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Antonio C. Marques [a] , Alvaro L. Peña Cantero [b] & Alvaro E. Migotto [c]

[a] Departamento de Zoologia , Instituto de Biociências, Universidade de São Paulo , São Paulo, Brazil

[b] Instituto Cavanilles de Biodiversidad y Biología Evolutiva , Universidad de Valencia , Valencia, Spain

[c] Centro de Biologia Marinha , Universidade de São Paulo , São Sebastião, Brazil

[d] Departamento de Zoologia, Instituto de Biociências , Universidade de São Paulo , CP 11461, 05422-970, São Paulo, SP, Brazil E-mail:
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Revision of the genus *Cryptolarella* Stechow, 1913 (Lafoeidae, Leptothecata, Hydrozoa)

ANTONIO C. MARQUES[1], ALVARO L. PEÑA CANTERO[2], & ALVARO E. MIGOTTO[3]

[1]*Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, São Paulo, Brazil,* [2]*Instituto Cavanilles de Biodiversidad y Biología Evolutiva, Universidad de Valencia, Valencia, Spain, and* [3]*Centro de Biologia Marinha, Universidade de São Paulo, São Sebastião, Brazil*

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Abstract
The bathyal genus *Cryptolarella*, comprising three known species, *Cryptolarella abyssicola* (Allman, 1888), *Cryptolarella diffusa* (Allman, 1888) and *Cryptolarella humilis* (Allman, 1888), is reviewed after the study of the holotypes of the species. A complete redescription and characterization of the species, including new data concerning morphometry and cnidome is presented, and its literature data reviewed. We conclude that all species are conspecific, resulting in a single valid species, *C. abyssicola*. The distinctive characters of the species are the growth habit, gonothecal arrangement and cnidome.

Keywords: *Deep-water, geographical distribution, hydroids, re-description, systematics, taxonomy*

Introduction

The genus *Cryptolarella* is relatively common in deep waters, and has been generally dealt with in monographic reviews of abyssal and bathyal hydroids (e.g. Vervoort 1966, 1985; Ramil and Vervoort 1992; Calder and Vervoort 1998). *Cryptolarella* was established by Stechow (1913a: 138) to accommodate those species originally assigned to the genus *Cryptolaria* Busk, 1857 by Allman (1888) that do not have coppinia or scapus.

The genus has a long history of inclusions and exclusions of species (cf. Stechow 1913a, 1921a, 1921b; Vervoort 1966, 1972; Calder and Vervoort 1998), due to difficulties in understanding its morphology in comparison to the other genera of the family Lafoeidae. In fact, the general aspect of colony and hydrotheca in both *Cryptolarella* and *Acryptolaria* Norman, 1875 are much alike, although their gonophores are absolutely distinct. This has confused taxonomists (e.g. Stechow 1921a, 1923) who did not perceive the boundaries between both genera. Indeed, the taxonomy of the family Lafoeidae, when based exclusively on trophosomal characters, is particularly limited due to its intrinsic restricted morphological variation. Moreover, it seems common to have parallelisms in different

Correspondence: Antonio C. Marques, Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, CP 11461, 05422-970, São Paulo, SP, Brazil. E-mail: marques@ib.usp.br

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stages of development of the trophosome, i.e. young stages of some genera can be similar to adult (or more developed) stages of others.

The study of reproductive characters, such as those of the coppiniae, may be useful in intrageneric and suprageneric determinations of the Lafoeidae. *Cryptolarella*, however, presents a unique situation among lafoeids. Although the trophosome of *Cryptolarella* resembles those of the genera included in the subfamily Lafoeinae, and part of those of the genera included in the subfamily Zygophylacinae, its gonothecae are solitary, i.e. not associated with each other. In this aspect, *Cryptolarella* seems to be more related to the Hebellinae, a subfamily with a completely dissimilar trophosome. Historically, the genus *Cryptolarella* was considered related to the Lafoeinae (Stechow 1921b, under the incorrect name Oswaldariinae; Naumov 1960, 1969; Bouillon 1985, under the incorrect name Eulafoeinae, see Calder 1991: 31; Calder and Vervoort 1998: 22, 25, under the correct name Lafoeinae).

In this study, besides the redescription of the holotypes of the species of *Cryptolarella*, we aim to evaluate the variability and taxonomic position of the genus.

Material and methods

The material studied belongs to the collections of the Natural History Museum (BMNH), London, UK; the United States National Museum of Natural History, Smithsonian Institution (USNM), Washington, DC, USA. The holotypes were examined, measured and photographed using microscope and stereomicroscope. The cnidome terminology follows Weill (1934) and Mariscal (1974); the nematocysts were measured non-discharged. Other study methods for Lafoeidae are from Peña and García-Carrascosa (1993) and Peña Cantero et al. (1998).

Genus *Cryptolarella* Stechow, 1913a

Cryptolarella Stechow 1913a: 138; 1923: 147; Millard 1975: 172.

Type species: *Cryptolarella abyssicola* (Allman 1888), as *Cryptolaria abyssicola* Allman 1888, by subsequent designation by Stechow (1923: 147).

Diagnosis

Colonies erect, without a definite pattern of ramification, with a creeping hydrorhiza. Hydrothecae sessile, tubular, arising singly from stem and branches, irregularly placed in several planes, curving outwards, with varied proportion between adnate and free adcauline part. Operculum, diaphragm and nematothecae absent. Gonothecae solitary, arising on stem and primary branches.

Remarks

The genus *Cryptolarella* was erected by Stechow (1913a: 138) to hold the species of *Cryptolaria* without coppinia or scapus, originally including the species *Cryptolaria abyssicola* Allman, 1888 and *Cryptolaria diffusa* Allman, 1888. Stechow (1913a: 138) also considered another species as *Cryptolarella*, *Cryptolaria conferta* Allman, 1877 in the sense of Quelch (1885: 3, Plate 2 Figure 1) and not in the original sense of Allman (1877). More recently, *Lafoea contorta* Nutting, 1905 was referred to *Cryptolarella* by Vervoort (1966), although previous authors (e.g. Stechow 1913a, 1913b; Yamada 1959: 51) assigned it to the genus *Filellum* Hincks 1868, an opinion followed by subsequent authors (e.g. Hirohito 1995; Peña Cantero et al. 1998). Vervoort (1966) also considered *Cryptolaria humilis* Allman, 1888 conspecific with *Cryptolarella abyssicola*. Finally, Vervoort (1972: 47–48) transferred *Cryptolaria flabellum* Allman, 1888 to the genus *Cryptolarella*. Therefore, six specific names were historically associated with the genus *Cryptolarella*.

Originally Stechow (1913a) did not assign a type species of *Cryptolarella*, doing this later (Stechow 1923: 147) when he selected *Cryptolaria abyssicola* Allman, 1888 as the type species of the genus. Among the three species considered by him into *Cryptolarella*, *Cryptolaria conferta*, in its original conception by Allman (1877), is currently referred to *Acryptolaria*, as *Acryptolaria conferta* (Allman 1877) (see Totton 1930). However, the specimen assigned to *Cryptolaria conferta* by Quelch (1885) represents, indeed, a *Cryptolarella*. We do not re-describe this species but tentatively include it in a list of synonyms of *C. abyssicola* below. The other species previously assigned to *Cryptolarella* by Stechow are re-described and discussed below.

Cryptolarella abyssicola (Allman, 1888)
(Figure 1; Table I)

Cryptolaria conferta: Quelch 1885: 3, Plate 2 Figure 1.

Cryptolaria abyssicola Allman 1888: 40, Plate 18 Figure 2, 2a; Levinsen 1893: 164; Marktanner-Turneretscher 1895: 404; von Campenhausen 1896a: 105; 1896b: 309; Hartlaub 1905: 593; Stechow 1913b: 29; 1923: 147; Bedot 1916: 87; 1918: 112; 1925: 160.

Cryptolaria diffusa Allman 1888: 42–43, Plate 21 Figure 1, 1a; Levinsen 1893: 164; Marktanner-Turneretscher 1895: 404; Ritchie 1907: 488; Bedot 1912: 87; 1918: 113; 1925: 161; Stechow 1913a: 138; 1913b: 29; Kramp 1951: 121, 122, 123; Vervoort 1966: 118; Calder and Vervoort 1998: 26.

Cryptolaria humilis Allman 1888: 39–40, Plate 18 Figure 1, 1a, b; Browne 1907: 16, 18, 29; Bedot 1912: 88; 1918: 114; 1925: 162; Rees and White 1966: 273; Vervoort 1966: 118; Calder and Vervoort 1998: 26.

Cryptolarella abyssicola: Stechow 1913a: 138; 1913b: 29; 1923: 147; Kramp 1951: 121, Plate 1 Figures 1–3; Vervoort 1966: 118–120, Figures 18–20; 1985: 268, 285–286, 294; Millard 1975: 172–174, Figure 57E–G; 1978: 191; 1980: 131; Dawson 1992: 15; Ramil and Vervoort 1992: 52; Calder and Vervoort 1998: 5, 25–28, Figure 12.

Cryptolarella diffusa: Stechow 1913a: 138; 1913b: 29; Kramp 1951: 123; Vervoort 1966: 118; Calder and Vervoort 1998: 26.

Cryptolarella humilis: Vervoort 1966: 118; Calder and Vervoort 1998: 26–27.

Cryptolarella flabellum: Vervoort 1972: 47–48, Figure 13a, b.

Not *Cryptolaria conferta* Allman 1877: 17, Plate 12 Figures 6–10 [=*Acryptolaria conferta* (Allman 1877)].

Not *Cryptolaria flabellum* Allman 1888: 40, Plate 19 Figure 1 [=*Acryptolaria flabellum* (Allman 1888)].

Not *Oswaldaria humilis*: Stechow 1921a: 229; 1923: 147 [=*Acryptolaria* sp.].

Material examined

Challenger St. 160, south of Australia, 42°42′S, 134°10′E, 2600 fms (=4755 m), fertile specimen, alcohol (BMNH 1888.11.13.26, holotype); *Challenger* St. 101, off Sierra Leone,

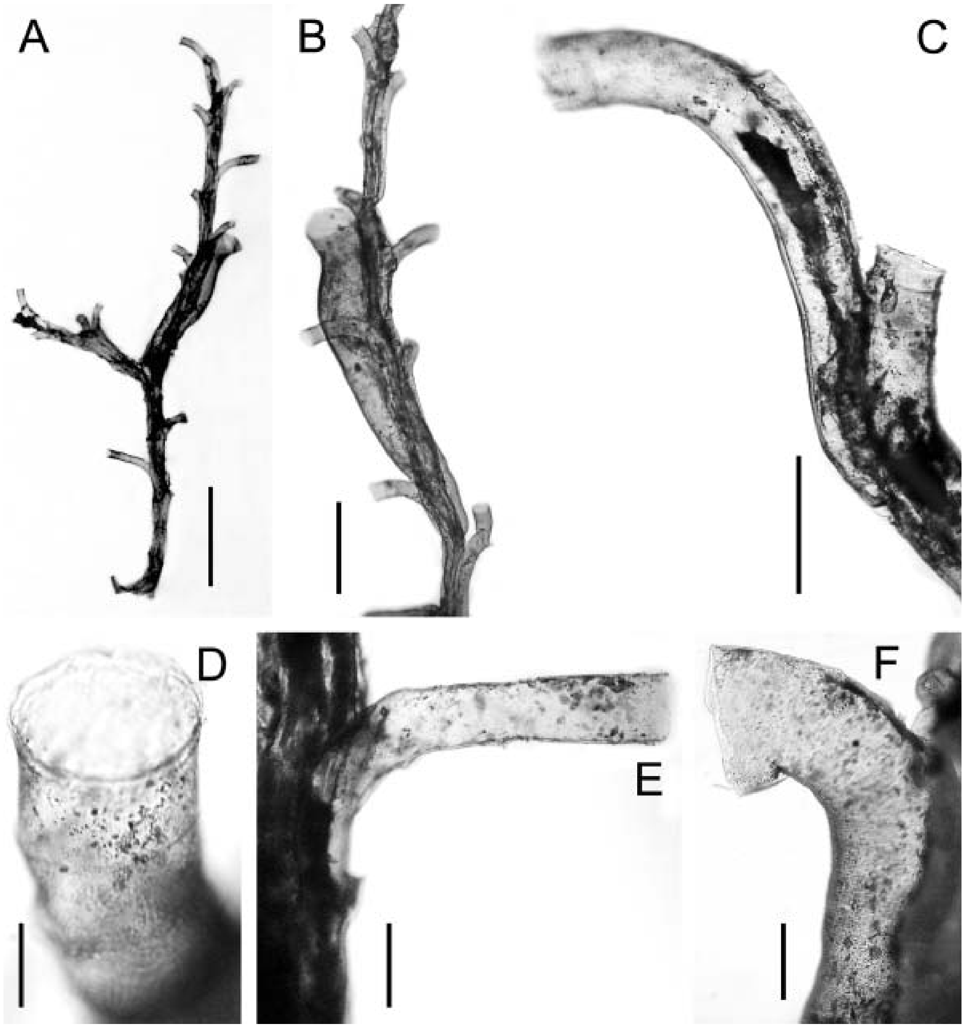

Figure 1. *Cryptolarella abyssicola* (Allman, 1888). (A) Fertile colony (*Eltanin* St. 27/1948); (B) gonotheca on stem (*Eltanin* St. 10/848); (C) hydrotheca with polyp inside; (D) hydrothecal aperture; (E) arising hydrotheca; (F) distal part of gonotheca (C–F from BMNH 1888.11.13.26). Scale bars: 2.0 mm (A); 1.0 mm (B, D); 0.3 mm (C, E, F).

04°48′N, 14°20′W, 2500 fms (=4572 m), fertile spirit specimen, badly preserved, being apparently dried out formerly (BMNH 1888.11.13.32, holotype of *Cryptolaria diffusa* Allman, 1888; cf. Allman 1888: 42; Vervoort 1966: 119); *Challenger* St. 73, near Azores, 38°30′N, 31°14′W, alcohol-preserved infertile material, 1000 fms (=1829 m) (BMNH 1888.11.13.25, type specimen of *Cryptolaria humilis* Allman, 1888; cf. Allman 1888: 39; Vervoort 1966: 120); *Eltanin* St. 10/848, south of Tierra del Fuego, 56°57′–56°56′S, 74°54′–74°43′W, 4209 m, one stem fragment ca 20 mm long; *Eltanin* St. 27/1948, Antarctic Ocean, 67°29′–67°33′S, 179°29′–179°34′E, 3495–3514 m, one stem fragment ca 23 mm long; Vema 15–69, tropical East Pacific, off Peru, 10°13′S, 80°05′W, 6324–6328 m, small fragments made up in a slide.

Table I. Morphometric data of previous records of *Cryptolarella* spp., presently assigned to *C. abyssicola* (in mm).

	C. abyssicola Holotype	*C. diffusa* Holotype	*C. humilis* Holotype	Browne (1907) (as *C. humilis*)	Kramp (1951)	Vervoort (1966)	Vervoort (1966)	Vervoort (1972) (as *C. flabellum*)	Millard (1975)	Vervoort (1985)	Calder and Vervoort (1998)
	S Australia	Sierra Leone	Off Azores	Bay of Biscay	NW Azores	Celebes Sea	Tasman Sea	W of Perú	South Africa	Bay of Biscay	Mid-Atlantic Ridge
Hydrothecae											
Length adnate part	**0.40–1.38**	0.59–0.92	0.83–0.88	0.60–0.70	1.10–1.80[a]	0.80–1.20	0.80–1.00	0.86–1.075	0.6–2.3[1]	0.90–1.00[b]	–
Length free part	0.25–0.90	**0.12**–0.25	0.20–0.28	0.56–0.90	–	0.40–0.80	0.60–1.40	1.10–**1.59**	–	0.60–0.72	–
Diameter at aperture	0.15–0.20	**0.11**–0.14	0.23–0.25	0.16–0.18	0.165–0.195	0.16–0.20	0.17–0.21	0.12–0.20	0.13–0.20	0.26–**0.30**	0.15–0.18
Gonothecae											
Length	**1.15**–3.25	1.50–2.05	–	–	2.10–2.70	2.20–2.40	**3.80**	**–**	–	–	–
Diameter at aperture	0.23–**0.55**	**0.18**–0.38	–	–	0.35–0.40	0.40–0.42	0.52	–	–	–	–
Maximum diameter	0.30–**0.85**	**0.23**–0.40	–	–	0.45–0.65	–	0.68	–	–	–	–

In bold are marked the extreme values recorded for the species.
[a]Total length of the hydrothecae; [b]Vervoort (1985, p 286) recorded "in the present material the length of the adnate hydrothecal wall varies between 1100 and 1350 μm" although he recorded different values in his table on page 286 (his data included in this table).

Type specimen

Holotype: *Cryptolaria abyssicola* Allman, 1888; fertile colony in alcohol, composed of several fragments (38, 25, 14, and 13 mm high), BMNH 1888.11.13.26.

Type locality

Challenger St. 160, 42°42′S, 134°10′E, south of Australia, 2600 fms (=4755 m) (Allman 1888: 40).

Description of holotype

Colony erect, shrubby and polysiphonic, with branches arising from a unique germinative tube; accessory tubes surrounding branching tube up to its distal parts. Germinative tube giving rise to hydrothecae in tetrapod branching (from each node, one branch giving rise to hydrotheca, other three to the sequence of the colony), and to gonothecae usually in a trifid branching (from a starting point, one branch constituting gonothecal pedicel, other two the sequence of the colony). No hydrorhiza present. Colony sparsely branched; branches in several planes, up to third order. Hydrothecae arising from both stem and branches. First-order branches (ca 20) up to 25 mm long, without a clear branching pattern; smallest branches monosiphonic, 1.13–3.75 mm (1.98 ± 0.79, $n=10$) apart from each other; largest branches polysiphonic, 0.25–0.53 mm (0.36 ± 0.09, $n=10$) in diameter, giving rise to a few branches in several planes. Lateral branches arising at angles of 45–90° in relation to main stem, sometimes with axillary hydrotheca at origin. Second- and third-order branches without a definite branching pattern. Stem (germinative and accessory tubes) and branches not divided into internodes, without apophysis; distal part of stem bearing only hydrothecae. Stem and branches deprived of nematothecae.

Hydrothecae sessile, tubular and curved outwards, arising in indistinct verticils or in an indefinite pattern, at variable distance from each other, though subsequent hydrotheca generally beginning at axil of previous one. Hydrothecae of stem and polysiphonic branches completely or partly surrounded by accessory tubes of fasciculation. Hydrothecae with more than half of their total adcauline length adnate to branches, free parts emerging from stem or branches at angles larger than 45°, usually 90°. Hydrothecae tubular, not widening distally, with smooth walls and thin perisarc; hydrothecal aperture circular, margin entire, with almost inconspicuous flaring rim and up to six renovations, 0.15–0.20 mm (0.18 ± 0.01, $n=10$) in diameter, perpendicular to long axis of free hydrothecal part. Adnate portion of hydrothecae, 0.90–1.38 mm (1.09 ± 0.16, $n=10$) long; free part 0.25–0.90 mm (0.51 ± 0.20, $n=10$) long; ratio adnate: free part 1.11–4.00:1 (2.44 ± 0.95, $n=10$). Hydranths badly preserved but, when retracted, lying in the adnate part of hydrothecae, parallel to long axis of branch.

Gonothecae arising at irregular intervals along stem and primary branches, solitary, on short pedicel; tubular to flask-shaped, ventricose at base, curving at median and distal parts. Highly varied in dimensions and shape, 1.15–3.25 mm (2.40 ± 0.81, $n=10$) long (from base to aperture through adcauline side), 0.30–0.85 mm (0.62 ± 0.15, $n=10$) maximum width at median region. Adcauline wall more or less parallel to longitudinal axis of branch; abcauline wall concave basally, convex in the middle, and again concave distally. Aperture circular, large, oblique to longitudinal axis of gonotheca and pointing upwards, 0.23–0.55 mm (0.47 ± 0.09, $n=10$) in diameter. Gonothecal perisarc with fine transverse striae (seen only at high magnification). Gonothecae rarely (three out of ca 20) upside-down in relation to growth of colony. Most gonothecae single, but two were seen arising together, with contiguous adcauline walls.

Nematocysts of one category, heterotrichous microbasic euryteles (seen discharged), 7.0–7.5 × 3.0–4.5 μm (7.25 ± 0.26 × 3.65 ± 0.58, *n*=10), bean-shaped, common, shaft 4 μm, discharged capsule 6 μm, ratio S/C=0.67:1.

Remarks

The species may be characterized by its unique gonophores, cnidome and colony shape. The gonothecae of the subfamilies Lafoeinae and Zygophylacinae are always aggregated, forming a coppinia. *Cryptolarella abyssicola* is unique because it bears solitary (or maximally paired) flask-shaped gonothecae much larger than the hydrothecae, instead of coppiniae. The cnidome of *C. abyssicola* includes only small microbasic euryteles. This type of cnidome contrasts with that of most Lafoeinae and Zygophylacinae, generally comprised of at least large microbasic mastigophores (personal observation).

Several genera of Lafoeinae and Zygophylacinae (namely *Abietinella* Levinsen, 1913, *Acryptolaria* Norman, 1875, *Cryptolaria* Busk, 1857, *Grammaria* Stimpson, 1854, and *Zygophylax* Quelch, 1885) have erect colonies in which the hydrothecae are regularly distributed along the branches, organized in two, four or six longitudinal rows. *Lafoea* Lamouroux, 1821 and *Cryptolarella* show a different organization, with hydrothecae scattered on hydrocaulus or, at most, with a tendency towards biserial arrangement (see Vervoort 1972: 47 and discussion on this material, below). Therefore, Stechow's (1913a) assertion that the hydrothecae in *Cryptolarella* are disposed in two rows is misleading as already noted by Kramp (1951: 121), and different from the original description of *C. abyssicola* by Allman (1888: 40, "hydrothecae disposed on all sides of stem"). *Cryptolarella*, however, shows some variation in the general appearance of the colony and the size of the hydrothecae, with colonies varying from "flexible with distinct but weak stems and main branches, all in one plane, some of such colonies have a bushy structure, whilst others have fairly rigid and comparatively thick main stem and branches" (Vervoort 1985: 286).

Vervoort (1966: 119) described the ontogeny of the colony of *C. abyssicola*: "the material from St. 574 includes a very youthful colony creeping on an Antipathariid. The (few) hydrothecae are tubular, slightly narrower than in the adult stage, the basal portion is slightly curved and inserts directly on the hydrorhiza. Each theca has 2 or 3 renovations (Figure 19 b)". Therefore, the initial growth of the species coincides with that of the adult stage of some species of *Filellum* (Lafoeinae), and possibly with many other younger stages of other Lafoeinae (namely *Lafoea*, *Acryptolaria*, *Grammaria*) or Zygophylacinae (namely *Zygophylax*, *Abietinella*, *Cryptolaria*). This similarity of form during ontogeny makes the identification of many young colonies of those genera and, therefore, the distribution of the species uncertain.

After examining creeping colonies from the *Galathea* Expedition that looked like young *Cryptolarella abyssicola*, Vervoort (1966: 120) considered *Lafoea contorta* Nutting 1905 as belonging to the genus *Cryptolarella*. As originally described *Lafoea contorta* represents stolonal colonies with emerging hydrothecae. Other authors (Stechow 1913a: 144; 1913b: 11, 110; 1923: 10; 1925: 458; Yamada 1959: 51; Hirohito 1995: 110) referred it to *Filellum*, and Peña Cantero et al. (1998: 301) considered it as a doubtful *Filellum* species, until the discovery of fertile colonies, a position we concur with. The use of the specific name *Cryptolarella contorta* was never repeated in the literature.

Cryptolaria diffusa, from Sierra Leone, was considered distinctive in its original description (Allman 1888) due to the presence of paired, tubular gonothecae. It was the second species assigned to *Cryptolarella* by Stechow (1913a). Vervoort (1966: 119) studied the holotype of the species remarking on the absence of such paired gonothecae, but with bodies on the branches that "could represent gonothecae though their apical parts have disappeared" and that they would be "almost certainly worm tubes". He concluded that there was no significant difference between *C. diffusa* and *C. abyssicola*, considering both conspecific (Vervoort 1966, 1985: 286). Vervoort (1966) was not sure that the structures described by Allman (1888) as "gonothecae" for both *C. abyssicola* and *C. diffusa*, and that he had also seen in the *Galathea* material (for *C. abyssicola*), differing from the coppinia of other Lafoeinae, were true gonothecae. Later he (Vervoort 1985: 286), however, reconsidered his previous position, stating, "I am now convinced that they do represent the gonothecae, though the nature of the gonophore is still a mystery".

We restudied the holotype of *C. diffusa* and found the paired gonothecae described by Allman (1888, Plate 21 Figure 1a). A full re-description of the species is given below.

Colony badly preserved, erect, shrubby, 19 mm in height (apical part broken), polysiphonic almost over its total length, 0.40 mm in diameter at base. No hydrorhiza present. Colony sparingly branched in several planes; up to third-order branches observed, arising from a unique germinative tube. Hydrothecae irregularly arising from stem and branches. Unique first-order branch perpendicular to stem, polysiphonic, 35 mm long and 0.43 mm in diameter at base, with few lower-order branches in several planes. Second- and third-order branches with no definite branching pattern. Stem (germinative and accessory tubes) and branches not divided into internodes, without apophyses; distal part of stem bearing only hydrothecae. Stem and branches without nematothecae. Hydrothecae badly preserved, sessile, tubular and curved outwards, not widening distally, with smooth walls and thin perisarc; rim even and smooth, with almost inconspicuously flaring border; aperture circular, 0.11–0.14 mm (0.13 ± 0.02, $n=3$) in diameter, perpendicular to long axis of free part of hydrotheca. Distribution of hydrothecae from nearly verticillate to an indefinite pattern; distance amongst hydrothecae variable, though subsequent ones generally arising at axil of previous one. Hydrothecae of stem and polysiphonic branches surrounded by accessory tubes. Hydrothecae with almost their total adcauline length adnate to branches; free part emerging from branches at angles larger than 45°. Adnate portion of hydrothecae 0.59–0.92 mm (0.74 ± 0.17, $n=3$) long; free part 0.12–0.25 mm (0.19 ± 0.07, $n=3$) long; ratio adnate: free part 1.09–2.80:1 (1.77 ± 0.71, $n=3$). Hydranths not preserved at all. Gonothecae irregularly arising along stem, primary and secondary branches; solitary, tubular and flask-shaped, with short pedicel, ventricose at base, curving at median and distal parts, highly variable in general dimensions and form, 1.05–2.05 mm (1.83 ± 0.26, $n=4$) long (from base to aperture at adcauline side), 0.23–0.40 mm (0.34 ± 0.09, $n=3$) maximum width at median region. Gonothecal adcauline wall more or less parallel to branch long axis, abcauline wall concave basally, convex in the middle, and concave again distally in relation to long axis of branch. Terminal aperture circular, large, oblique to long axis of gonotheca, 0.18–0.38 mm ($n=2$) in diameter. Gonothecal perisarc with striae perpendicular to gonothecal long axis. There are two gonothecae arising together, with contiguous adcauline walls.

The "bodies" mentioned by Vervoort (1966) are difficult to characterize, though we believe they could represent abnormal or damaged gonothecae. Kramp (1951: 122) and Vervoort (1966: 119–120) considered the presence of paired gonothecae as incidental or an abnormality. However, we also found paired gonothecae in the holotype of *C. abyssicola*, proving the event not to be rare. We concur with Kramp (1951), Vervoort (1996), and Calder and Vervoort (1998: 26) in regarding both species as conspecific.

A third species, also described by Allman (1888) as *Cryptolaria humilis*, was later transferred to the genus *Cryptolarella*. It was not originally included in the genus by Stechow (1913a), possibly because Allman's material was infertile. The species was recorded by Allman (1888) for the Azores region and, after that, was only recorded by Browne (1907: 29) for the Bay of Biscay. Browne was inclined to consider *C. humilis* conspecific with *Cryptolaria conferta* Allman, 1877 [currently *Acryptolaria conferta* (Allman, 1877)] and with *Cryptolaria crassicaulis* Allman, 1888 [currently *Acryptolaria crassicaulis* (Allman, 1888)].

Stechow (1921a: 229; 1923: 147) assigned *C. humilis* to the genus *Oswaldaria* Stechow 1921b (type species *Cryptolaria crassicaulis* Allman, 1888), as the binomen *Oswaldaria humilis* (Allman, 1877). For Stechow (1921a, 1921b) those species of *Cryptolaria* without diaphragm (especially in the sense of Allman 1877, 1888; see Stechow 1921b: 256) demanded the erection of a new generic name (Stechow 1921b: 256; 1923: 147), because the names *Acryptolaria*, *Scapus* and *Perisiphonia* were not available. As far as we know, the only authors who used the binomen *O. humilis*, besides Stechow himself, were Calder and Vervoort (1998: 25), in their list of synonyms of *C. abyssicola*. Currently, *Oswaldaria* is considered a synonym of *Acryptolaria* Norman, 1875.

Cryptolaria humilis was included in the genus *Cryptolarella* as a synonym of *C. abyssicola* by Vervoort (1966: 118; 1985: 285) and Calder and Vervoort (1998: 25–27), a view hesitantly adopted by Ramil and Vervoort (1992: 52). The record of *O. humilis* by Stechow (1921a: 229; 1923: 147), however, is accompanied by the description of a coppinia, and these specimens at least should be assigned to another species of the genus *Acryptolaria*, as acknowledged by Stechow himself (1923).

We have had the opportunity to re-study the holotype of *Cryptolaria humilis* Allman, 1888 and a complete re-description is given below.

Colony badly preserved, erect, shrubby, 24 mm in height, polysiphonic though branches arising from a unique germinative tube, accessory tubes surrounding branching tube almost up to its distal part. Hydrorhiza composed of many long rhizoidal tubes. Colony scarcely branched in several planes, branches up to second order, hydrothecae arising from both stem and branches. Unique first-order branch 10 mm long, polysiphonic, 0.35 mm in diameter, branching of lower-order branches in several planes. Lateral branches arising at angles of 45–90° in relation to main stem, sometimes with axilar hydrotheca at origin. Stem (germinative and accessory tubes) and branches not divided into internodes, deprived of apophyses, distal part of stem bearing only hydrothecae; stem and branches without nematothecae. Hydrothecae sessile, tubular and curved outwards, irregularly arranged in several planes, with variable distance from each other though subsequent hydrotheca generally arising at axil of previous one. Hydrothecae of stem and polysiphonic branches surrounded by accessory tubes. Hydrothecae with more than half of their total length adnate to branches, free part emerging from long axis of branches at angles greater than 45°, usually 90°. Adnate portion of hydrothecae tubular, 0.83–1.88 mm ($n=2$) long, perisarc smooth; free part cylindrical, smooth, 0.20–0.28 mm ($n=2$) long, ratio adnate: free part 3.14–4.15:1 ($n=2$); perisarc thin; hydrothecae not widening distally, margin even and smooth, with up to five shallow–medium renovations, with almost inconspicuously flaring rim; hydrothecal aperture circular, 0.23–0.25 mm ($n=2$) in diameter, perpendicular to long axis of free part of hydrotheca. Hydranths not preserved at all. Gonothecae not seen. Nematocysts of one category, heterotrichous microbasic euryteles (not seen discharged), $5.0–5.5 \times 2.0–2.5$ μm, bean-shaped.

The colony studied by Allman (1888) is badly preserved, but general dimensions and the analysis of the cnidome of remnant tissue, as well as the habit of the colony, could be studied. These characteristics are not different from those of *C. abyssicola*, corroborating Vervoort's (1966) decision.

Allman (1888: 40) described, as *Cryptolaria flabellum*, a new species of hydroid based on infertile material. His description is very poor in details: ''Colony attaining a height of about one inch; hydrocaulus rigid, rooted by a thick disc-like expansion, ramification in a single plane, and irregular. Hydrothecae alternate, distichous, very long and slender. Gonosome not known''. The species was considered well marked by Allman (1888: 40) because ''its long curved hydrothecae resemble slender lateral branches, while its rigid habit, and the fact of the ramification being all in one and the same plane, call to my mind the general aspect of certain Gorgonian Corals''. Nevertheless, the original description and figures of *C. flabellum* make it clear the species does not belong to the genus *Cryptolaria*. Indeed, Stechow (1923: 147) assigned most of the species of *Cryptolaria* described by Allman (1877, 1888) to the genus *Oswaldaria* (presently considered a synonym of *Acryptolaria*), including *Acryptolaria flabellum*. This specific name was also quoted by Fraser (1944: 212) and Vervoort (1968: 99), both referring to Allman's material.

The binomen *Cryptolaria flabellum* is still adopted in a series of papers for the northern seas (namely Naumov 1960; Filatova and Barsanova 1964; Belousov 1975a—as *Cryptolaria flabellata*—and 1975b). The only taxonomic paper of this series, Naumov (1960), has the description and figures of material sampled in the Bering and Okhotsk Seas. Vervoort (1972) considered Naumov's material belonging to a new species distinct from *C. flabellum*, because of the hydrothecal length, the more dense sets of hydrothecae, the lack of the initial arrangement in slightly displaced pairs, and the extremely high number of distal hydrothecal renovations. Naumov's material seems to be similar to the type species of *Cryptolarella abyssicola*, except by the presence of the numerous renovations in the older (=basal) hydrothecae. However, in the absence of gonothecae in the Russian material (cf. Naumov 1960), there is even the possibility of Naumov's material being a species of *Acryptolaria*.

Vervoort (1972) transferred *Acryptolaria flabellum sensu* Vervoort (1968) to the genus *Cryptolarella*. The description in Vervoort (1972) is based on fertile material collected from deep water off Peru, in the tropical eastern Pacific, during the Vema Expedition, for which the gonotheca was described (p 48, Figure 13a, b), undoubtedly indicating that it belongs to the genus *Cryptolarella*. We have re-studied part of this material, without gonothecae, deposited in the Nationaal Natuurhistorisch Museum (Leiden, The Netherlands), and observed the hydrothecal arrangement in many planes, a characteristic of *Cryptolarella*. Vervoort (1972) did not inspect Allman's type. We have also studied the type material of *Cryptolaria flabellum* [BMNH 1888.11.13.27; ''Challenger'' St. 24, 18°38′30″N, 65°05′30″W, off Culebra Island, West Indies, 390 fms (=713 m); Allman 1888: 40] and confirmed the material is indeed an *Acryptolaria* species, as proposed by Fraser (1944) and Vervoort (1968), especially based on the alternate pattern of hydrothecal arrangement, different from that found in the genus *Cryptolarella* and in Vervoort's (1972) material.

As Vervoort's (1972) *Cryptolarella* is correctly assigned to this genus, it is important to consider whether it deserves a new name. The most characteristic feature of Vervoort's material is the very long free part of the hydrothecae (1.10–1.59 mm) especially if compared to the adnate part (0.86–1.075 mm). Vervoort (1972: 47) himself noticed the ''length depending on the number of renovations being present''. Measurements without considering hydrothecal renovations show another perspective: abcauline length 1.127–1.4 mm; free adcauline length 0.403–0.550 mm; adnate adcauline length 0.950–1.127 mm; adcauline length 1.497–1.530 mm; diameter at aperture 0.161–0.190 mm. Nevertheless, although the type specimen of *C. abyssicola* is smaller (free part 0.25–0.90 mm; adnate part encompassing Vervoort's material, 0.40–1.38 mm), there is a high variation of the free part, from 0.12 mm (type of *C. diffusa*) to 1.40 mm (*C. abyssicola* for the Tasmanian Sea; Vervoort 1966). The development of the free part may be a variable trait, greatly influenced by environmental conditions. The proportion adnate: free part of the hydrotheca (0.67–0.78) also overlaps with material already recorded as *C. abyssicola*, that reach 0.71 (*C. abyssicola* for the Tasmanian Sea; Vervoort 1966) and 0.77 ("*C. humilis*" by Browne 1907 from the Bay of Biscay, see Vervoort 1966) (Table I). All other dimensions given by Vervoort (1972) are also similar to those of *C. abyssicola*. Therefore, we presently regard *Cryptolarella flabellum sensu* Vervoort (1972) as *C. abyssicola*.

The morphometric data of the recorded and studied material of *Cryptolarella abyssicola* reveals its highly variable dimensions (cf. Vervoort 1985: 286) (Table I). However, a closer examination of the holotype of the species shows that most of this variation is included in the range of the holotype variation. The most striking exception to these inclusions is the generally smaller size (namely length of free adcauline hydrothecal wall, diameter of hydrothecal aperture, maximum diameter of gonothecae, and diameter of gonothecae at aperture) of the holotype of *C. diffusa*, although some of these dimensions overlap. Other differences are the wider hydrothecal aperture in the holotype of *C. humilis* (this study) and of *C. abyssicola* from the Bay of Biscay (Vervoort 1985: 286), and the longer free part of the hydrothecae in *C. abyssicola* from the Tasman Sea (Vervoort 1966: 118–120, due to repeated renovations in those colonies) and Peru (Vervoort 1972: 47–49). Vervoort (1985: 286; probably following Millard 1975: 172) correlated the length of the adnate hydrothecal wall with depth, "the largest dimensions being usually found in deep water material". However, the variation of the dimensions in the holotype makes this unlikely.

Cryptolarella abyssicola is known from deep water; considered to be a "true bathyal hydroid" (Vervoort 1985: 294), it also inhabits abyssal bottoms. There are scattered records of the species for the Atlantic, Pacific, Indian, and Antarctic Oceans. Kramp (1951: 122) noted that in "several other groups of marine animals we know that the abyssal species frequently have a very extensive geographical distribution". The records of the species vary from 200 to 6328 m (ca 900 m from North Atlantic after Quelch 1885; 4755 m from south of Australia, 4500 m from Sierra Leone, 1829 m from near Azores after Allman 1888; 742 m from Bay of Biscay after Browne 1907; 4540–4600 m from North Atlantic after Kramp 1951; 4940–4970 m from Celebes Sea, 3710–4670 m from Tasman Sea, 2470 m from Kermadec Trench after Vervoort 1966; 6324–6328 m from Peru after Vervoort 1972; 200–2740 m from South Africa after Millard 1975; 1980–4715 m from Bay of Biscay after Vervoort 1985; 2100 m from Bay of Biscay after Ramil and Vervoort 1992; 4578 m from the Mid-Atlantic Ridge after Calder and Vervoort 1998). The species was found on rock (Kramp 1951), worm tubes and anthipathariids (Vervoort 1966).

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