**Research Article**

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

Thaís Pires Miranda¹, Amanda Ferreira Cunha¹ & Antonio C. Marques¹
¹Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo
Rua do Matão Trav. 14, 101, 05508-090, São Paulo, Brazil

**ABSTRACT.** Lovenella gracilis Clarke, 1882 is one of the 15 nominal species referred to the genus Lovenella Hincks, 1868, a genus 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.

**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 (Tables 1 and 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 polyp with hydrotheca well demarcated by a basal line, separating it from the operculum (Fraser, 1944; Kramp, 1959; Bouillon and Boero, 2000).

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 and Boero (2000) and Bouillon et al. (2004) did not agree with this proposal, arguing that the medusa 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.xii.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; MZUSP4265, 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.vi.2004; MZUSP5357, MZUSP5358, with gonophores, 15.ix.2004; MZUSP5359, with gonophores, 9.iii.2004.

Description. Colonies stolonal or erect, up to 19 mm (n = 10) in height, arising directly from creeping hydrothiza 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>
<thead>
<tr>
<th>Species</th>
<th>Shape of colony</th>
<th>Growth</th>
<th>Septa per internode</th>
<th>Annulations on pedicel</th>
<th>Hydrothecae</th>
<th>Frequency of hydrothecae regeneration</th>
<th>Shape of operculum valves</th>
<th>Number of operculum valves</th>
<th>Diaphragm</th>
<th>Nematophores</th>
<th>Gonothecae</th>
<th>Arising of gonothecae</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>L. chiquitita</em></td>
<td>Stolonal or erect</td>
<td>Sympodial</td>
<td>-</td>
<td>Throughout</td>
<td>Deep-campanulate</td>
<td>Occasionally</td>
<td>Triangular with rounded base</td>
<td>8-10</td>
<td>Oblique</td>
<td>Absent</td>
<td>Smooth, elongated, widening distally</td>
<td>From hydrorhiza (Millard, 1957, 1975)</td>
<td></td>
</tr>
<tr>
<td><em>L. clausa</em> (Löven, 1836)</td>
<td>Stolonal or erect</td>
<td>Sympodial</td>
<td>-</td>
<td>2-5 on proximal and distal regions</td>
<td>Cylindrical, widening distally</td>
<td>2-3 times</td>
<td>Triangular with rounded base</td>
<td>8-10</td>
<td>Transversal</td>
<td>Absent</td>
<td>Smooth, elongated, widening distally</td>
<td>Axillary from pedicel</td>
<td>García Corrales <em>et al.</em> (1979); Cornelius (1995)</td>
</tr>
<tr>
<td><em>L. corrugata</em> Thornely, 1908</td>
<td>Erect</td>
<td>Sympodial</td>
<td>-</td>
<td>3-6 on proximal and distal regions</td>
<td>Deep-campanulate, corrugated proximally</td>
<td>2-4 times</td>
<td>Triangular with rounded base</td>
<td>8-12</td>
<td>Oblique</td>
<td>Absent</td>
<td>Ringed, spindle shaped</td>
<td>Axillary from pedicel</td>
<td>Vervoort (1959); Millard (1980)</td>
</tr>
<tr>
<td><em>L. gracilis</em> Clarke, 1882</td>
<td>Erect</td>
<td>Sympodial</td>
<td>3-4</td>
<td>1-2 on proximal and distal regions</td>
<td>Campanulate</td>
<td>-</td>
<td>Conical</td>
<td>8</td>
<td>Transversal</td>
<td>Smooth, clavate</td>
<td>Axillary from pedicel</td>
<td>Clarke (1882); Calder (1971, 1975)</td>
<td></td>
</tr>
<tr>
<td><em>L. grandis</em> Nutting, 1901</td>
<td>Erect</td>
<td>Sympodial</td>
<td>-</td>
<td>Not specified</td>
<td>Cylindrical, widening distally</td>
<td>-</td>
<td>Triangular with rounded base</td>
<td>10-12</td>
<td>-</td>
<td>Absent</td>
<td>Smooth, elongated, widening distally</td>
<td>Axillary from pedicel</td>
<td>Nutting (1901); Fraser (1941)</td>
</tr>
<tr>
<td><em>L. nodosa</em> Fraser, 1938</td>
<td>Erect</td>
<td>Sympodial</td>
<td>-</td>
<td>2-3 on distal region</td>
<td>Cylindrical, widening distally</td>
<td>-</td>
<td>Triangular with rounded base</td>
<td>8</td>
<td>-</td>
<td>Absent</td>
<td>Smooth, tubular, widening distally</td>
<td>Axillary from pedicel</td>
<td>Fraser (1938)</td>
</tr>
<tr>
<td><em>L. paniculata</em> (G.O. Sars, 1874)</td>
<td>Erect</td>
<td>Sympodial</td>
<td>-</td>
<td>On proximal region</td>
<td>Cylindrical, widening distally</td>
<td>-</td>
<td>Conical</td>
<td>-</td>
<td>Oblique</td>
<td>Absent</td>
<td>-</td>
<td>Sars (1874)</td>
<td></td>
</tr>
<tr>
<td><em>L. producta</em> (G.O. Sars, 1874)</td>
<td>Stolonal</td>
<td>Monopodial</td>
<td>-</td>
<td>3-8 on proximal and distal regions, sometimes, in the middle</td>
<td>Cylindrical, widening distally</td>
<td>-</td>
<td>Conical</td>
<td>Up to 12</td>
<td>Transversal</td>
<td>Present</td>
<td>-</td>
<td>Sars (1874); Cornelius (1995)</td>
<td></td>
</tr>
<tr>
<td><em>L. rugosa</em> Fraser, 1938</td>
<td>Stolonal or erect</td>
<td>Sympodial</td>
<td>-</td>
<td>Throughout</td>
<td>Deep-campanulate</td>
<td>-</td>
<td>Triangular with rounded base</td>
<td>9-10</td>
<td>Oblique</td>
<td>Absent</td>
<td>Smooth, elongated, widening distally</td>
<td>From hydrorhiza</td>
<td>Fraser (1938)</td>
</tr>
</tbody>
</table>

**Taxonomical position of Lovenella gracilis Clarke, 1882**
<table>
<thead>
<tr>
<th>Species</th>
<th>Umbrella</th>
<th>Velum</th>
<th>Manubrium</th>
<th>Number of gonads</th>
<th>Position of gonads</th>
<th>Morphology of gonads</th>
<th>Number of tentacles</th>
<th>Number of statocysts</th>
<th>Number of marginal vesicles</th>
<th>Number of marginal bulbs</th>
<th>Number of cirri</th>
<th>Position of cirri</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>L. annae</em> (von Lendenfeld, 1884)</td>
<td>Broader than high</td>
<td>-</td>
<td>Small, globular, with 4 interradial spots</td>
<td>4</td>
<td>Near radial canals</td>
<td>Oval</td>
<td>8</td>
<td>-</td>
<td>-</td>
<td>8</td>
<td>2 clusters</td>
<td>On each side of tentacles</td>
<td>Kramp (1961)</td>
</tr>
<tr>
<td><em>L. assimilis</em> (Browne, 1905)</td>
<td>Broader than high</td>
<td>Narrow</td>
<td>Short</td>
<td>4</td>
<td>On distal end of radial canals</td>
<td>Oval</td>
<td>4</td>
<td>-</td>
<td>-</td>
<td>5-7</td>
<td>2 clusters</td>
<td>On each side of tentacles</td>
<td>Browne (1905); Hirano &amp; Yamada (1985)</td>
</tr>
<tr>
<td><em>L. bermudensis</em> (Fewkes, 1883)</td>
<td>Wide, low, without raised apex</td>
<td>-</td>
<td>Short and wide</td>
<td>4</td>
<td>On stomach</td>
<td>Spherical</td>
<td>4-8</td>
<td>-</td>
<td>-</td>
<td>4</td>
<td>2</td>
<td>On each side of tentacles</td>
<td>Fewkes (1883); Kramp (1959)</td>
</tr>
<tr>
<td><em>L. chiquitita</em> Millard, 1957</td>
<td>Higher than wide</td>
<td>-</td>
<td>Short</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>8</td>
<td>-</td>
<td>8</td>
<td>8</td>
<td>-</td>
<td>-</td>
<td>Millard (1975)</td>
</tr>
<tr>
<td><em>L. clausa</em> (Löven, 1836)</td>
<td>Hemispherical</td>
<td>ca. ¼ of the bell radius</td>
<td>Short and small</td>
<td>4</td>
<td>On distal end of radial canals</td>
<td>Oval and longitudinally divided</td>
<td>16-24</td>
<td>-</td>
<td>16-23</td>
<td>1-3</td>
<td>On each side of tentacles</td>
<td>Kramp (1959); Cornelius (1995)</td>
<td></td>
</tr>
<tr>
<td><em>L. gracilis</em> Clarke, 1882</td>
<td>Hemispherical</td>
<td>Wide</td>
<td>Short</td>
<td>4</td>
<td>On midway of 2 radial canals</td>
<td>Spherical</td>
<td>21</td>
<td>-</td>
<td>33</td>
<td>4</td>
<td>-</td>
<td>-</td>
<td>Clarke (1882); Calder (1971)</td>
</tr>
<tr>
<td><em>L. haichangensis</em> Xu &amp; Huang, 1983</td>
<td>Hemispherical</td>
<td>-</td>
<td>Short</td>
<td>4</td>
<td>On 2/3 of the distal portion of radial canals</td>
<td>Slender linear</td>
<td>8</td>
<td>-</td>
<td>16</td>
<td>24</td>
<td>1-2 pairs</td>
<td>On each side of tentacles and marginal bulbs</td>
<td>Xu &amp; Huang (1983)</td>
</tr>
<tr>
<td><em>L. sinuosa</em> Lin, Xu, Huang &amp; Wang, 2009</td>
<td>Flatter than hemispherical</td>
<td>-</td>
<td>-</td>
<td>4</td>
<td>On proximal portion of manubrium</td>
<td>Linear, longitudinally divided</td>
<td>4</td>
<td>7-8</td>
<td>-</td>
<td>4</td>
<td>8-10 pairs</td>
<td>On each side of tentacles</td>
<td>Lin et al. (2009)</td>
</tr>
</tbody>
</table>
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: Thornely (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 µm), 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 µm), d) detail of the hydrothecae and hydrocaulus (Scale: 100 µm).

87.5-160 µm (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 µm (n = 10), diameter 75-120 µm (n = 10). Hydrotheca campanulate, 350-740 µm (n = 10) deep from rim to base, 215-340 µm (n = 10) wide at margin, 100-180 µm (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 µm (n = 10), diameter at margin 150-270 µm (n = 10), diameter at base 100-200 µm (n = 10); walls smooth, distal region of gonothecae deepened, with a central aperture. Gonothecal pedicels short, length 60-300 µm (n = 10), diameter 60-120 µm (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 µm X 1.5-2 µm (n = 10, undischarged capsules).

**Distributional range.** North Atlantic (Clarke, 1882; Brooks, 1882; Fraser, 1910, 1912, 1944; Calder, 1971,
Taxonomical position of *Lovenella gracilis* Clarke, 1882


**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* (Löven, 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 *Eucheilota hartlaubi* by Russell (1936a). However, as explained by Calder (1971: 64) “*Eucheilota* 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](image) Scanning electron microscopy of *Lovenella gracilis* Clarke, 1882. a) General aspect of the colony (Scale: 200 µm), (b-d) detail of the hydrothecae (Scales: b, c, 100 µm; d, 50 µm), e) detail of the demarcation between hydrotheca and operculum (Scale: 50 µm). f) gonotheca arising from hydrocaulus (Scale: 100 µm).
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 (?)modosa*, 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.

**ACKNOWLEDGEMENTS**

We would like to thank Dr. Helena Matthews-Cascon (Universidade Federal do Ceará) for providing material from Rio Grande do Norte, Dr. Peter Schuchert (Muséum d'Histoire Naturelle) and Dr. Yayoi Hirano (Chiba University) for the help with literature, and Enio Mattos (Universidade de São Paulo) for technical support. This study was supported by CAPES Procad, Prodoc e Pró-Equipamentos 1887/2007, CNPq (Proc. 490348/2006-8, 304720/2009-7, 304720/2009-7, 562143/2010-6, 563106/2010-7) and FAPESP (Proc. 2004/09961-4, 2006/58226-0, 2010/06927-0). This is a contribution of NP-BioMar, USP.

**REFERENCES**


Taxonomical position of *Lovenella gracilis* Clarke, 1882


Received: 16 May 2011; Accepted: 22 October 2012