

## DISCUSSION

Clarke (1882: 139) described the polyp and medusa of *Lovenella gracilis* for Chesapeake Bay, uncertain of its “relationships and systematic position” when compared to *L. clausa* (Lóven, 1836). Indeed, Fraser (1910, 1912) mistakenly assigned North Carolina and Massachusetts specimens of *L. gracilis* to *L. clausa*; but he corrected himself after examining further material, noting that both species are distinct and that “the European species *L. clausa* has not been observed in the Western Atlantic” (Fraser, 1944: 174).

Concomitantly to Clarke’s description of *L. gracilis*, Brooks (1882) described the new genus *Dipleuron*, and its type-species *D. parvum*, based on a medusa found at North Carolina coast. Huvé (1952), based on Mediterranean material, considered *L. gracilis* and *D. parvum* similar, adopting the name *Dipleuron gracilis* because *Lovenella* would not be a valid genus since the type species *L. clausa* was linked to the medusa of *Euceilota hartlaubi* by Russell (1936a). However, as explained by Calder (1971: 64) “*Euceilota* and *Lovenella* are not congeneric, and the medusa *E. hartlaubi* has since been shown to be a *Lovenella* [...]”.

Life cycle studies of *L. gracilis* eventually revealed that its medusa stage is indistinguishable from *D. parvum* as described by Brooks (1882) (Calder, 1971). Then, *Dipleuron* was reaffirmed as junior synonym of *Lovenella*, with the actual name *L. gracilis* Clarke,



**Figure 4.** Scanning electron microscopy of *Lovenella gracilis* Clarke, 1882. a) General aspect of the colony (Scale: 200  $\mu\text{m}$ ), (b-d) detail of the hydrothecae (Scales: b, c, 100  $\mu\text{m}$ ; d, 50  $\mu\text{m}$ ), e) detail of the demarcation between hydrotheca and operculum (Scale: 50  $\mu\text{m}$ ). f) gonotheca arising from hydrocaulus (Scale: 100  $\mu\text{m}$ ).



1882 having priority over *Dipleuron parvum* Brooks, 1882. However, Calder (1991) reconsidered this synonymy when referring to *L. gracilis*, arguing that *Dipleuron* and *Lovenella* would be distinct because of “differences in the morphology of their opercula” (Calder, 1991: 3).

Under light microscopy, the operculum of *L. gracilis* is a continuation of the hydrothecal wall, without demarcation (*cf.* Calder, 1971, 1975; Bouillon *et al.*, 2004). The original definition of the genus *Lovenella* has no mention to a basal line demarcating the operculum (Hincks, 1868), therefore potentially accommodating *L. gracilis*. Amending diagnoses, however, have defined *Lovenella* by the presence of this line demarcating the operculum (Calder, 1991; Cornelius, 1995), a notable characteristic of most of the species of the genus (Millard, 1957; Cornelius, 1995). Based on this pattern, the absence of the demarcation in *L. gracilis* justified its transference to *Dipleuron* (Calder, 1991).

A refinement of the morphological study was necessary. We have found specimens representing the first record of *L. gracilis* for the South Atlantic and Brazilian coast (*cf.* Migotto *et al.*, 2002), even though Stechow (1914) recorded *Gonothyraea* (?) *nodosa*, a disputable and inconclusive similar hydroid for Rio de Janeiro coast, to which we prefer not to make inferences about its taxonomic status. Scanning electron microscopy of this Brazilian *L. gracilis* revealed the presence of a tenuous line separating the operculum from the hydrotheca (Fig. 4), making it clear it is a *Lovenella* species. Therefore, considering the troubled taxonomy of the family Lovenellidae and the new evidence presented herein, we propose the maintenance of the genus *Dipleuron* Brooks, 1882 as a junior synonym of *Lovenella* Hincks, 1868.

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