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Title: When morphometry meets taxonomy: morphological variation and species boundaries in Proboscoida (Cnidaria: Hydrozoa)

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Short running title: Morphometry and species boundaries in Proboscoida

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When morphometry meets taxonomy: morphological variation and species boundaries in Proboscoida (Cnidaria, Hydrozoa)

Abstract

Species delimitation in marine taxa is often problematical given wide intraspecific variation. Based on extensive genetic sampling from specimens of the families Campanulariidae, Clytiidae and Obeliidae recently published, we evaluated morphological variation in this group, correlating morphometric and phylogenetic patterns for species delimitation. Several species within Campanulariidae were confidently delimited based on differences in size (e.g., *Bonneviella* species, *Tulpa tulipifera* and *Rhizocaulus verticillatus*) while others were reidentified and corroborated based on differences in perisarc thickness (e.g., *Silicularia rosea*, *Orthopyxis* and *Campanularia* species). In Clytiidae, the length and diameter of hydrothecae, height of hydrothecal cusps and perisarc thickness delimited the species *Clytia linearis*, *C. elsaeoswaldae* and *C. noliformis*, among others. However, few characters reliably differentiated the lineages associated with the nominal species *C. gracilis* and *C. hemisphaerica*. In Obeliidae, *Obelia geniculata* was distinctive for its higher perisarc thickness, and corroborated as a widely distributed species. *Obelia longissima* and lineages refered to *O. dichotoma* were subtly distinguished, showing a few differences in size and branching of colonies. The taxonomic implications of these results are broadly discussed. With a few exceptions, species could be delimited based on morphometric patterns, once morphological variation was investigated in a comparative manner.

Keywords: morphometrics – Campanulariidae – Clytiidae – Obeliidae – diagnostic characters – morphology – size – perisarc thickness – hydrothecae – hydrothecal cusps – branching

Introduction

Marine taxa frequently have highly variable morphology and/or a paucity of diagnostic characters, often rendering their species delimitation problematic (Yoshioka, 1982; Trussell, 1996; Bruno & Edmunds, 1997; Kaandorp, 1999; Bell & Barnes, 2000; Todd, 2008). Integrative approaches have helped to resolve incongruencies between molecular and morphological data, and many traditional characters considered to be diagnostic are often found to be uninformative (Fukami *et al.*, 2004, 2008; Forsman *et al.*, 2009, 2010; Budd *et al.*, 2010; DeBiasse & Hellberg, 2015; Pérez-Barros *et al.*, 2015). Presumably cosmopolitan species are often found to comprise several cryptic lineages (e.g., Klautau *et al.*, 1999; Barroso *et al.*, 2010; Kawauchi & Giribet, 2014), but excessive splitting of taxa may also occur (e.g., Prada *et al.*, 2014; Willette *et al.*, 2015). Contemporary studies use integrative approaches as taxonomic standards for species delimitation, but delimiting species remains far from simple because population-level variation may commonly be mistaken as interspecific variation or vice-versa, and these patterns are often not easy to differentiate (e.g., Meroz-Fine *et al.*, 2003; Prada *et al.*, 2008; Forsman *et al.*, 2010; Stefani *et al.*, 2011; see also Schuchert, 2014; Cunha *et al.*, 2016).

Species delimitation in Hydrozoa involves similar problems (reviewed by Cunha *et al.*, 2016). Their planktonic medusa stage and hydroid rafting has been for long considered to widen the dispersal capabilities of species (Ralph, 1961; Cornelius 1981a, 1992a; Boero & Bouillon, 1993; Calder, 1993), theoretically enhancing gene flow and supporting the traditional view that most hydrozoan species have nearly cosmopolitan distributions (Cornelius, 1981a, 1992b). However, molecular studies are showing that genetic diversity in Hydrozoa is higher than previously assumed (Schuchert 2005, 2014; Miglietta *et al.*, 2007, 2009, 2015; Postaire *et al.*, 2016; Moura *et al.*, 2018), and that samples from different, usually distant, localities often likely represent their own lineages (Schuchert 2014; Postaire *et al.*, 2017a, b; Boissin *et al.*, 2018). Molecular studies have also revealed the need for major changes in the classification of the group at several taxonomic levels (Collins *et al.*, 2004, 2006, 2008; Cartwright *et al.*, 2008; Leclère *et al.*, 2009; Maronna *et al.*, 2016; Moura *et al.*, 2018), allowing the description of new species (e.g., Schierwater & Ender, 2000; Cunha *et al.*, 2015) as well as revalidations of former synonyms (e.g., Schuchert, 2005; Miglietta *et al.*, 2007, 2009; Lindner *et al.*, 2011; Moura *et al.*, 2012; Cunha *et al.*, 2015).

Hydroids that were formerly included in the family Campanulariidae Johnston, 1836 have been the subject of important recent taxonomic changes. Because of the supposedly wide intraspecific variation in this group (e.g., Ralph, 1956, 1957; Cornelius, 1982, 1995), taxonomists have frequently disagreed on the importance of diagnostic characters for the species and genera, and many nominal species were either split or lumped excessively (Nutting, 1915; Ralph, 1957; Millard, 1975; Östman, 1982a, 1987; Cornelius, 1975, 1990, 1982, 1995; Calder, 1991; Boero *et al.*, 1996). Recent molecular analyses have shown that several species comprise cryptic lineages, and that intraspecific variation has been overestimated (Govindarajan *et al.,* 2005, 2006; Lindner *et al.*, 2011; Cunha *et al.*, 2015). Additionally, their phylogenetic relationships and extensive morphological diversity have led to campanulariids being split into three families within the suborder Proboscoida Broch, 1910: Campanulariidae Johnston, 1836, Clytiidae Cockerell, 1911, and Obeliidae Haeckel, 1879 (Maronna *et al.*, 2016).

Several morphological characters used in traditional diagnoses have proven to be uninformative to delimit species and genera in these families (Cunha *et al.*, 2017). Besides information from the cnidome (Östman 1982a, 1999; Lindner & Migotto, 2001) and life cycles (Lindner & Migotto, 2002; Lindner *et al.*, 2011; Zhou *et al.*, 2013; He *et al.*, 2015), morphometric data are also promising to delimit species boundaries in the group (e.g., Cunha *et al.*, 2015), especially if the range of variation of morphological characters is investigated (Cunha *et al.*, 2016).

This study aimed to evaluate patterns of morphological variation correlated with species delimitation in the suborder Proboscoida (*sensu* Maronna *et al.*, 2016). Morphometric patterns of nearly all specimens included in a previous phylogeny (Cunha *et al.*, 2017) were analyzed based on their phylogenetic relationships, integrating morphological, morphometric and molecular data for the delimitation of species of Campanulariidae, Clytiidae and Obeliidae.

Material and Methods

Taxonomic sampling

The specimens used in this study are the same vouchers that were included in the molecular phylogenetic analysis by Cunha *et al.* (2017), with a few exceptions (Supporting Information, Table S1). Therefore, materials used for DNA analyses were also used in morphometric analyses whenever possible, and the results of the two studies can be directly compared. Also, vouchers of previously published sequences, deposited in the National Museum of Natural History (USNM), Smithsonian Institution (Govindarajan *et al.*, 2006; Lindner *et al.*, 2011), Muséum d'Histoire Naturelle de Genève (MHNG) (Leclère *et al.*, 2009), and Museu de Zoologia da Universidade de São Paulo (MZUSP) (Cunha *et al.*, 2015) were studied. Additional type and non-type materials from these and other museum collections (see Supporting Information, Table S1) were studied, enhancing taxon sampling and comparisons to delimit specific lineages.

In total, we analyzed morphometric data for 291 specimens of the suborder Proboscoida, comprising 16 species of Campanulariidae (and all currently accepted genera, cf. Schuchert, 2019), 16 species of Clytiidae (and one out of two accepted genera), and 14 species of Obeliidae (covering all accepted genera). We tried to include in the analysis as many individuals of each species as possible, but this was determined by the number of sequences available for each species, as it was important to have a direct comparison between morphometric data and molecular lineages. In some cases only one individual representing the species was measured (e.g., *Clytia paulensis*), whereas in other cases up to 26 different individuals were included for comparison (e.g., *Orthopyxis sargassicola*). Additionally, some collection lots had two to three polyps of the same colony (individual) measured, allowing for intracolony comparisons (see Supporting Information, Table S1).

Morphological and morphometric analyses

We studied morphological characters of the polyps of species of Proboscoida, in accordance with the previous phylogeny of the group (Cunha *et al.*, 2017). We were not able to study vouchers of published sequences that came from medusae (Zhou *et al.*, 2013; Laakmann & Holst 2014; He *et al.*, 2015). However, their original publications, as well as some additional studies, provided important information on medusa characters that improved the discussion (e.g., Lindner & Migotto, 2002; Lindner *et al.*, 2011; Zhou *et al.*, 2013; Laakmann & Holst, 2014; He *et al.*, 2015).

Morphological characters were initially chosen based on measurements of polyps of Proboscoida reported in species descriptions that have been considered informative for species delimitation (e.g., Millard, 1975; Cornelius, 1982, 1990, 1995; Calder, 1991; Migotto, 1996; Lindner & Migotto, 2002; Lindner *et al.*, 2011). Based on our previous experience with the genus *Orthopyxis* (Cunha *et al.*, 2015) and morphological variation in Proboscoida (Cunha *et al.*, 2016), further characters were added to the analysis to capture more of the interspecific variation, specially regarding size and shape of hydrothecae and gonothecae, as well as the thickness of the perisarc (by measuring the diameter and thickness in three different positions, see Table 1). Gonosomal characters were included whenever these structures were available, but the identification of their contents was rarely possible because of their state of maturation and/or preservation. Hydranth characters (e.g., number of tentacles, length and diameter of column) were not considered because all materials studied were preserved in ethanol or formalin, and hydranths were frequently retracted or absent.

Specimens and the corresponding scales were photographed under stereo- and/or compound microscopes for morphometric analysis, and measurements were subsequently taken using Image J (Schneider *et al.*, 2012). Morphometric data were analyzed with a Principal Component Analysis (PCA, see Legendre & Legendre, 1998; Borcard *et al.*, 2011) using the *vegan* package (Oksanen *et al.*, 2015) for the R programming language (R Core Team, 2019). The PCA was conducted on a correlation matrix, and distance biplots were generated for a graphical view of the results. The analysis comprised different levels of comparison within each family, including the complete dataset as well as subsets of data, in order to have a more detailed investigation of patterns of morphological variation in these groups.

Results

Family Campanulariidae

The PCA with all species shows that several measurements of length and diameter (LH, DHMa, DHMe, DHB, LP, TLT) are responsible for the largest amount of variation in the data (PC1), while the presence of cusps (NC, HCMax, HCMin) and perisarc thickness (PPMe, PHMe, PSS) explain another direction of high variation among species (PC2, Fig. 1A, B; Table 1). Differences in size separate *Tulpa tulipifera*, *Bonneviella superba*, *B. ingens* and *B. regia* from other Campanulariidae, based on their larger hydrothecae and pedicels (Figure 1A, C). Similarly, *Rhizocaulus verticillatus* can be distinguished from *Campanularia* and *Orthopyxis* by its larger hydrothecae and trophosome (Fig. 1D, E). Differences in size are not only informative to delimit different genera, but are considerably variable among *Bonneviella* species (Supporting Information, Table S2). The dimensions of the specimens of *B. regia* (USNM 1106181, Govindarajan *et al.*, 2006) are congruent with the type material of this species, while measurements of the unidentified specimens (*Bonneviella* sp.2 and sp.4, Govindarajan *et al.*, 2006) are closer to type materials of the other species examined (Supporting Information, Table S2). *Bonneviella* sp.2 (USNM 1106182), here reidentified as *B. superba*, and *B. grandis* are among the species with larger hydrothecae and trophosome, while *Bonneviella* sp.4 (USNM 1106187), here reidentified as *B. ingens*, have hydrothecae and trophosome almost half the size of the three previous species (Supporting Information, Table S2, Fig. 2A-C).

Perisarc thickness, as well as the number and height of hydrothecal cusps, separate several species within Campanulariidae (Fig. 1B). *Silicularia rosea* is clearly distinct from *Campanularia, R. verticillatus, Tulpa* and *Bonneviella* due to its thicker perisarc (Fig. 1C, 2D). Species of *Campanularia*, in contrast, can hardly be differentiated by any of the characters included in the analysis, since they have similar morphological patterns (Fig. 1D). The exception is *C. hincksii*, slightly set apart from the remaining *Campanularia* by its taller hydrothecal cusps (HCMax, HCMin, Fig. 1D), a character that shows little or no overlap among the species when intraspecific variation is considered (Fig. 3B). The remaining characters, however, do not show this pattern (Fig. 3A, C-D).

Perisarc thickness is also informative to separate *Orthopyxis* from species of *Campanularia*, although morphological variation may attenuate this difference. Several specimens of *O. sargassicola* and *O. crenata* group together with *Campanularia* because of their thinner perisarc and presence of hydrothecal cusps, compared to the remaining species of *Orthopyxis* (Fig. 1E and Supporting Information, Fig. S1C). Indeed, although *O. sargassicola* and *O. crenata* have a thicker perisarc on average, their range of variation may overlap with *Campanularia* (Fig. 4A). Species of *Campanularia* have, on average, a thinner perisarc in comparison to most other *Orthopyxis* (except for *O. mianzani*, Fig. 4B), and when there is overlap in the range of variation of perisarc thickness, these taxa can be distinguished by the hydrothecal length and length:diameter ratio (Fig. 4C, D).

When considering only species of *Orthopyxis* without hydrothecal cusps, the variation in size and perisarc thickness distinguish all individual lineages (Figs. 1F): *Orthopyxis mianzani* has larger polyps with larger hydrothecae and a thinner perisarc; *O. asymmetrica* (see reidentified materials in Table 2) have shorter polyps and hydrothecae, with thinner perisarcs; *O. caliculata* has shorter polyps and hydrothecae, but a thicker perisarc; and *O. integra* (see reidentified material in Table 2) have larger polyps and hydrothecae, with thicker perisarcs. The specimen from the Aleutian Islands (USNM 1106184, Govindarajan *et al.*, 2006; Cunha *et al.*, 2017, as *Orthopyxis integra*_1_USA) is distinguished by its larger hydrothecae and pedicels (Figs. 1E-F, 4D). However, variation occurs in all species, and some may overlap in their ranges, sometimes contradicting the separation of the lineages (e.g., *O. caliculata* and *O. asymmetrica*, *O. integra* and *O. caliculata*, see Figs. 1F, 4). Additional comparisons with type species and descriptions from the literature (Supporting Information, Table S3) show that the morphological patterns of the specimens identified as *Orthopyxis* sp.1, *O. everta* and *O. integra*_IT by Govindarajan *et al.*, (2006) and Cunha *et al.*, (2017) are congruent with that of *O. asymmetrica* (Stechow, 1919). Differences in hydrothecal length, perisarc thickness and length:diameter ratio of the basal chamber confirm their distinction from *O. angulata* Bale, 1914, *O. compressa* (Stechow, 1919), and *O. caliculata* (Hincks, 1853) (Supporting Information, Table S3).

Additional principal components were evaluated, but they did not show clear patterns of differentiation among species (Supporting Information, Fig. S1). A PCA including only data from specimens with gonothecae separated *S. rosea* for its longer gonothecae, as well as

Orthopyxis and *Bonneviella* for their broader gonothecae (see Supporting Information, Fig. S1F).

Family Clytiidae

When all species of *Clytia* are compared, the PCA shows that most of the variation (PC1) is related to the presence of erect colonies, and the number, length, diameter, and perisarc thickness of the internodes (NIS, LIS, DIS, PIS) separate *Clytia linearis* and some specimens of *C. elsaeoswaldae*, *C.* cf. *gracilis* sp.1, and *C.* cf. *hemisphaerica* sp.1 from the remaining Clytiidae (Fig. 5A). However, when data for species of *C.* cf. *gracilis* and measurements related to internodes are excluded from the analysis, further morphological patterns among species with erect colonies appear (Fig. 5C-D). *Clytia linearis* is distinguished by its longer hydrothecae and cusps (LH, HCMax, HCmin, Figs. 5C-D), although the range of variation of the cusps height overlaps with those of other species (Fig. 6A-B). Likewise, *C. elsaeoswaldae* is separated by the larger hydrothecal diameter (DHMa, DHMe, DHB, DBC, Fig. 5A, C-D), but this character is more informative when compared to species of *C.* cf. *gracilis* and *C.* cf. *hemisphaerica*, with which it shows less overlap (Fig. 6C). Further comparisons show that *C. elsaeoswaldae* has a thicker diaphragm on average than *C. linearis*, as well as species of *C.* cf. *gracilis* and *C.* cf. *hemisphaerica* (Fig. 6D). However, morphological variation is high and certainly attenuates these differences, leading to large overlaps among species.

The second direction accounting for most variation (PC2, Fig. 5A-B) is related to perisarc thickness (PHMa, PHMe, PHB, PPMe) and length:diameter ratio of the hydrotheca (HRatio). It sets apart *Clytia* sp.2 and *Clytia noliformis* for their thicker perisarc, and *Clytia* sp.1, *C.* cf. *gracilis* sp.5 and *C. paulensis* for their more cylindrical hydrothecae (Figs. 5A, 6E-F). Although evident when directly compared among these species, differences in HRatio are not evident in all PCAs, probably because of the slight variation shown by the remaining species of *Clytia* (Fig. 6F).

Species of *C.* cf. *gracilis*, though not clearly individualized, can be set apart from each other when compared as a group: *C.* cf. *gracilis* sp.B , *C.* cf. *gracilis* sp.1 and sp.2 have larger hydrothecae and pedicels (LH, DHMa, DHMe, DHB, DP) with higher and more numerous cusps (NC, HCMax, HCMin), while *C.* cf. *gracilis* sp.3 and sp.4 have, in general, lower values for those characters (Fig. 5E-F). If measurements related to erect colonies are excluded from the analysis (LIS, PIS, NIS, DIS), *C.* cf. *gracilis* sp.1 and *C.* cf. *gracilis* sp.B can be further separated from *C.* cf. *gracilis* sp.2 by the length (LH) and length:diameter ratio of the hydrotheca (HRatio, Fig. 5F), although these differences are too small to be informative and delimit lineages. Specimens of *C.* cf. *gracilis* sp.5 spread along the four quadrants of the graph because of their high variation in the characters examined (Figure 5E-F). Additional comparisons with literature descriptions show that morphological variation is pronounced in the presumably typical *C. gracilis*, and the lineages analyzed here could fit one or more descriptions (Supporting Information, Table S4).

Species of *C.* cf. *hemisphaerica* are not separated by any of the morphological measurements, showing intermediate values for most of the characters evaluated (Fig. 5A-D, Supporting Information, Fig. S2). Characters that are important to differentiate other species of *Clytia* are uninformative for lineages of *C.* cf. *hemisphaerica*, especially because of their wide range of variation and extensive overlap. This variability is also seen when descriptions from the literature are compared (Supporting Information, Table S5 and Fig. S4).

Additional PCAs, including characters from the gonotheca, show less conspicuous patterns of differentiation among species (Supporting Information, Fig. S2). *Clytia hummelincki* has been shown to not be part of Clytiidae in previous phylogenetic analysis (Cunha *et al.*, 2017), and, therefore, was not included in the PCAs with this family.

Family Obeliidae

Patterns of morphological variation in Obeliidae are mostly congruent among the different datasets examined (Fig. 7). Considering all species, perisarc thickness (PHMA, PHMe, PHB, PPMe, TD) explains most of the data variation, separating *Obelia geniculata* by its thicker perisarc (Figs. 7A-B). This character also set apart *O. geniculata* from the remaining species when only the genus *Obelia* is considered (Fig. 7C). In addition, *Obelia geniculata* has the widest range of variation of perisarc thickness, when *Laomedea* and *Obelia* are compared (Fig. 8A). For the remaining genera, perisarc thickness does not notably contribute to the differentiation of the species, because of its extensive overlap (Fig. 8A). Measurements of diameter (DHMa, DHMe, DHB, DBC, DP) explain another direction of variation of the data, and mainly differentiate *L. flexuosa* from the remaining Obeliidae by its broader hydrothecae (Figs. 7A-B, D, 8B). Species of *Laomedea* also show a wide range of variation and overlap in pedicel length (LP, Fig. 8C), but their pedicels are on average longer than in *Obelia*.

Obelia longissima is distinguished from the remaining Obeliidae by its larger measurements of first- and second-order branches (LIS, DIS, NIS, LIB, DIB, NIB, Fig. 7A-C). It also has a wider range of variation in the hydrothecal length compared to the remaining species, and it cannot be distinguished based on this character because of the extensive overlap with other species (Fig. 8D). Erect and branched colonies also differentiate *Hartlaubella gelatinosa* and *Gonothyraea loveni*, though to a lesser extent; this pattern is clearly observed when *Obelia* is excluded from the analysis (Fig. 7D). These species, together with *O. bidentata* and *Obelia* sp.1, also differ from the remaining Obeliidae in their more cylindrical hydrothecae (higher values of HRatio) and taller hydrothecal cusps (Figs. 7B-D, 8 E, F). The exception is Obeliida indet., which has the tallest hydrothecal cusps when all these species are compared (Fig. 8F). In general, Obeliida indet. has similar morphometric patterns to *O. longissima*, mostly related to the presence of erect colonies and hydrothecal length (Fig. 7B, D). The hydrotheca is typically longer in Obeliida indet., but morphological variation attenuates this difference (Fig. 8D).

It is evident from most of the analyses that lineages of *Obelia* cf. *dichotoma* are not distinguished from each other by any of the measurements, showing intermediate values for all characters evaluated (Fig. 7A-C, E). Many specimens of *O. longissima* cannot be distinguished from the lineages of *O.* cf. *dichotoma* as well, and although some are differentiated by their larger erect and branched colonies, variations in these characters prevent a complete separation of the species (Fig. 9A). *Obelia longissima* also has longer hydrothecae and taller hydrothecal cusps on average, but their range of variation overlap among the species (Fig. 9B, D). *Obelia* cf. *dichotoma* sp.3 and *O.* cf. *dichotoma* sp.4 are grouped together and slightly separated from the remaining species of *Obelia*, probably because of their smaller and less branched colonies, but no further patterns of differentiation are seen among these lineages (Fig. 7E). Indeed, when compared to literature descriptions, the size and branching of colonies seem to be among the few characters that could fairly differentiate some of the lineages of *O.* cf. *dichotoma*, which are similar to the descriptions of other nominal species (Supporting Information, Table S6).

Characters related to the gonothecae do not differentiate the species of *Obelia*, but species of *Laomedea* can be distinguished by their larger gonothecae (LG, DGD, DGMe, DGB, DGP, Fig. 7F). Additional PCAs do not show further patterns of differentiation among Obeliidae (Supporting Information, Fig. S3).

Discussion

At first glance, morphometric patterns in the suborder Proboscoida are not discriminative, and most species would be indistinguishable. Indeed, several characters that have been historically considered as variable (e.g., colony size, perisarc thickness, height of hydrothecal cusps; Ralph, 1956; Cornelius, 1975, 1982; Millard, 1975) were corroborated as such in our current analysis, especially when different populations were included (see *Campanularia volubilis*, Fig. 3). However, we also demonstrated the existence of consistent morphological patterns when characters are investigated at different levels of comparison and their range of variation is fully considered in the analysis. Below, we discuss the main morphometric patterns observed, and how they can be informative to delimit lineages within Proboscoida.

Size differences in Campanulariidae

In Campanulariidae, the length and diameter of the trophosome, pedicels, and hydrothecae can reliably distinguish *Bonneviella*, *T. tulipifera*, and *R. verticillatus* from the genera *Campanularia*, *Silicularia*, and *Orthopyxis*, which in turn can be characterized by differences in perisarc thickness (see below). Indeed, several species of *Bonneviella* Broch, 1909 were originally assigned to *Campanularia* Lamarck, 1816, and distinguished by their "enormous" size or "immense" hydrothecae (Allman, 1876, as *Campanularia grandis*; Nutting, 1901, as *C. regia*). Later, the pre-oral cavity on the hypostome of these species was considered the main diagnostic character of the group (Bonneviellidae, Broch, 1909; Nutting, 1915). *Tulpa tulipifera* (Allman, 1888) and *Rhizocaulus verticillatus* (Linnaeus, 1758) were also originally assigned to *Campanularia* (Linnaeus, 1758; Allman, 1888), and subsequently defined as separate genera based on differences in hydrothecal size and shape, and the presence of polysiphonic colonies, respectively (Stechow, 1920, 1921). The generic value of these characters, however, has been questioned by some authors, especially given the similarities in the hydrothecae and gonothecae between *Campanularia volubilis* (Linnaeus, 1758) and *R. verticillatus* (Rees & Thursfield, 1965; Boero *et al.*, 1996, but see Cornelius, 1982: 57, 1999). The phylogenetic relationships of these species support their separation (Cunha *et al.*, 2017), and our current analysis confirmed that they differ consistently in size, which should also be considered for their delimitation. *Tulpa tulipifera*, in addition to size, can be differentiated from *Campanularia* species by the absence of a subhydrothecal spherule (Vervoort, 1972; El Beshbeeshy & Jarms, 2011). However, conclusions as to whether these differences should be considered at the genus or species level must rely on future taxonomic decisions regarding the genus *Campanularia*, especially because it is not monophyletic (see next section for further discussion).

Because of the considerable interspecific variation in *Bonneviella*, differences in size may also be informative to delimit the species examined in this study. As pointed out by Nutting (1915), *Bonneviella regia* (Nutting, 1901) can be differentiated from *Bonneviella grandis* (Allman, 1876) by the shapes of their gonothecae and the noticeably smaller hydrothecae of *B. regia* (Supporting Information, Table S2). *Bonneviella superba* Nutting, 1915 has the largest hydrothecae among *Bonneviella* species, while hydrothecae in *Bonneviella ingens* Nutting, 1915 are intermediate in size, but considerably different in shape from those of *B. superba* (Nutting, 1915; Naumov, 1969). The morphometric patterns of the type materials support the hypothesis that the vouchers of *Bonneviella* sp. (USNM 1106182 and 1108187, Govindarajan *et al.*, 2006) are close to *B. superba* and *B. ingens*, respectively (Supporting Information, Table S2). This is a tentative identification, however, because both materials lack reproductive structures. Also, intraspecific variation in *Bonneviella* was not investigated because of the small number of specimens studied (*B. regia*: N=3, *B. superba* and *B. ingens*: N=1), making it difficult to determine whether the range of variation of these characters could overlap among the species examined.

The clade comprising *C. volubilis*, *R. verticillatus*, and *Bonneviella* may represent a local radiation, and it is necessary to examine additional material from other localities (Govindarajan *et al.*, 2006). Although *C. volubilis* was not differentiated from any other *Campanularia* species based on characters related to size, both *R. verticillatus* and *Bonneviella* were characterized by their larger size (Fig. 1A, D), and all their records come from the Aleutians (Supporting Information, Table S1). *Rhizocaulus verticillatus* was originally recorded from Cumberland, England (Cornelius, 1981, 1982), and is known for its arctic-boreal distribution (Antsulevich, 1992; Calder, 2003; Schuchert, 2001; Stepanjants *et al.*, 2006; Ronowicz, 2007). Species of *Bonneviella* were originally and have been subsequently recorded in arctic and subarctic regions (type localities for *B. regia*, *B. grandis*, *B. ingens* and *B. superba* are Prince William Sound, Tsugaru Strait, Simushir Island, and Bering Sea, respectively; Broch, 1910; Kramp, 1913; Nutting, 1901, 1915; Naumov, 1969; Yamada, 1969; Schuchert, 2001). Even though these genera have a close phylogenetic relationship (Govindarajan *et al.*, 2006; Cunha *et al.*, 2017), their large size may be related to their occurrence in colder waters, a relationship previously described for other species of Proboscoida (e.g., *Obelia geniculata*, *Silicularia bilabiata*, *Orthopyxis integra*; Ralph & Thomson, 1956; Ralph, 1957; Naumov, 1969). The same occurs with *T. tulipifera*, which was originally recorded from Heard Island in Antarctica (Allman, 1888; Stechow, 1921) and has a Kerguelen-Patagonian distribution (Peña Cantero & García Carrascosa, 1999; Soto Àngel & Peña Cantero, 2015), indicating that its larger size is probably a convergence. Nevertheless, further comparisons with additional material from different populations are essential to evaluate the intraspecific range of variation of these characters and their relationship to the species geographic distribution.

Trends in perisarc thickness and size/shape of hydrothecae

Our results show that perisarc thickness is among the most variable characters (e.g., Millard, 1975; Cornelius, 1982, 1995; Cunha *et al.*, 2015), but yet most informative to delimit *Silicularia*, *Campanularia*, and *Orthopyxis*. Besides the unique bilaterally symmetrical hydrothecae of *Silicularia* Meyen, 1834, a conspicuous character to delimit the genus (Ralph, 1956, 1957; Blanco, 1967), *S. rosea* can also be delimited by the comparatively thicker perisarc of its hydrothecae and pedicels. *Silicularia rosea* Meyen, 1834 is widely distributed in antarctic and subantarctic waters, and was considered synonymous with *S. bilabiata* (Coughtrey, 1875) (Vervoort & Watson, 2003), a species shown by Ralph (1956, 1957) to have wide intraspecific variation and comprise several nominal species within *Silicularia*. A previous molecular analysis of nuclear and mitochondrial genes showed that specimens of *S. rosea* from Argentina and New Zealand were closely related (Cunha *et al.* 2017), and we found similar morphological patterns among these specimens (Fig. 1). All these lines of evidence indicate that *S. rosea* is a widely distributed species, although Galea *et al.* (2014) recently assigned previous records of *S. rosea* from Chile (Galea *et al.*, 2009) and Tristan da Cunha (Galea, 2010) to *S. bilabiata* and *S. hemisphaerica* (Allman, 1888), respectively. All specimens that we studied had an oblique hydrothecal aperture (Fig. 2D) as is typical of *S. rosea* (Vervoort & Watson, 2003; Galea *et al.*, 2014), but the hydrothecae of specimens from New Zealand were smaller (398.5μm on average) than in Argentinean specimens (790.4μm). These differences are similar to those reported by Galea *et al.* (2014, =length raised wall) for *S. rosea* and *S. hemisphaerica*. However, considering the absence of gonothecae in New Zealand specimens and their close phylogenetic relationship with specimens from Argentina, which could indicate intraspecific variations, it is essential to evaluate additional material to corroborate these proposals.

Campanularia, on the other hand, was not found to be monophyletic in previous molecular analyses (Cunha *et al.*, 2017). *Campanularia volubilis* (type locality Brighton, England, Cornelius 1981, 1982) is the type species of the genus (Cornelius, 1981b, ICZN 1985), but the clade comprising this species is hypothesized to represent a local radiation (Govindarajan *et al.*, 2006), as discussed above. In addition, the specimens included in the phylogenetic analysis come from Monterey, USA (Govindarajan *et al.*, 2006; Cunha *et al.*, 2017), and can not be assumed to represent the type species. For this reason, we refrain from any taxonomic decision regarding *Campanularia* until more and unequivocal material of the type species is available. Presently, a possible conclusion derived from the results would be to merge *Bonneviella* and *Rhizocaulus* into *Campanularia*, but this decision is contraindicated by the several morphological differences among these genera. Although not monophyletic, all species of *Campanularia* have similar morphological patterns, and most of their similarities could be considered symplesiomorphic character states. Also, differences in size of the hydrothecae between *C. hincksii* Alder, 1856 and *C. volubilis* can be masked by intraspecific variation (see Cornelius, 1982, 1995), especially when different populations are evaluated (Fig. 3). Species included in this study can only be reliably delimited by their gonothecae (Millard, 1971, 1975; Cornelius, 1982, 1995), although the height of the hydrothecal cusps in *C. hincksii* might also be distinctive.

Orthopyxis L. Agassiz, 1862 is a monophyletic genus (Cunha *et al.*, 2017), and despite several past taxonomic disputes as to whether it should be considered a synonym of *Campanularia* (Millard, 1975; Cornelius, 1982, 1995; Hirohito, 1995; Bouillon *et al.*, 2004), *Orthopyxis* was considered valid mainly based on the gonophore producing a reduced medusa (medusoid, Agassiz, 1862; Cornelius, 1995). Our analysis showed that *Orthopyxis* could also be distinguished from *Campanularia* based on trophosomal characters, such as perisarc thickness and length:diameter ratio of hydrothecae. However, *Campanularia* may fall into the range of variation of *O. sargassicola* (Nutting, 1915) and *O. crenata* (Hartlaub, 1901), because the perisarcs in these two *Orthopyxis* species vary from thin to thick, and their hydrothecae from campanulate to cylindrical (Vervoort & Watson, 2003; Cunha *et al.*, 2015, 2016). *Campanularia* and *Orthopyxis* can be reliably delimited based on these characters if their ranges of variation are evaluated, especially when there is overlap between the different species.

Indeed, variation in *O. crenata* is conspicuous. In molecular phylogenies, specimens of *O. crenata* from New Zealand clustered with unidentified *Orthopyxis* specimens from Argentina (see 16S and COI phylogenies, Cunha *et al.*, 2017). This clade forms a monophyletic group with specimens of *O. crenata* from Brazil (concatenated phylogenies, Cunha *et al.*, 2017). Our results showed that, despite their affinities, specimens from New Zealand and Argentina show clear differences in the perisarc thickness (Fig. 4A), as well as size and shape of the hydrothecae in comparison with *O. crenata* from Brazil. However, the close phylogenetic relationship with *O. crenata* from New Zealand, the type locality of the species (Hartlaub, 1901; Vervoort & Watson, 2003), led us to consider these morphological differences as intraspecific variations, also because they are commonly reported for this species (Ralph, 1957; Millard, 1975; Cornelius, 1982; Vervoort & Watson, 2003; Galea *et al.*, 2009). This decision, however, may be changed in the future, with additional evidence from morphology, ecology and genetics/genomics.

Distinct lineages of *Orthopyxis* with the traditional morphological diagnostic characters of *O. integra* (MacGillivray, 1852) were shown to be delimited by the degree of perisarc thickening and the size and shape of the hydrothecae (Cunha *et al.*, 2015). Our results corroborate these patterns, and further attest that the clade comprising the specimen of *O. integra* from the Aleutian Islands ("*Orthopyxis integra*_1_USA", USNM 1106184, see Cunha *et al.*, 2017 and Supporting Information, Table S1), with spirally grooved gonothecae (Fig. 10A), has morphological patterns that are commonly regarded as distinctive for *O. integra* (MacGillivray, 1842), such as larger and more cylindrical hydrothecae (Nutting, 1915; Bale, 1934; Hirohito, 1995; Calder *et al.*, 2014). Although we could not verify the presence of spirally grooved gonothecae in the Argentinean specimens ("Campanulariidae sp. indet." and "*O. integra*_PT20", see Supporting Information, Table S1), they are here regarded as *O. integra* given their morphological and phylogenetic patterns (Table 2), contradicting the hypothesis that this species does not occur in the southwestern Atlantic (Cunha *et al.*, 2015). Also, perisarc thickness can be much variable in *O. integra*, showing extensive overlap with *O. caliculata* (Fig. 4B).

In addition to *O. integra*, our analysis also showed that Mediterranean specimens identified as *O. integra*_IT, *O. everta* and *Orthopyxis* sp.1 by Govindarajan *et al.* (2006) and Cunha *et al.,* (2017), and that form a clade in the molecular phylogeny of the group (Cunha *et al.*, 2017), have similar morphological patterns and can be delimited by their shorter hydrothecae and thinner perisarc, in comparison to other *Orthopyxis* species (Figs. 1F, 10B). Although their perisarc is not as thick as described by Stechow (1919), we believe that these specimens should be assigned to *Orthopyxis asymmetrica* Stechow, 1919, a species commonly reported in the Mediterranean (Piraino & Morri, 1990; Peña Cantero & García Carrascosa, 2002; Bouillon *et al.*, 2004). Even though this species was proposed to be a synonym of *O. integra* (e.g., Cornelius, 1982; Östman *et al.*, 1987), our findings support *O. asymmetrica* as a distinct and valid species (see Table 2 for reidentifications).

Morphometric patterns in the delimitation of *Clytia* species

With some exceptions, several species of *Clytia* have morphometric differences congruent with their phylogenetic patterns (Cunha *et al.*, 2017). *Clytia linearis*, for instance, is monophyletic in all phylogenetic analyses (Cunha *et al.*, 2017), with consistent morphometric patterns shared by the specimens, corroborating it as a widely distributed species (Rees & Vervoort, 1987; Medel & Vervoort, 2000). Classically, *C. linearis* (Thornely, 1900) is distinguished by the hydrothecal inward folds (cf. Calder, 1991; Lindner & Migotto, 2002; Schuchert, 2003). However, this species can also be differentiated from other members of *Clytia* by its erect colonies and the size of the hydrothecae, even though its “deep” hydrothecae, frequently mentioned in descriptions, are also commonly reported as variable in size (e.g., Cornelius, 1982; Altuna, 1994). Our analyses showed that the range of intraspecific variation of the size of the hydrothecae in *C. linearis* does not overlap with those of other species (Fig. 6A), and this character can also be useful to delimit the species.

Clytia elsaeoswaldae Stechow, 1914 was also shown to be a distinct, monophyletic lineage (Lindner *et al.*, 2011; Cunha *et al.*, 2017). It is differentiated from *C. gracilis* (M. Sars, 1850) and *C. hemisphaerica* (Linnaeus, 1767) by its occasional polysiphonic colonies, inclined hydrothecal cusps, and smooth gonothecae growing exclusively on the hydrorhiza of the polyps, and by its smaller medusae (Lindner *et al.*, 2011). The morphometric patterns of *C. elsaeoswaldae* shown in this study further support its delimitation, since it can be differentiated from species of *C.* cf. *gracilis* and, to a lesser extent, *C.* cf. *hemisphaerica* by its hydrothecal diameter (Fig. 6C). The rounded basal portion of the hydrothecae (cf. Lindner *et al.*, 2011) seems to be another distinctive character of the species, probably related to its broader hydrothecae. However, some specimens of *C.* cf. *hemisphaerica* fall into its range of variation (Fig. 6C).

Clytia noliformis (McCrady, 1859) has been confounded with *C. hemisphaerica*, but it was considered distinct from the latter by several authors (e.g., Östman *et al.*, 1987; Calder, 1991; Lindner & Calder, 2000). The shape of the hydrothecae and gonothecae, as well as the distinct annulations (= subhydrothecal spherules) and the presence of merotrichous isorhizae (a unique type of nematocyst) differentiate *C. noliformis* from its congeners (Calder, 1991; Linder & Migotto, 2001, 2002). We found that the perisarc thickness, a character rarely described in the literature (but see Calder, 1991), can also be used to delimit this species (Fig. 6E).

Similarly, *Clytia paulensis* (Vanhöffen, 1910) is regarded as distinctive because of the shape of its hydrothecal cusps (Millard, 1975; Cornelius, 1982, 1995), but we noted that the species also has a more cylindrical hydrotheca in comparison with some other members of

Clytia (HRatio, Fig. 6F). The length:diameter ratio of the hydrothecae of *C. paulensis* is known to be variable, though, ranging from 1.5 to 4 in different populations (Millard, 1966; Cornelius, 1982). Since we were able to study the intracolony variation of only one specimen of *C. paulensis*, this character should be considered with caution for the delimitation of the species.

Molecular analyses of *C. gracilis* resulted in several cryptic lineages in previous studies (Govindarajan *et al.*, 2006; Lindner *et al.*, 2011; Cunha *et al.*, 2017). The polyp of *C. gracilis* is distinguished from *C. hemisphaerica* mainly by the inclined and pointed triangular cusps and the smooth gonothecae, contrasting with the non-inclined, rounded cusps and the spirally ribbed gonothecae in *C. hemisphaerica* (Calder, 1991; Cornelius, 1995). We found, however, that the height, number and shape of the hydrothecal cusps vary within the different lineages of *C. gracilis*, as do the hydrothecal length and length:diameter ratio (Figs. 2E-G, 11). The same variations are found among specimens of *C. gracilis* described in the literature from presumably different populations (Vervoort, 1959; Calder, 1991; Cornelius, 1995; Schuchert, 2001; Peña Cantero & García Carrascosa, 2002), and the lineages analyzed herein could fit into one or more of these descriptions (Supporting Information, Table S4). This emphasizes the difficulties in correlating the morphometric patterns of these lineages with the type of *C. gracilis*, especially considering that its original description was based on two species, currently *C. gracilis* and *Gonothyraea loveni* (Allman, 1859) (M. Sars, 1850, 1857; cf. Cornelius, 1982; Cornelius & Östman, 1986; Calder, 1991). Although a lectotype of *C. gracilis* was designated by Cornelius (1982: 94), it was based on the original illustration provided by M. Sars (1857), and information on its diagnostic characters remains subjective and incomplete. For a sound delimitation of the type species, it is now essential to obtain specimens of *C. gracilis* from the type locality (Lofoten and Finnmark, Norway; Sars, 1850, 1857; Calder, 1991) and correlate their phylogenetic (molecular) and morphometric patterns to the cryptic lineages. The delimitation of a neotype would also be beneficial, since the type series seems to be based on original illustrations (cf. Cornelius, 1982; Cornelius & Östman, 1986).

Clytia hemisphaerica also comprises several cryptic lineages (Cunha *et al.*, 2017). We were unable to differentiate them by their morphometric patterns (Supporting Information, Fig. S4), although all lineages have the diagnostic characters that are generally attributed to polyps of *C. hemisphaerica* (Fig. 2H-I; Calder, 1991; Cornelius, 1995). They also fit into one or more published descriptions, impeding the delimitation and identification of characters from the type of *C. hemisphaerica* (Supporting Information, Table S5), which was recorded from "Belgian seas" (cf. Linnaeus, 1767; Cornelius, 1982). The three lineages of *C. hemisphaerica* analyzed in this study were geographically structured, comprising specimens from Belize, the United States, and the Mediterranean/North Sea, and forming a monophyletic group in most of the concatenated phylogenies (Cunha *et al.*, 2017, Supporting Information, Table S1). These results raise doubts as to whether *C. hemisphaerica* should indeed be considered a species complex, or a species with pronounced population subdivisions (see Schuchert, 2014; Postaire *et al.*, 2017).

Recently, two new species of *Clytia* were described from China, together with information on their life cycles and nematocysts (Zhou *et al.*, 2013; He *et al.*, 2015). *Clytia xiamenensis* Zhou *et al.*, 2013 was shown to be closely related to *C. hemisphaerica*, also clustering with specimens of *C.* cf. *gracilis* sp.A from the USA (Lindner *et al.*, 2011; Zhou *et al.*, 2013). This pattern was corroborated by Cunha *et al.* (2017), although in their study additional specimens of *C. hemisphaerica* from the USA clustered with *C. xiamenensis* (see 16S phylogenies, Cunha *et al.*, 2017). Originally, the hydroid of *C. xiamenensis* was differentiated from *C. hemisphaerica* by its pointed and inclined hydrothecal cups, as well as its smaller B-type microbasic mastigophores (Zhou *et al.*, 2013). We showed, however, that specimens of *C. hemisphaerica* from the same clade (*C.* cf. *hemisphaerica* sp.1, see Supporting

Information, Table S1) do not have inclined hydrothecal cusps (Fig. 2H), even though their cusps are not as rounded as those of *C.* cf. *hemisphaerica* sp.2 (compare with Fig. 2I). Indeed, inclined cusps can be variable in some species (*C. gracilis*, see below), and the definition of the shape of hydrothecal cusps does not seem reliable to differentiate *C. hemisphaerica* and *C. xiamenensis*. We lack information on the nematocysts and life cycle of these specimens, which may support the separation of the species, as suggested by Zhou *et al.* (2013). However, it is important that the diagnostic characters of the type of *C. hemisphaerica* are clearly defined before the two species can be confidently differentiated. This would envolve the analysis of specimens of *C. hemisphaerica* from the type locality, and the comparison of their phylogenetic and morphometric patterns, as well as life cycle and nematocysts with those of the clade comprising *C. xiamenensis*. If this clade indeed proves to be distinct from the other lineages, then specimens from the USA should be assigned to *C. xiamenensis*.

Similarly, *Clytia gulangensis* He & Zheng, 2015 (He *et al.*, 2015) clustered with specimens of *C. gracilis* from Brazil (*C.* cf. *gracilis* sp.5, Supporting Information, Table S1) in the phylogenetic analysis of Cunha *et al.* (2017). Brazilian specimens do not have all the diagnostic characters of *C. gulangensis*, at least in the polyp stage, because some specimens have non-inclined hydrothecal cusps and smaller hydrothecae, with a length:diameter ratio near two (Supporting Information, Table S4, Fig. 2E-G). In fact, the shape of the hydrothecal cusps showed wide variation among the different Brazilian specimens (Fig. 11). He *et al.*, (2015) differentiated the polyp of *C. gracilis* from *C. gulangensis* based on the presence of asymmetric and inclined cusps (tilted, cf. Schuchert, 2003) in *C. gracilis*; however, some Brazilian specimens clustering with *C. gulangensis* had asymmetric and inclined cusps (Fig. 11B, C, E). Therefore, we conclude that the polyps of *C. gulangensis* cannot be confidently delimited from those of *C. gracilis* until the diagnostic characters of *C. gracilis* (M. Sars, 1850) are reliably determined. Nevertheless, information on the nematocysts and life cycle is still lacking for

Brazilian specimens, and these characters may prove to be distinctive for *C. gulangensis* (cf. He *et al.*, 2015).

Size and perisarc thickness differences in Obeliidae

One of the main variations found among species of Obeliidae was related to perisarc thickness, setting apart *O. geniculata* from all its congeners, as well as the remaining Obeliidae. Indeed, *O. geniculata* (Linnaeus, 1758) is a relatively easy species to identify because of its characteristic asymmetrical thickening of the internodes (Cornelius, 1975, 1990, 1995; Schuchert, 2001; Calder, 2012). Our study shows that the range of variation of perisarc thickness in *O. geniculata* is the widest among the Obeliidae (Fig. 8A), corroborating several literature descriptions that reported colonies with thin to strongly thickened perisarc (e.g., Millard, 1975; Migotto, 1996; Vervoort & Watson, 2003; Calder, 2013). Although *O. geniculata* has been suggested to represent a complex of cryptic species (Govindarajan *et al.*, 2005), molecular phylogenies including mitochondrial and nuclear markers supported its monophyly (Govindarajan *et al.*, 2006; Cunha *et al.*, 2017), showing low intraspecific distances when compared to other species of *Obelia* (see Cunha *et al.*, 2017). Similarly, our study corroborates the perisarc thickness as its distinctive character, and the nematocysts were also shown to be diagnostic (Östman, 1982a, 1999). These results indicate that there is currently little support for the delimitation of distinct species within its molecular lineages, and *O. geniculata* could be considered a widely distributed species.

Laomedea flexuosa was differentiated from the remaining members of Obeliidae by the diameter of its hydrothecae and pedicels (Fig. 8B). Indeed, this species is frequently described with a robust hydrotheca, having its length nearly equal to its width (Cornelius, 1982, 1995). *Laomedea flexuosa* was also distinguished from other members of Obeliidae by its isoenzyme patterns and nematocysts, further supporting its delimitation (Östman, 1982a, b). *Laomedea* *angulata* and *L. calceolifera*, on the other hand, do not show clear patterns of differentiation, except for the shape and position of their gonothecae, probably the most conspicuous character for their delimitation (cf. Cornelius, 1982). All species of *Laomedea* included in our analysis could be confidently distinguished from *Obelia* based on their longer pedicels (Fig. 8C), even though the genus did not prove to be monophyletic in previous molecular phylogenies (Govindarajan *et al.*, 2006; Cunha *et al.*, 2017). Because *L. flexuosa* (Alder, 1857) is the type species of the genus *Laomedea* (Cornelius 1981b, ICZN 1985), the best decision at present would be to assign *L. calceolifera* and *L. angulata* to *Obelia*, if the clade comprising all these species (Cunha *et al.*, 2017) contains the type species of *O. dichotoma* (Linnaeus, 1758) (taken as conspecific with *O. spherulina* Péron & Lesueur, 1810, the type species of *Obelia* Péron & Lesueur, 1810 (Cornelius, 1975, 1982)). However, this action is presently premature because there is no sequence of *O. dichotoma* from its type locality (southwestern England, Cornelius, 1975), and the delimitation of this species is unclear (see below).

Erect colonies and differences in shape and number of hydrothecal cusps

The species *G. loveni, H. gelatinosa* and *O. longissima*, the last to a greater extent, are separated from the remaining Obeliidae by their typically erect, branched colonies (Cornelius, 1982, 1990, 1995). *Hartlaubella* Poche, 1914 is distinguished from *Obelia* by its fixed gonophores (free medusa in *Obelia*; Cornelius, 1990; Boero *et al.*, 1996; Stepanjants, 1998), and *H. gelatinosa* (Pallas, 1766) can also be differentiated by its paired branches that are successively arranged at right angles on opposite sides of the polysiphonic main stem (Cornelius, 1995). However, this feature is also present in large colonies of *O. bidentata* Clark, 1875 (Cornelius, 1995), which has contributed to some confusion in the past (Cornelius, 1982, 1990). *Hartlaubella gelatinosa* and *G. loveni* can be differentiated from *O. bidentata* by the shape and number of cusps, which are taller and more numerous in the latter (Fig. 8F). *Obelia bidentata* also has a more cylindrical hydrotheca than *H. gelatinosa* and *G. loveni* (Fig. 8E).

Obelia bidentata is assumed to have wide intraspecific variation, particularly in erect colonies, which vary from small and monosiphonic to large and polysiphonic; and in the shape of the hydrothecal cusps, with deep or shallow embayments (Cornelius, 1975, 1982, 1990, 1995; Millard, 1975; Mammen, 1965; Calder, 1991). This variation led to some dispute on the validity of several nominal species that have been frequently synonymized with *O. bidentata*, basically due to misinterpretation of intra- or interspecific variations (e.g., *Obelia longicyatha* Allman, 1877, *Obelia austrogeorgiae* Jäderholm, 1904; Cornelius, 1975, 1982; Calder, 1991). Calder (2013) recently regarded *O. oxydentata* Stechow, 1914 as a valid species based on the smaller size of the monosiphonic colonies from the tropical and subtropical western Atlantic (<1 cm high). In our study, we found that small (0.3-1 cm high) monosiphonic colonies and large (>6 cm high) polysiphonic colonies (USNM 1106185, from the North Sea) are related in nearly all topologies analyzed in previous molecular studies (Govindarajan *et al.*, 2006; Cunha *et al.*, 2017), partially contradicting the idea that these variations could indicate interspecific differences (see Calder, 2017). However, as pointed out by Cunha *et al.* (2017), *O. bidentata* exhibits intraspecific genetic distances that are comparable to interspecific distances in other clades, and this could be evidence of either extensive population differentiation or the occurrence of a species complex (as in *C. hemisphaerica*, see above).

Obeliida indet. was ambiguously positioned at the base of Obeliidae and Clytiidae plus Obeliidae in the phylogenetic analysis of Cunha *et al.* (2017). In that study, this species was tentatively assigned to *Clytia stolonifera* Blackburn, 1938. We show that it can be differenciated from the remaining Obeliidae by its longer hydrothecae and taller hydrothecal cusps (Table 2). However, the inclusion and comparison of more specimens is necessary to confirm this identification and ascertain if this species should be considered in the genus *Clytia* or *Obelia*.

Morphometric patterns of *Obelia dichotoma* and *O. longissima*

Differences in size, branching patterns, tanning of the main stem, and the shapes of the hydrothecae and hydrothecal rim have long been used to distinguish *Obelia longissima* (Pallas, 1766) and *O. dichotoma* (Linnaeus, 1758) (Alder, 1857; Hincks, 1868; Nutting, 1915; Kramp, 1935). Currently, besides the differences in their nematocysts (Östman, 1982a), *O. longissima* is characterized by having predominantly monosiphonic colonies with usually longer stems and branches roughly uniform in length, as well as a dark and flexuous main stem. *Obelia dichotoma*, on the other hand, has polysiphonic stems in older colonies, with branches often nearly as long as the main stem, giving the colony a bushy appearance (Östman, 1987; Cornelius, 1990, 1995; Schuchert, 2001; Calder, 2012). Additionally, the hydrotheca in *O. dichotoma* is often polygonal in cross-section, with an even to crenate rim; while the hydrotheca in *O. longissima* is round with the rim castellate to sinuous (Cornelius, 1990, 1995). The hydrothecal diaphragm varies from transverse to oblique in both species (Cornelius, 1990, 1995). Previous molecular studies showed that *O. dichotoma* comprises several cryptic lineages (Cunha *et al.*, 2017), and *O. longissima* was corroborated as a monophyletic and widely distributed species (Govindarajan *et al.*, 2006; Cunha *et al.*, 2017). Our results revealed that some characters support the separation of the species (Supporting Information, Table S6), viz. (1) size of the colony, with *O. longissima* usually larger than species of *O.* cf. *dichotoma*, although some lineages of the latter exceeded the former in the number of branches; (2) length of internodes, longer on average in *O. longissima* but with some overlap with lineages of *O.* cf. *dichotoma*; (3) hydrothecal length, usually longer in *O. longissima* but with some overlap with species of *O.* cf. *dichotoma*; (4) shape of the hydrothecal rim, varying from smooth to crenate in all lineages of *O.* cf. *dichotoma*, and invariably sinuous in *O. longissima*. Morphological variation may obscure some of these differences, but colonies of *O. longissima* can be reliably delimited by these characters when intraspecific variation is considered.

Contrastingly, cryptic lineages of *O.* cf. *dichotoma* do not show morphometric differences, presenting extensive variation and overlap in their characters (Fig. 9). Although *O.* cf. *dichotoma* sp.3 and sp.4 could be distinguished from the remaining lineages by their smaller and less branched colonies (Fig. 9A, Supporting Information, Table S6), in some cases colonies varied from unbranched to branched within the same lineage, indicating that these characters vary intra- and interspecifically. This also partially contradicts the idea that the amount of branching of the colonies could support the validation of former synonyms of *O. dichotoma* (e.g., *Obelia hyalina* Clarke, 1879, *Obelia griffini* Calkins, 1899; see Calder, 2013; Calder *et al.*, 2014), although their size and the shape of the hydrothecae are probably distinctive. For instance, Calder (2013) showed that colonies of *O. hyalina* are usually small and occur in tropical and warm-temperate waters. We found that all specimens of Brazilian *O.* cf. *dichotoma* are also small (~4-11 mm) and have few branches, although some have a slightly crenate hydrothecal rim (*O.* cf. *dichotoma* sp.3, Fig. 10C, Supporting Information, Table S6), in contrast to the even hydrothecal rim of *O. hyalina* (Clarke, 1879; Calder, 2013). Similarly, all specimens of *O.* cf. *dichotoma* sp.4 have rounded hydrothecae in cross section and an even hydrothecal rim (Fig. 10D, Supporting Information, Table S6), in accordance with the diagnostic characters of *O. griffini*, recently revalidated by Calder *et al.* (2014). Although these identifications are tentative and need further confirmation, our results could support the revalidation of former synonyms of *O. dichotoma* to accommodate these cryptic lineages. Better knowledge of the nematocysts of these lineages might be particularly important for their corroboration, especially given that I_D and I_d-type isorhizae are diagnostic for *O. dichotoma* and assumed to be invariably present in the species (Östman, 1982a, 1987; Cornelius, 1990).

Conclusions

This study demonstrates the usefulness of morphometric data to delimit species in Proboscoida. We showed that morphometric characters related to size, perisarc thickness, shape of hydrothecae, and hydrothecal cusps may contribute to the delimitation of several species, although in some cases (e.g., *Campanularia* spp., *Clytia gracilis*, *Clytia hemisphaerica*, *Laomedea* spp., *Obelia dichotoma*), morphometric differences are masked by intraspecific variation (see summary in Table 2 and phylogenetic hypothesis with the species reidentified in this study in Fig. 12). Considering that our study was limited to the hydroid stage, extending this approach to investigate characters of the medusa stage and nematocysts is promising, and may shed light on some of the remaining difficult cases. However, some attention and specific procedures should be taken into consideration for this taxonomic approach. Even though many marine groups have wide intraspecific variation, consistent differences in morphometric patterns may be uncovered once this variation is comparatively investigated. This might be difficult to persue at first, without access to data from different populations and morphological characters. However, this problem will be gradually overcome once taxonomic descriptions that include morphometric characters and their amplitude of variation are more often linked to molecular data of voucher specimens. Morphometric characters are usually simple to obtain with the aid of compound or stereo microscopes and digital cameras, and in most cases they will be more informative for the identification if considered in conjunction with other discrete diagnostic characters, as well as information on genetic differentiation of populations.

Thorough investigations using morphometric data for voucher specimens and molecular trees, complemented by broader inferences in population morphological and morphometric variation, will improve delimitations of species and, as a corollary, result in more complete and precise taxonomic descriptions that allow for accurate identifications. This approach will directly impact our current knowledge on Hydrozoa (as well as Medusozoa and other marine taxa), refining our assessments of marine species diversity.

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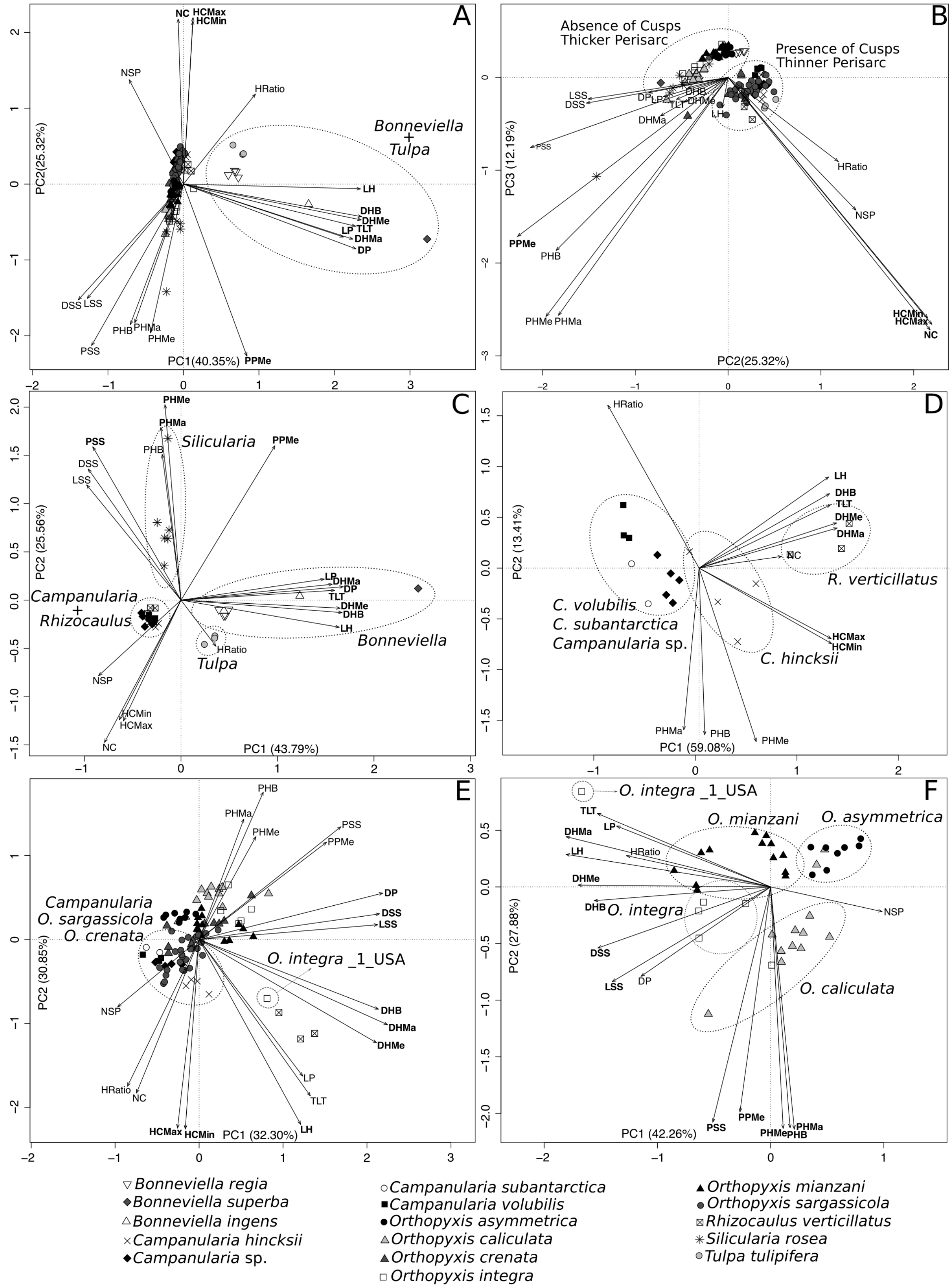

Figure 1. Distance biplots of the Principal Component Analysis (PCA) comprising data for Campanulariidae. A. First and second principal components (PCs) of the PCA with the

complete dataset; B. Second and third PCs of the PCA with the complete dataset; C. First and second PCs of the PCA without the genus *Orthopyxis*; D. First and second PCs of the PCA with *Campanularia* and *Rhizocaulus*; E. First and second PCs of the PCA with *Campanularia* and *Orthopyxis*; F. First and second PCs of the PCA with *Orthopyxis*, but excluding *O. sargassicola* and *O. crenata*. In E and F, position of the specimen *Orthopyxis integra*_1_USA is shown (see Supporting Information, Table S1). Numbers in parentheses indicate percentages of variation explained by each principal component. Abbreviations of morphometric variables as in Table 1, and those in bold indicate measurements that were correlated with each principal component (Pearson correlation >0.7 and <-0.7).

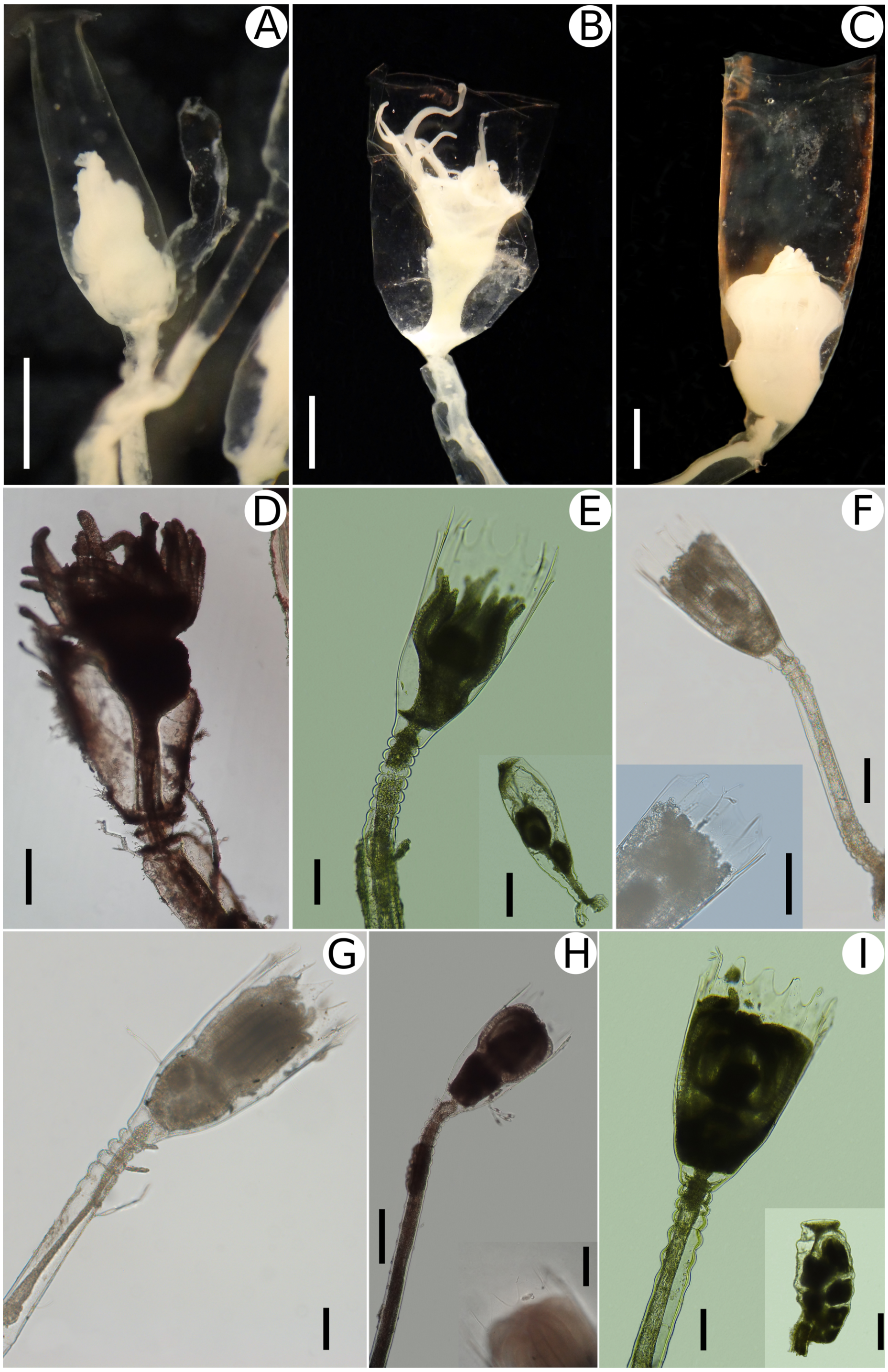

Figure 2. General morphology of species of Campanulariidae and Clytiidae. A. *Bonneviella regia* (USNM 1106181); B. *Bonneviella superba* (USNM 1106182); C. *Bonneviella ingens* (USNM 1106187); D. *Silicularia rosea* (PT11_ARG); E. *Clytia* cf. *gracilis* sp.1 (EL32_SLV), with gonotheca; F. *Clytia* cf. *gracilis* sp.3 (EL05_SLV), with detail of hydrothecal cusps; G. *Clytia* cf. *gracilis* sp.5 (PAF03_BRA); H. *Clytia* cf. *hemisphaerica* sp.1 (FLT03_USA), with

detail of hydrothecal cusps; I. *Clytia* cf. *hemisphaerica* sp.2 (EL06_SLV), with gonotheca. Scales: A, C = 1 mm; B = 2mm; = 300 μm; F (both), G, H (cusps), I (trophosome) = 100 μm; D, E (both), H (trophosome), I (gonotheca) = 200 μm.

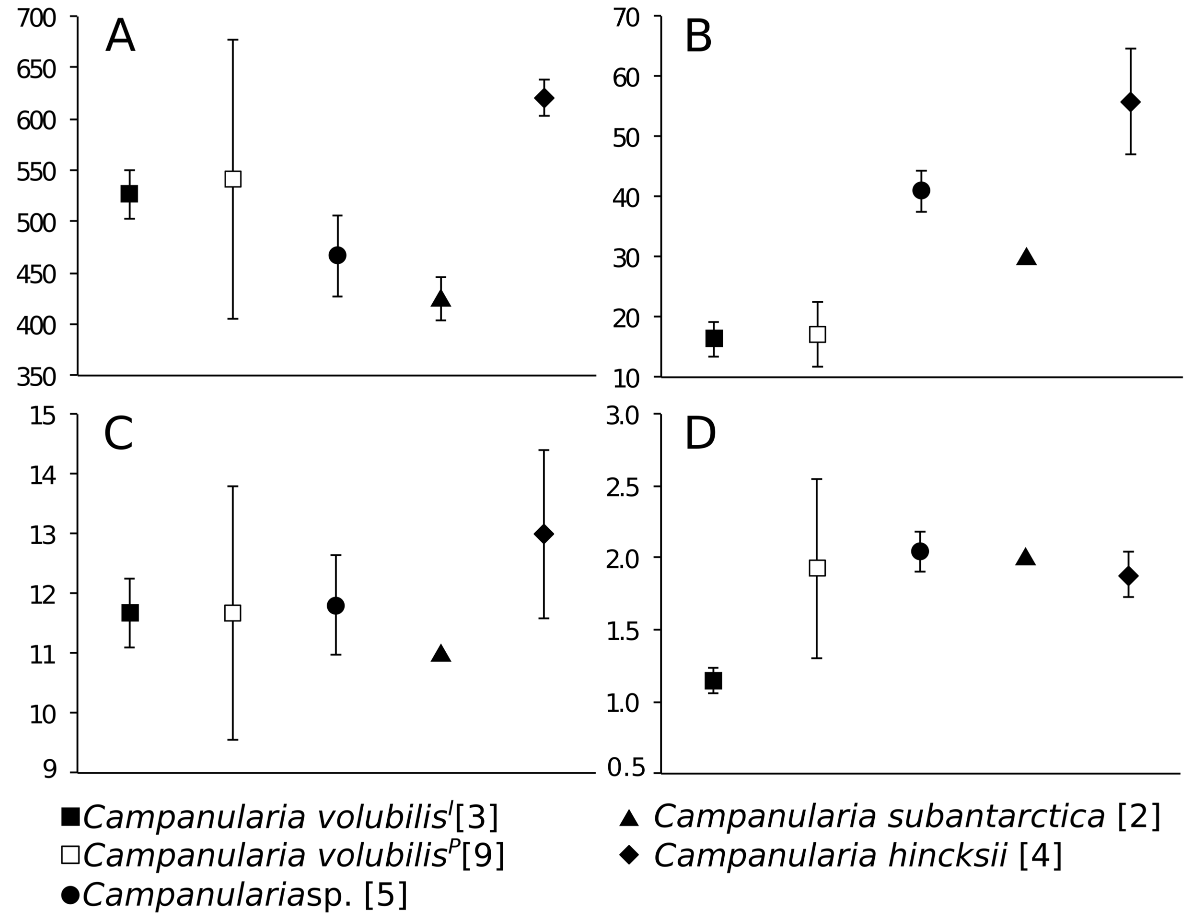

Figure 3. Mean ± standard deviation of morphometric data for *Campanularia*. Morphological variation in *C. volubilis* is presented as intracolony (^{I}) and population variation (^{P}, ZMUC and USNM 29217, see Table S1) for comparison. A. Length of hydrothecae (LH, µm); B. Maximum height of hydrothecal cusps (HCMax, µm); C. Number of hydrothecal cusps (NC); D. Length:diameter ratio of hydrotheca (HRatio). Brackets = [number of specimens measured].

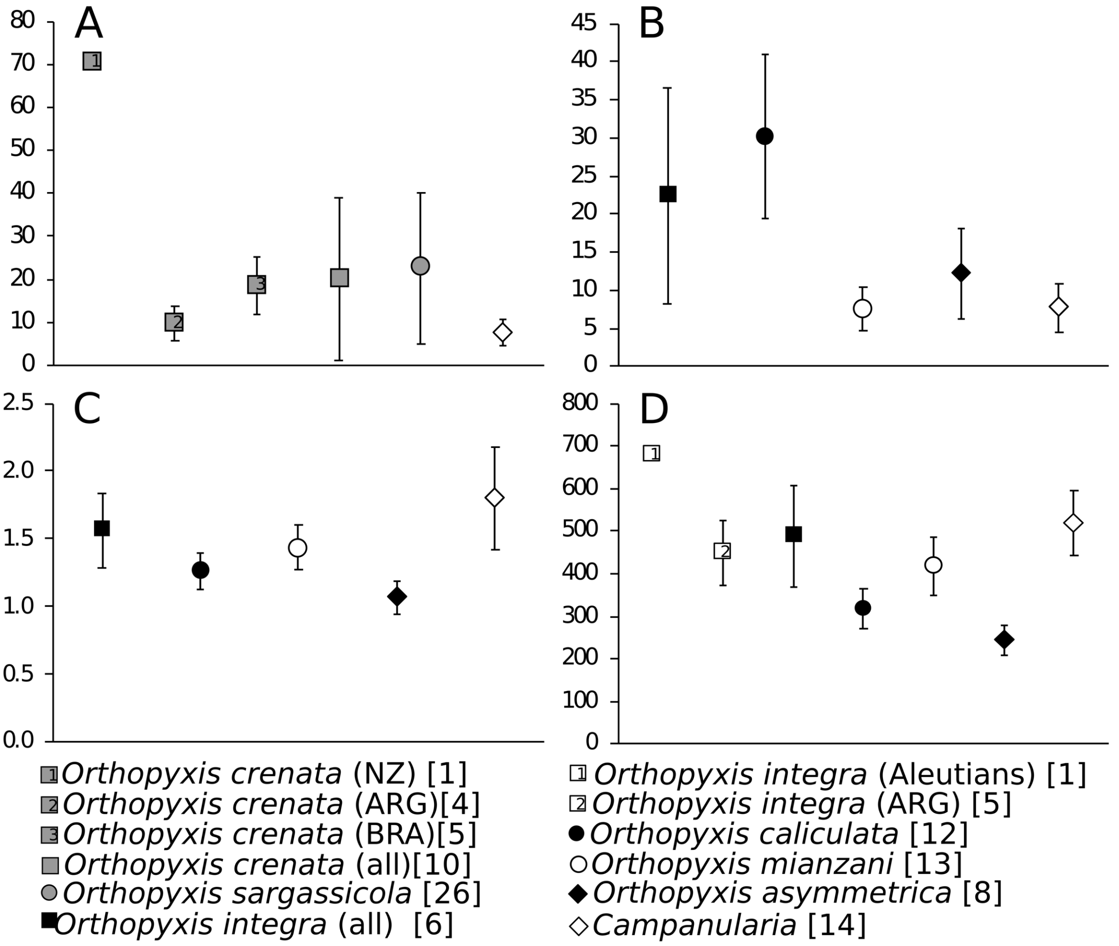

Figure 4. Mean ± standard deviation of morphometrica data for *Orthopyxis*, including a comparison with species of *Campanularia* (ie., *C. subantarctica*, *C. hincksii* and *Campanularia* sp., Supporting Information, Table S1). Morphological variation in *O. crenata* and *O. integra* is presented separately for some populations and combined ("all"), for comparison. Data for specimens of *O. crenata* from New Zealand, Argentina and Brazil are represented with numbers 1 to 3, respectively. Similarly, data for specimens of *O. integra* from the Aleutian Islands and Argentina are represented with number 1 and 2, respectively. A, B. Maximum perisarc thickness of hydrotheca at medial portion (PHMe, µm); C. Length:diameter ratio of hydrotheca (HRatio); D. Length of hydrotheca (LH, µm). Brackets = [number of specimens measured].

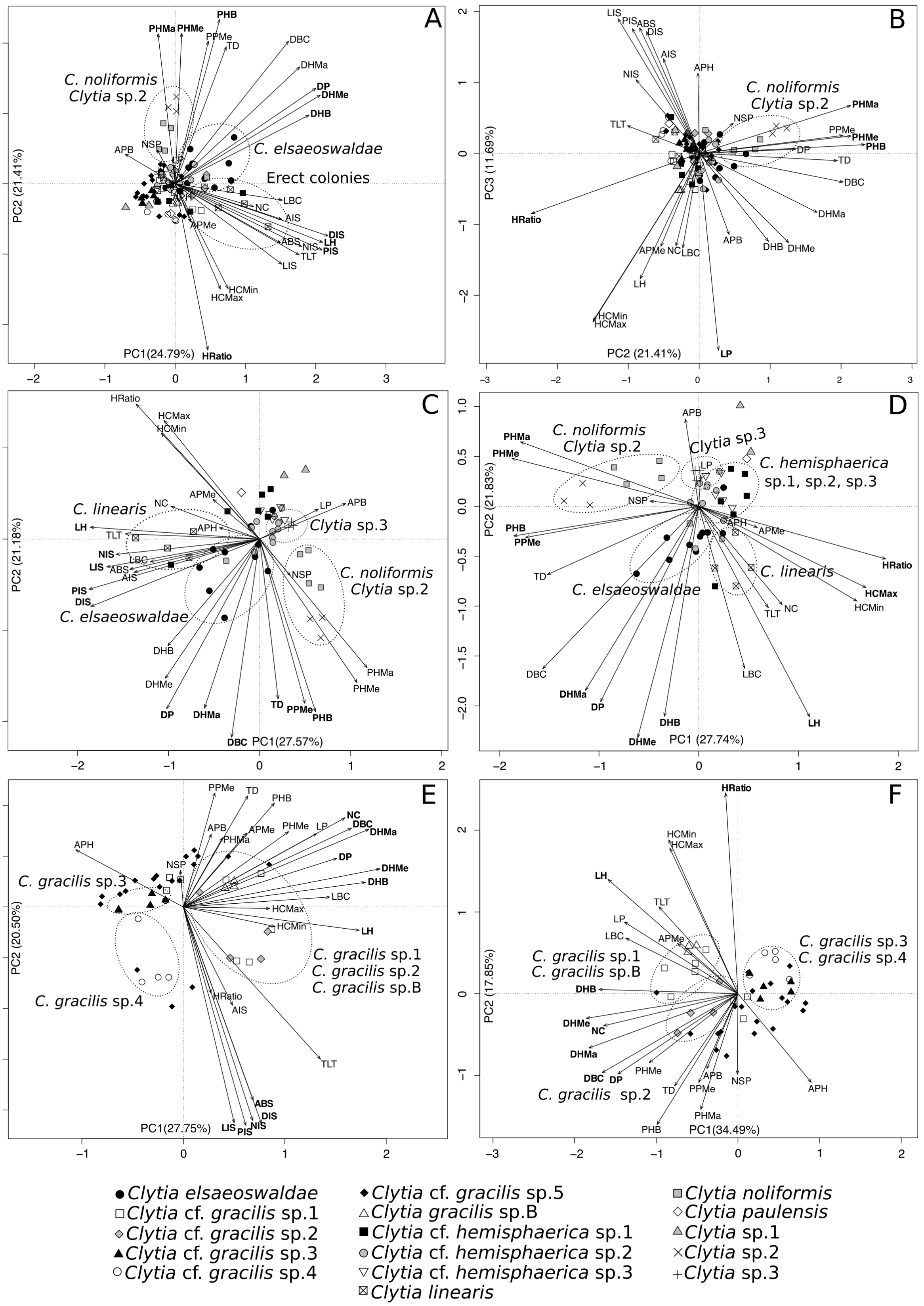

Figure 5. Distance biplots of Principal Component Analysis (PCA) comprising data for Clytiidae. A. First and second principal components (PCs) of the PCA with the complete

dataset; B. Second and third PCs of the PCA with the complete dataset; C. First and second PCs of the PCA without *Clytia* cf. *gracilis* lineages; D. First and second PCs of the PCA without *C.* cf. *gracilis* lineages and measurements related to internodes of erect colonies (NIS, LIS, AIS, PIS, DIS); E. First and second PCs of the PCA with lineages of *C.* cf. *gracilis*; F. First and second PCs of the PCA with lineages of *C.* cf. *gracilis*, excluding measurements related to internodes of erect colonies (NIS, LIS, AIS, PIS, DIS). Numbers in parentheses indicate percentages of variation explained by each principal component. Abbreviations of morphometric variables as in Table 1, and those in bold indicate measurements that were correlated with each principal component (Pearson correlation >0.7 and <-0.7).

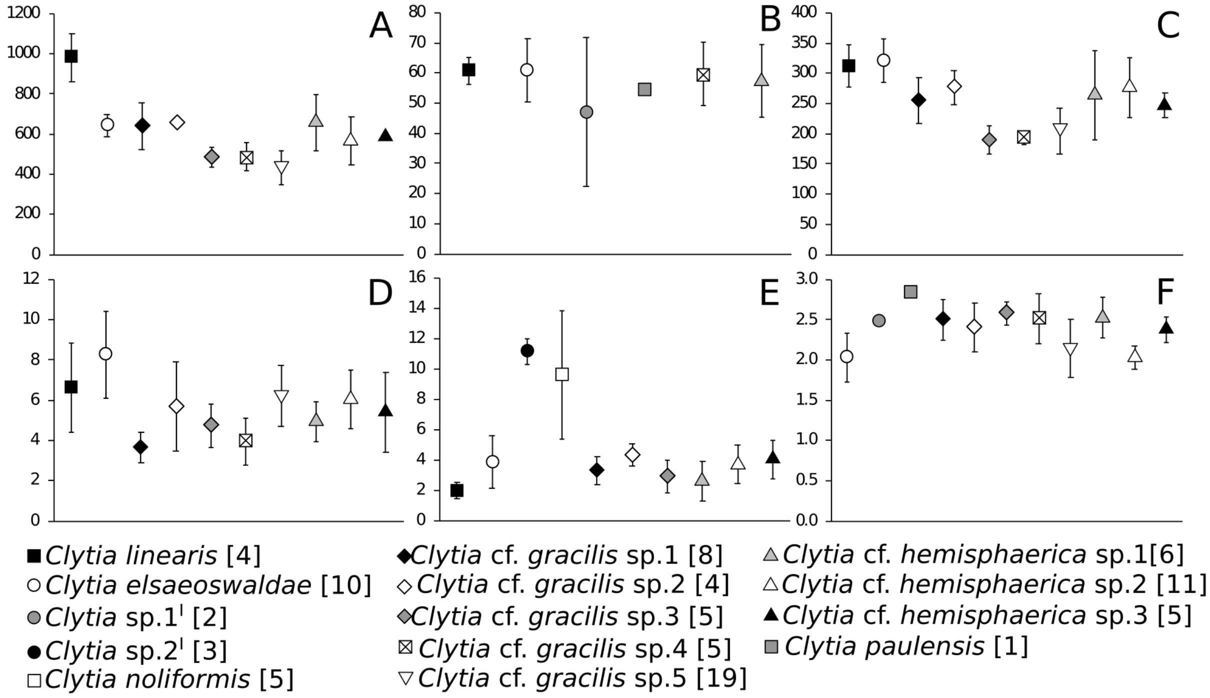

Figure 6. Mean ± standard deviation of morphometric data for *Clytia* species. Data for *Clytia* sp.1 and sp.2 refers to intracolony (^{I}) variation. A. Length of the hydrotheca (LH, µm); B. Maximum height of hydrothecal cusps (HCMax, µm); C. Maximum diameter of hydrotheca at medial portion (DHMe, µm); D. Thickness of diaphragm (TD, µm); E. Maximum hydrothecal perisarc thickness at margin (PHMa, µm); F. Length:diameter ratio of hydrotheca (HRatio). Brackets = [number of specimens measured].

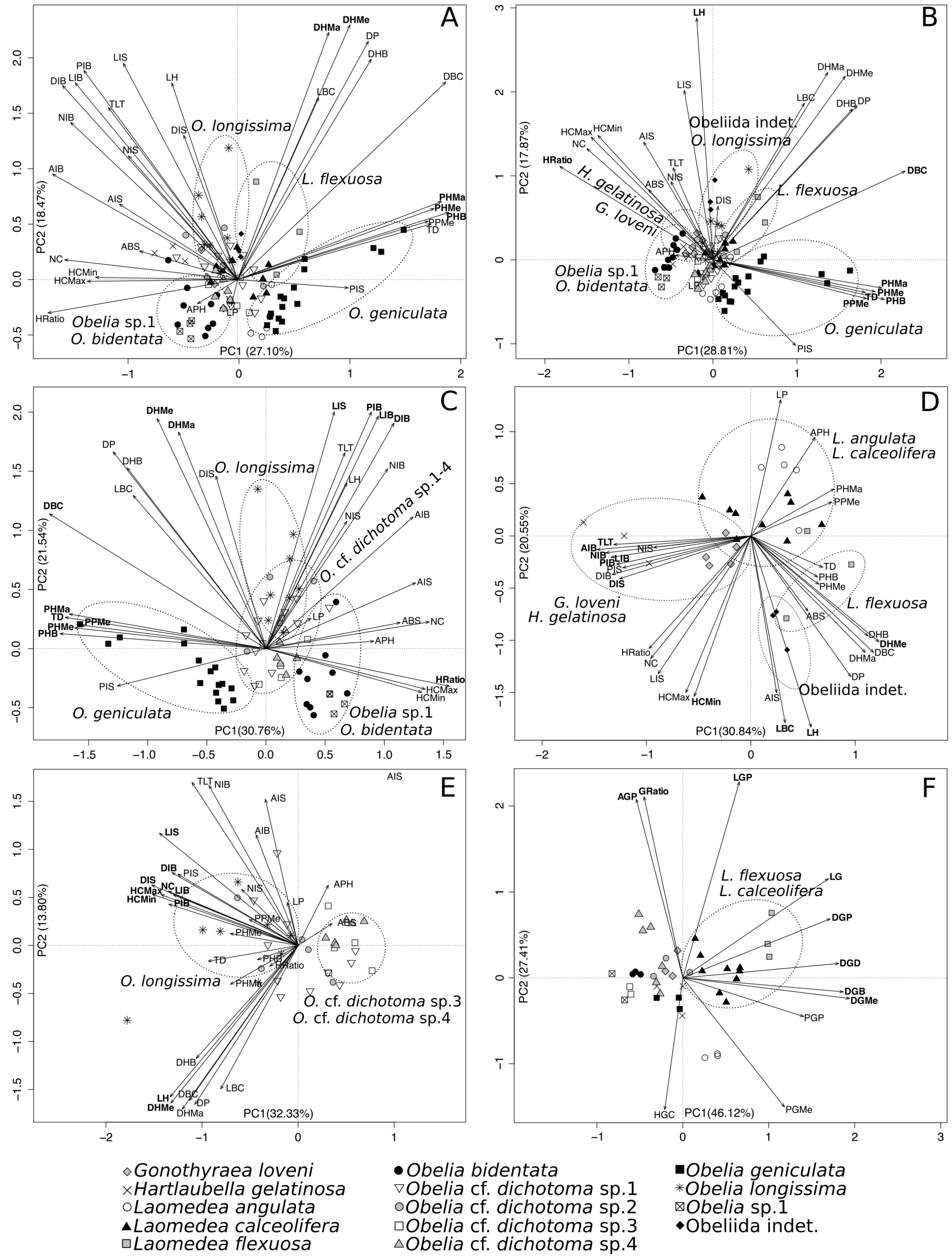

Figure 7. Distance biplots of the Principal Component Analysis (PCA) comprising data for the family Obeliidae. A. First and second principal components (PCs) of the PCA with the complete dataset; B. First and second PCs of the PCA with the complete dataset, excluding

measurements related to second-order branches of erect colonies (NIB, DIB, AIB, LIB, PIB); C. First and second PCs of the PCA with species of *Obelia* only; D. First and second PCs of the PCA without species of *Obelia*; E. First and second PCs of the PCA with lineages of *O.* cf. *dichotoma* and *O. longissima*; F. First and second PCs of the PCA with measurements of the gonothecae. Numbers in parentheses indicate percentages of variation explained by each principal component. Abbreviations of morphometric variables as in Table 1, and those in bold indicate measurements that were correlated with each principal component (Pearson correlation >0.7 and <-0.7).

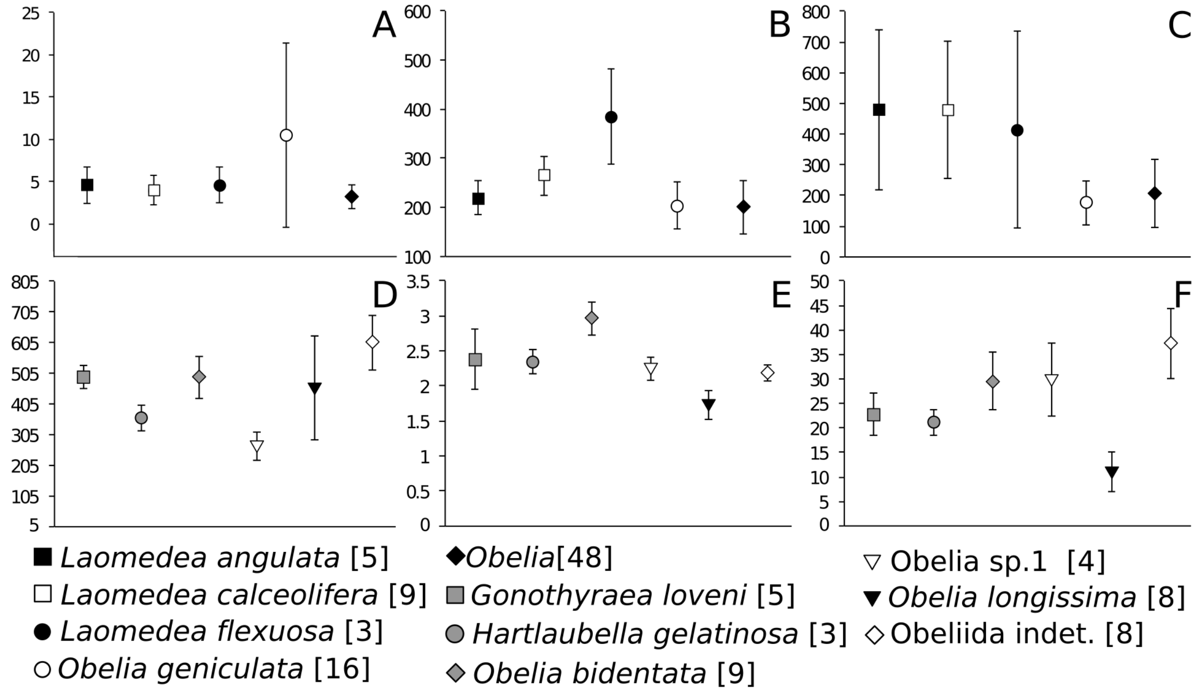

Figure 8. Mean ± standard deviation of morphometric data for Obeliidae. Data for the genus *Obelia* comprises all species included in this study, except *O. geniculata*. A. Maximum hydrothecal perisarc thickness at margin (PHMa, µm); B. Maximum hydrothecal diameter at margin (DHMa, µm); C. Length of pedicel (LP, µm); D. Length of the hydrotheca (LH, µm); E. Length:diameter ratio of the hydrotheca (HRatio); F. Maximum height of hydrothecal cusps (HCMax, µm). Brackets = [number of specimens/colonies measured].

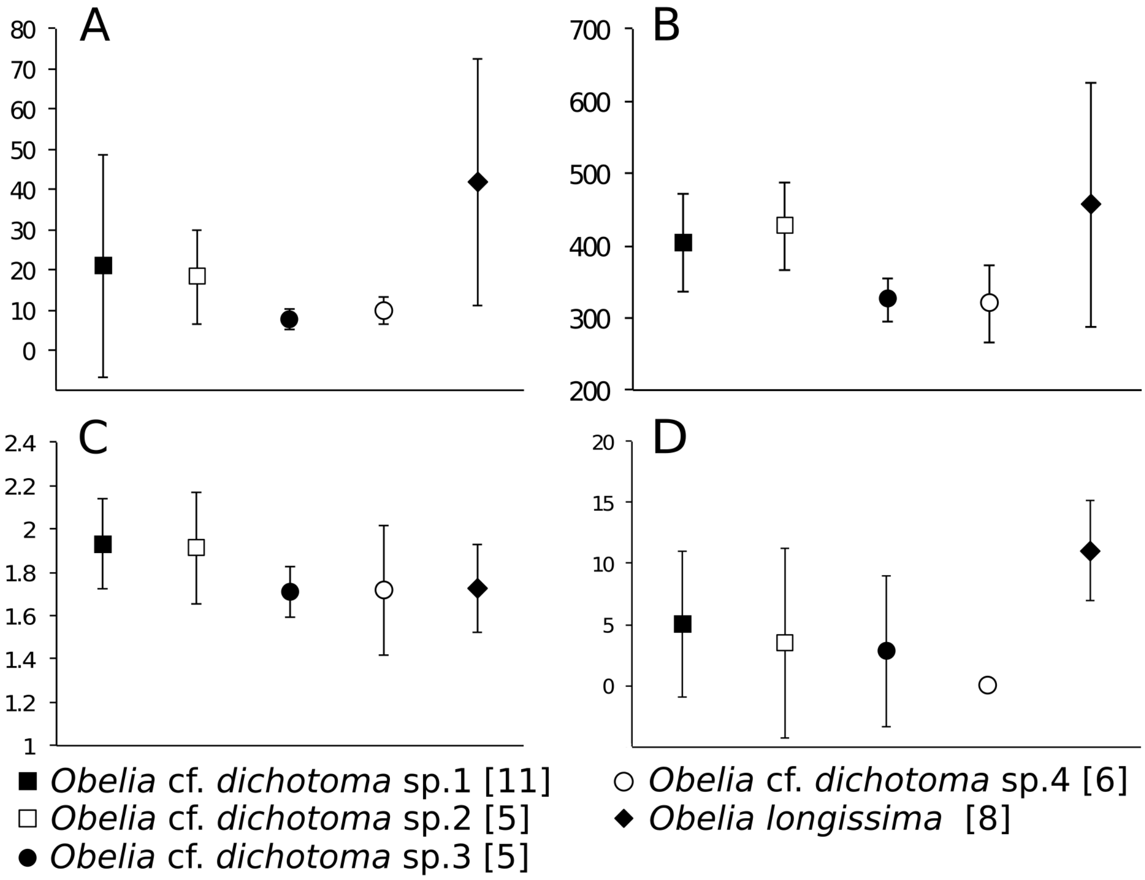

Figure 9. Mean ± standard deviation of morphometric data for the lineages identified as *Obelia* cf. *dichotoma.* A. Total length of the trophosome (TLT, mm); B. Length of the hydrotheca (LH, µm); C. Length:diameter ratio of the hydrotheca (HRatio); D. Maximum height of hydrothecal cusps (HCMax, µm). Brackets = [number of specimens/colonies measured].

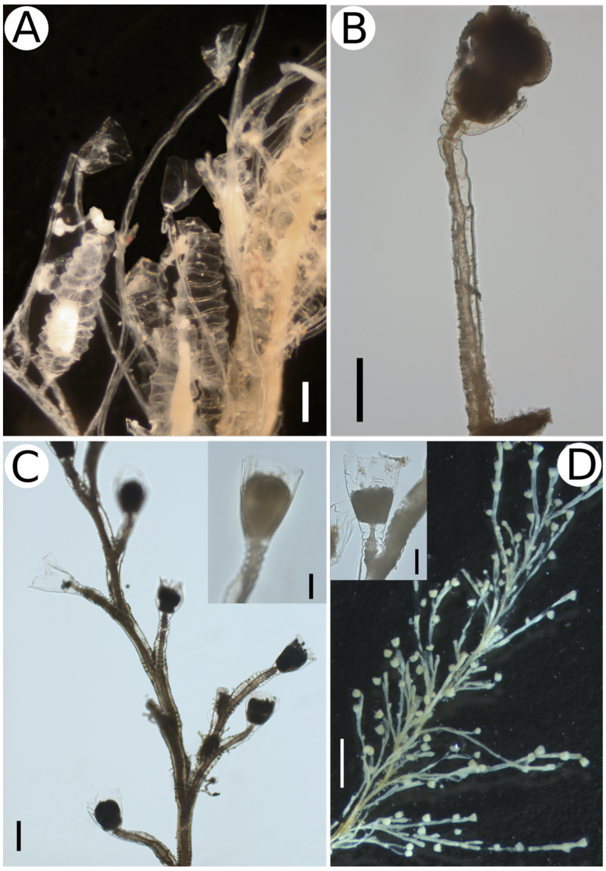

Figure 10. A. *Orthopyxis integra*_1_USA (USNM 1106184), with gonothecae; B. *Orthopyxis asymmetrica* (EL02_SLV); C. *Obelia* cf. *dichotoma* sp.3 (PAF07_BRA), with detail of hydrotheca; D. *Obelia* cf. *dichotoma* sp.4 (Site 1.1_USA), with detail of hydrotheca; Scales: A= 500 µm; B, C (colony) = 200 µm; C, D (hydrotheca) = 100 µm; D (colony) = 1 mm. For specimens and codes see Supporting Information, Table S1.

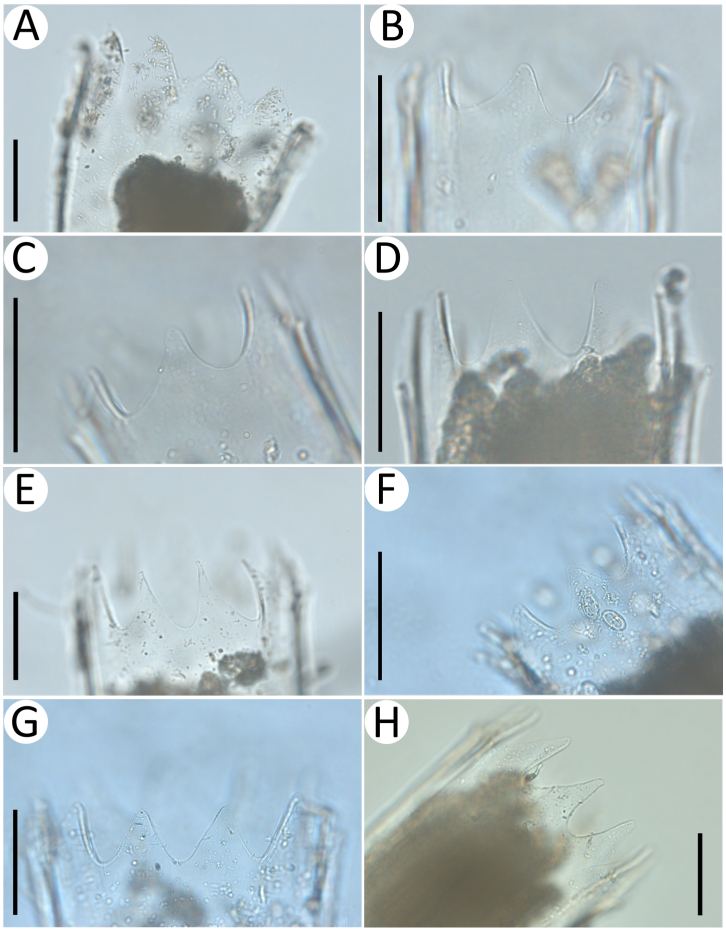

Figure 11. Variation in the shape of hydrothecal cusps of *Clytia* cf. *gracilis* sp.5. A, B. Specimens from Fortaleza, Brazil (CE2_BRA, CE5_BRA); C, D. Specimens from Cascavel, Brazil (CE1_BRA, CE3_BRA); E, F. Specimens from São Luís do Maranhão, Brazil (MAP01_BRA, MAP11_BRA); G. Specimen from Trairi, Brazil (T1_BRA); H. Specimen from Salinópolis, Brazil (PAF03_BRA). Scale: 100 µm.

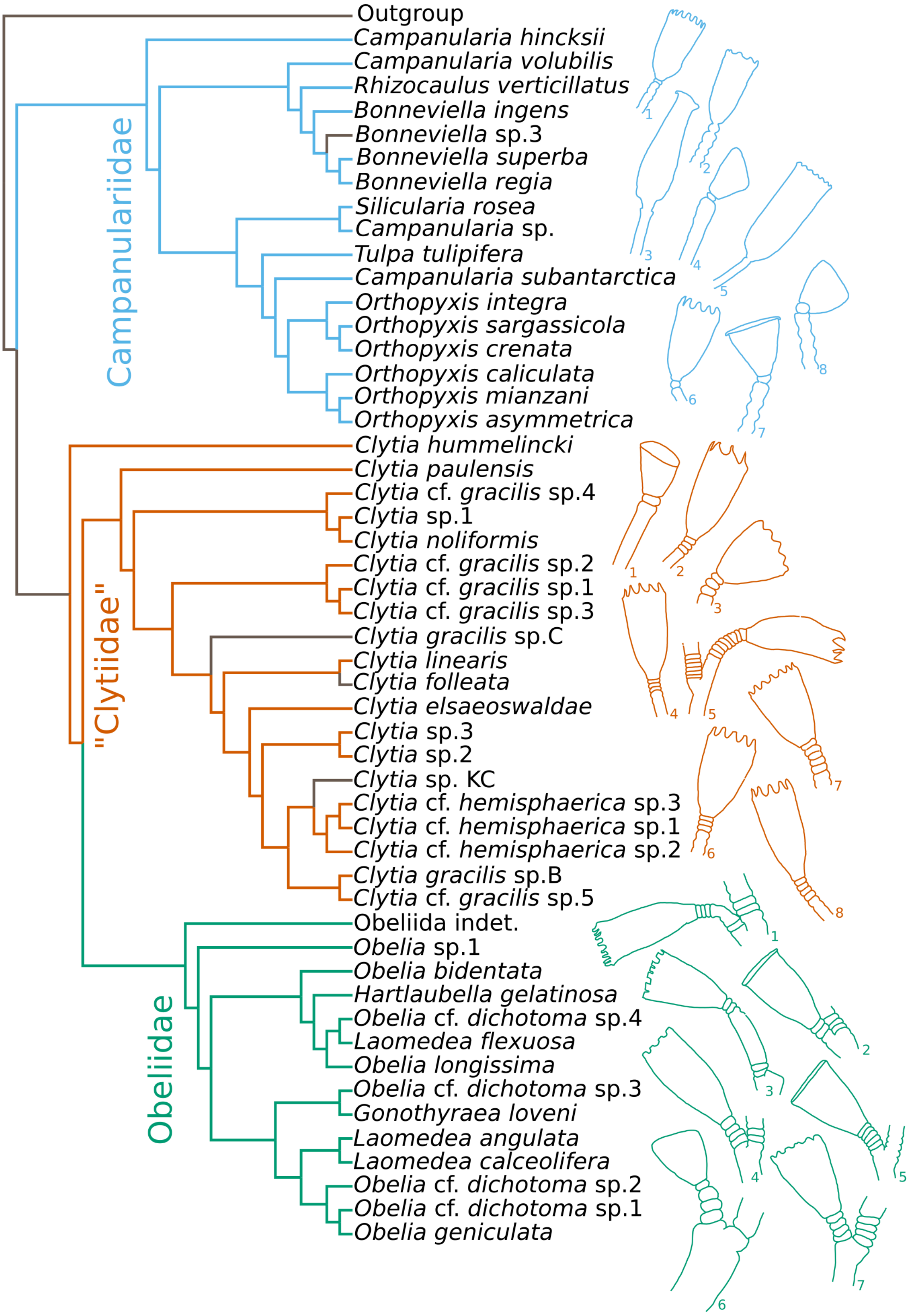

Figure 12. Phylogenetic hypothesis of Proboscoida based on the Maximum Likelihood phylogeny of Cunha *et al.* (2017, Fig. 2 therein), including the reidentifications proposed in this study. Branches in grey indicate lineages not analyzed in this study. Specimens codes (also

see Supporting Information, Table S1): Campanulariidae - 1. *Campanularia hincksii* (IT); 2. *C. volubilis* (USNM 29217); 3. *Bonneviella regia*; 4. *Silicularia rosea* (PT11); 5. *Tulpa tulipifera* (PT18); 6. *Orthopyxis sargassicola* (PTY1); 7. *O. caliculata* (PAB3); 8. *O. asymmetrica* (EL04); Clytiidae – 1. *Clytia hummelincki* (CBC42); 2. *C.* cf. *gracilis* sp.4 (CBC20); 3. *C. noliformis* (SP3); 4. *Clytia* sp.1 (IT13); 5. *C. linearis* (PY10); 6. *C.* cf. *hemisphaerica* sp.2 (EL06); 7. *C. elsaeoswaldae* (Me26); 8. *C.* cf. *gracilis* sp.5 (PAF03); Obeliidae – 1. *Obelia bidentata* (MAR02); 2. *O.* cf. *dichotoma* sp.4 (UR6); 3. *Hartlaubella gelatinosa* (PT16); 4. *Gonothyraea loveni* (SWM03); 5. *Laomedea calceolifera* (ROW03); 6. *Obelia geniculata* (UNH01); 7. *O.* cf. *dichotoma* sp.2 (MMA03). Outlines not to scale.

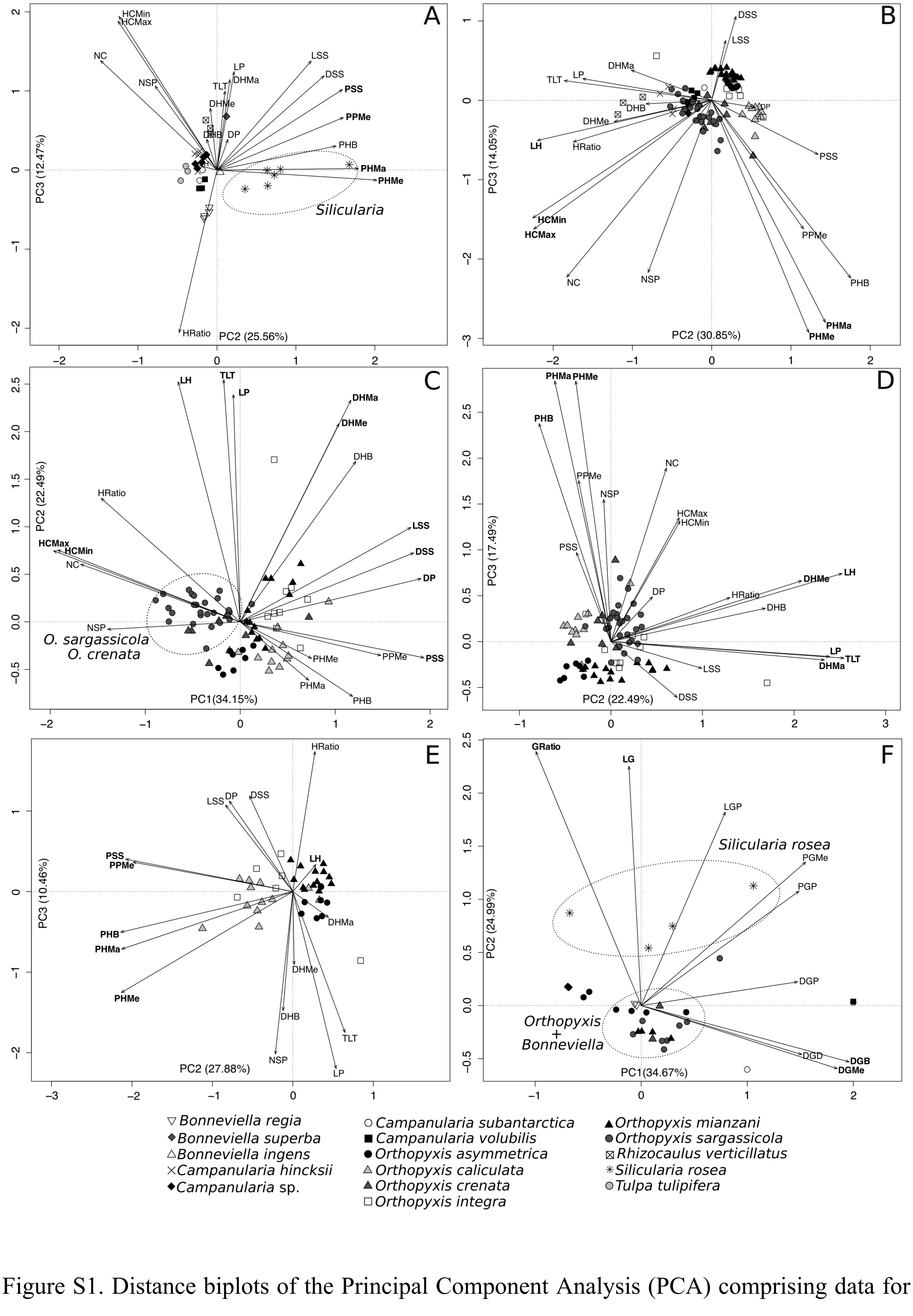

Figure S1. Distance biplots of the Principal Component Analysis (PCA) comprising data for Campanulariidae. A. Second and third principal components (PCs) of the PCA without the genus *Orthopyxis*; B. Second and third PCs of the PCA with *Campanularia* and *Orthopyxis*; C. First and second PCs of the PCA including only *Orthopyxis*; D. Second and third PCs of the PCA with *Orthopyxis*; E. Second and third PCs of the PCA with *Orthopyxis,* but excluding *O. sargassicola* and *O. crenata*; F. First and second PCs of the PCA with measurements of the gonothecae. Numbers in parentheses indicate percentages of variation explained by each principal component. Abbreviations of morphometric variables as in Table 1, and those in bold indicate measurements that were correlated with each principal component (Pearson correlation >0.7 and <-0.7).

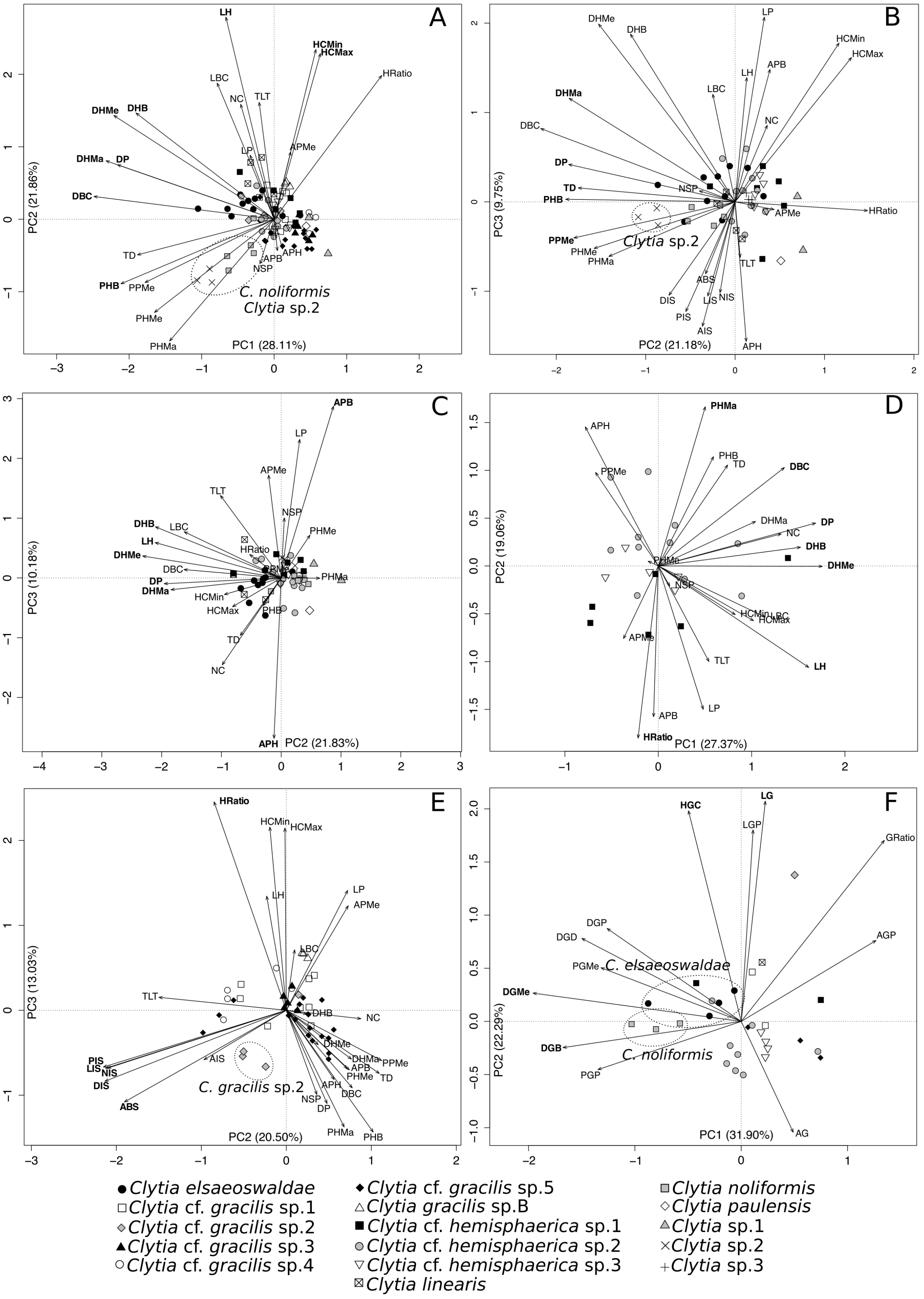

Figure S2. Distance biplots of the Principal Component Analysis (PCA) comprising data for Clytiinae. A. First and second principal components (PCs) of the PCA with the complete dataset, and without measurements related to internodes of erect colonies (NIS, LIS, AIS, PIS, DIS, ABS); B. Second and third PCs of the PCA without lineages of *Clytia* cf. *gracilis*; C. Second and third PCs of the PCA without *C.* cf. *gracilis* and measurements related to internodes of erect colonies; D. First and second PCs of the PCA with lineages of *C.* cf. *hemisphaerica*, but without measurements related to internodes of erect colonies; E. Second and third PCs of the PCA with lineages of *C.* cf. *gracilis*; F. First and second PCs of the PCA with measurements of the gonothecae. Numbers in parentheses indicate percentages of variation explained by each principal component. Abbreviations of morphometric variables as in Table 1, and those in bold indicate measurements that were correlated with each principal component (Pearson correlation >0.7 and <-0.7).

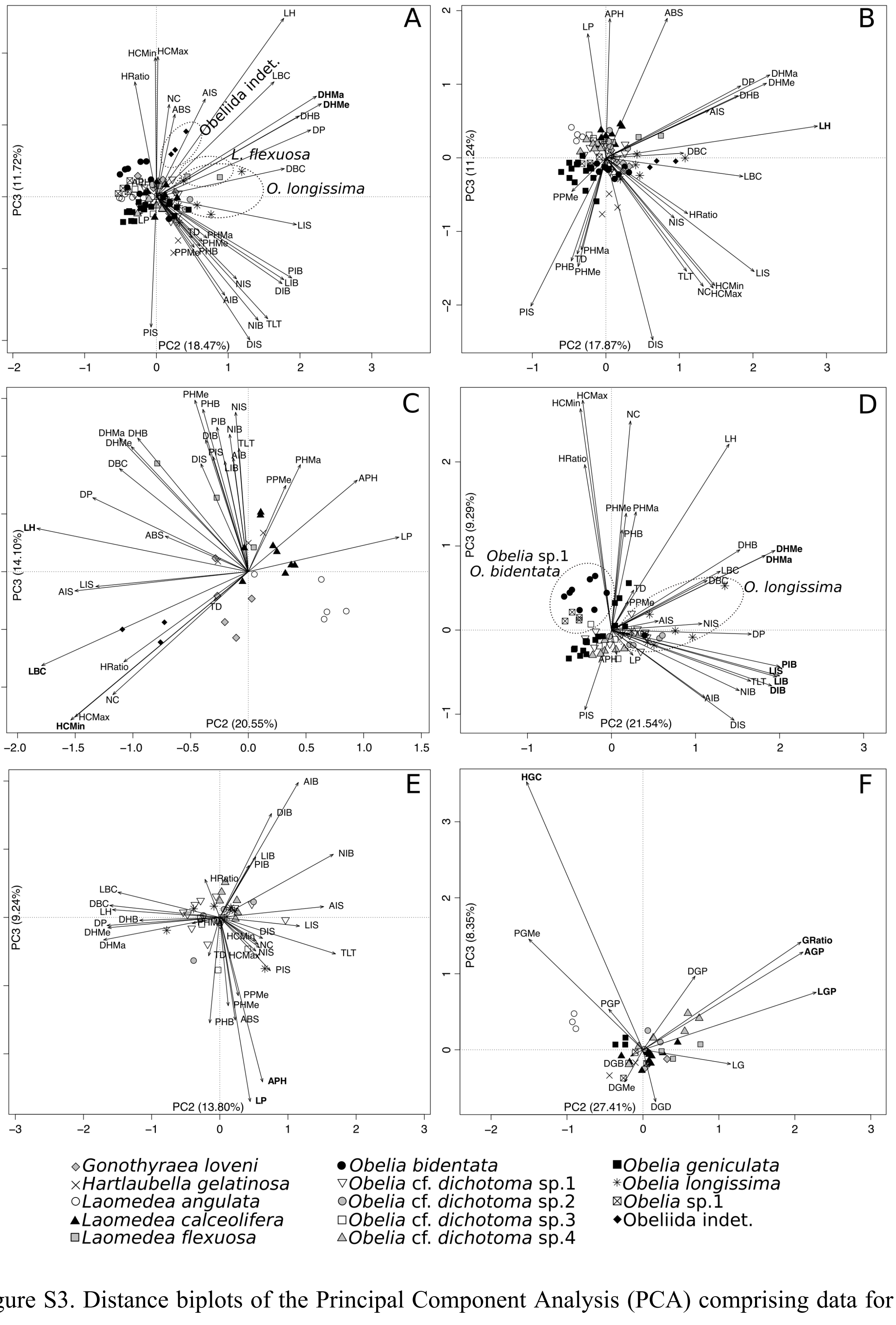

Figure S3. Distance biplots of the Principal Component Analysis (PCA) comprising data for Obeliidae. A. Second and third principal components (PCs) of the PCA with the complete dataset; B. Second and third PCs of the PCA with the complete dataset, but excluding measurements related to second-order branches of erect colonies (NIB, DIB, AIB, LIB, PIB); C. Second and third PCs of the PCA without species of the genus *Obelia*; D. Second and third PCs of the PCA with species of the genus *Obelia* only; E. Second and third PCs of the PCA with lineages of *O.* cf. *dichotoma* and *O. longissima*; F. Second and third PCs of the PCA with measurements of the gonothecae. Numbers in parentheses indicate percentages of variation explained by each principal component. Abbreviations of morphometric variables as in Table 1, and those in bold indicate measurements that were correlated with each principal component (Pearson correlation >0.7 and <-0.7).

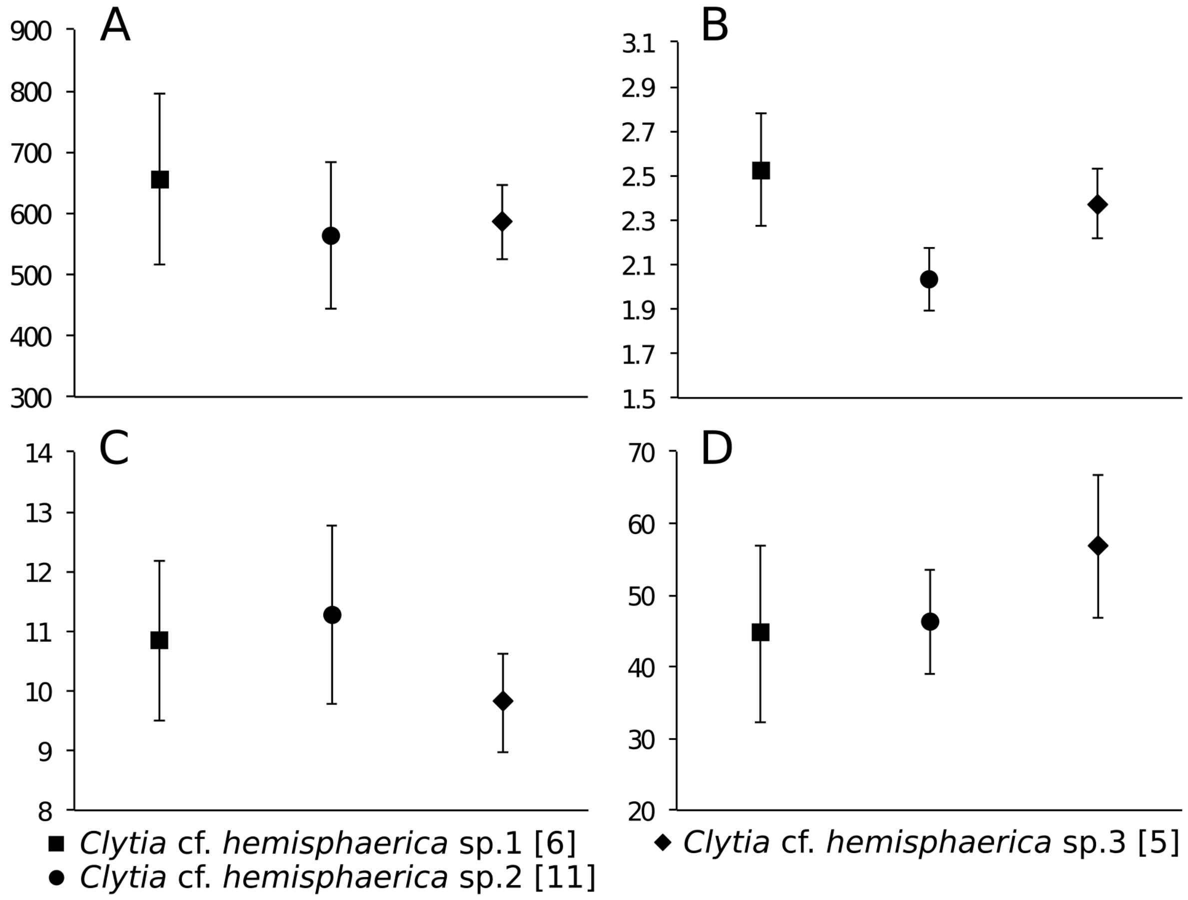

Figure S4. Mean ± standard deviation of morphometric data for species identified as *Clytia* cf. *hemisphaerica*. A. Length of the hydrotheca (LH, µm); B. Length:diameter ratio of hydrotheca (HRatio, µm); C. Number of hydrothecal cusps (NC); D. Maximum height of hydrothecal cusps (HCMax, µm). Brackets = [number of specimens/colonies measured].

Table 1. Measurements included in the morphometric analysis (codes are in alphabetical order).

Code	**Measurement**
AG	Number of Gonothecal Annuli
AGP	Number of Annuli of Gonothecal Pedicel
AIB	Maximum Number of Annuli of the Internodes of Side Branches
AIS	Maximum Number of Annuli of the Internodes of Main Stem
APB	Number of Pedicel Annuli at Base
APH	Number of Pedicel Annuli below Hydrotheca
APMe	Number of Pedicel Annuli at Medial Portion
DBC	Diameter of Hydrothecal Basal Chamber (at diaphragm)
DGB	Maximum Gonothecal Diameter at Base
DGD	Maximum Gonothecal Diameter at Distal Portion
DGMe	Maximum Gonothecal Diameter at Medial Portion
DGP	Maximum Diameter of Gonothecal Pedicel at Medial Portion
DHB	Maximum Hydrothecal Diameter at Base
DHMa	Maximum Hydrothecal Diameter at Margin
DHMe	Maximum Hydrothecal Diameter at Medial Portion
DIB	Maximum Diameter of Internode of Side Branches at Medial Portion
DIS	Maximum Diameter of Internode of Main Stem at Medial Portion
DP	Maximum Diameter of Pedicel at Medial Portion
DSS	Maximun Diameter of Subhydrothecal Spherule
GRatio	Length:Diameter (at medial portion) Ratio of Gonotheca
HCMax	Maximum Height of Hydrothecal Cusps
HCMin	Minimum Height of Hydrothecal Cusps
HGC	Height of Gonothecal Collar

Code	**Measurement**
HRatio	Length:Diameter (at medial portion) Ratio of Hydrotheca
LBC	Length of Hydrothecal Basal Chamber
LG	Length of Gonotheca
LGP	Length of Gonothecal Pedicel
LH	Length of Hydrotheca
LIB	Length of Internode of Side Branches
LIS	Length of Internode of Main Stem
LP	Length of Pedicel
LSS	Length of Subhydrothecal Spherule
NC	Number of Hydrothecal Cusps
NIB	Maximum Number of Internodes of Side Branches
NIS	Total Number of Internodes of Main Stem
NSG	Number of Gonothecal Sinuosities (crenations)
NSP	Maximum Number of Pedicel Sinuosities (crenations)
PGMe	Maximum Gonothecal Perisarc Thickness at Medial Portion
PGP	Maximum Perisarc Thickness of Gonothecal Pedicel at Medial Portion
PHB	Maximum Hydrothecal Perisarc Thickness at Base
PHMa	Maximum Hydrothecal Perisarc Thickness at Margin
PHMe	Maximum Hydrothecal Perisarc Thickness at Medial Portion
PIB	Maximum Perisarc Thickness of Internode of Side Branches at Medial Portion
PIS	Maximum Perisarc Thickness of Internode of Main Stem at Medial Portion
PPMe	Maximum Perisarc Thickness of Pedicel at Median Portion
PSS	Maximum Perisarc Thickness of Subhydrothecal Spherule
TD	Thickness of Diaphragm

Code	Measurement
TLT	Total Length of Trophosome

Table 2. Summary of species delimited in this study and their morphometric characters. This symbol * indicate groups that were monophyletic in most, but not all of the phylogenies in Cunha *et al.* (2017). The species *Orthopyxis integra* (MacGillivray, 1842) is not monophyletic in its traditional sense (see text). The genera *Rhizocaulus*, *Tulpa*, *Gonothyraea* and *Hartlaubella* were represented by only one species, therefore their monophyletism needs confirmation (Cunha *et al.*, 2017). When referring to family or genus, comparative conclusions on distinctive morphometric characters are limited to the species analyzed in this study.

Taxon	**Specimen(s) (see Table S1)**	**Monophyletic? (Cunha *et al.*, 2017)**	**Morphometric diagnostic characters**	**Morphometric characters are distinctive when compared to**
Infraorder Campanulariida Bouillon, 1984		yes		
Family Campanulariidae Johnston, 1836		yes		
Genus *Bonneviella* Broch, 1909		yes*	Total length of the trophosome, length of the pedicel and hydrotheca	Campanulariidae
Bonneviella ingens Nutting, 1915	*Bonneviella* sp.4 (USNM 1106187)	yes	Size and shape of hydrotheca	Campanulariidae

Taxon	**Specimen(s) (see Table S1)**	**Monophyletic? (Cunha *et al.*, 2017)**	**Morphometric diagnostic characters**	**Morphometric characters are distinctive when compared to**
Bonneviella regia (Nutting, 1901)	USNM 1106181	yes	Size of hydrotheca	Campanulariidae
Bonneviella superba Nutting, 1915	*Bonneviella* sp.2 (USNM 1106182)	yes	Size of hydrotheca (the largest in *Bonneviella*)	Campanulariidae
Genus *Campanularia* Lamarck, 1816		**no**	Perisarc thickness, length and length:diameter ratio of hydrotheca	*Orthopyxis*, except for some specimens of *O. sargassicola* and *O. crenata*
Campanularia hincksii Alder, 1856	MZUSP 2759-60; USNM 1106157	yes	Height of hydrothecal cusps	other species of *Campanularia*
Campanularia subantarctica	MZUSP 2639, 2643	yes	Distinctive morphometric characters not found	-
Campanularia sp.	MZUSP 2641-42, 2761	yes	Distinctive morphometric characters not found	-
Campanularia volubilis	USNM 1106166	yes	Distinctive morphometric characters not	-

Taxon	**Specimen(s) (see Table S1)**	**Monophyletic? (Cunha *et al.*, 2017)**	**Morphometric diagnostic characters found**	**Morphometric characters are distinctive when compared to**
Genus *Orthopyxis* L. Agassiz, 1862		yes*	Perisarc thickness, length and length:diameter ratio of hydrotheca	*Campanularia*
Orthopyxis asymmetrica Stechow, 1919	*Orthopyxis* sp.1, *Orthopyxis everta*, *Orthopyxis integra*_IT (MZUSP 3360-63; USNM 1106159-80)	yes	Length of hydrotheca and pedicel, perisarc thickness, length:diameter ratio of hydrothecal basal chamber	other species of *Orthopyxis*
Orthopyxis caliculata (Hincks, 1853)	MZUSP 2612-15, 2550, 2552, 2554, 2556, 2563, 2565, 4177, 4265	yes	Length of hydrotheca and pedicel, perisarc thickness	other species of *Orthopyxis*
Orthopyxis crenata (Hartlaub,	MZUSP 2551, 2560,	yes	Number and height of hydrothecal cusps	other species of *Orthopyxis*,

Taxon	Specimen(s) (see Table S1)	Monophyletic? (Cunha *et al.*, 2017)	Morphometric diagnostic characters	Morphometric characters are distinctive when compared to
1901)	2598, 2601, 2633, 3359, *Orthopyxis* sp. (MZUSP 2644); *Orthopyxis integra*_NZ (USNM 1106163)		(but may eventually present even hydrothecal rim)	except for *O. sargassicola*
Orthopyxis integra (MacGillivray, 1842)	MZUSP 3358, USNM 1106184, Campanulariidae sp. indet. (MZUSP 2638, 2640)	yes	Length of hydrotheca and pedicel, perisarc thickness, length:diameter ratio of hydrotheca	other species of *Orthopyxis*
Orthopyxis mianzani Cunha, Genzano & Marques, 2015	MZUSP 2559, 2570-80; USNM 1259970	yes	Length of hydrotheca and pedicel, perisarc thickness	other species of *Orthopyxis*
Orthopyxis sargassicola	MZUSP 2593-97,	yes	Number and height of hydrothecal cusps	other species of *Orthopyxis,*

Taxon	**Specimen(s) (see Table S1)**	**Monophyletic? (Cunha *et al.*, 2017)**	**Morphometric diagnostic characters**	**Morphometric characters are distinctive when compared to**
(Nutting, 1915)	2599-2600, 2602-03, 2605-11, 2617-20, 2627-2630, 2632, 4597			except for *O. crenata*
Genus *Rhizocaulus* Stechow, 1919		yes*		
Rhizocaulus verticillatus (Linnaeus, 1758)	USNM 1106183	yes	Total length of trophosome, length of hydrotheca	*Campanularia* and *Orthopyxis*
Genus *Silicularia* Meyen, 1834		yes		
Silicularia rosea Meyen, 1834	MZUSP 3365, 3364; USNM 1106164	yes	Perisarc thickness	Campanulariidae, except for *Orthopyxis*
Genus *Tulpa* Stechow, 1921		yes*		
Tulpa tulipifera (Allman,	MZUSP 3366	yes	Size of hydrotheca	Campanulariidae

Taxon	**Specimen(s) (see Table S1)**	**Monophyletic? (Cunha *et al.*, 2017)**	**Morphometric diagnostic characters**	**Morphometric characters are distinctive when compared to**
1888)				
Infraorder Obeliida Maronna *et al.*, 2016		yes		
Obeliida indet.	USNM 1420685, 1420678	yes	Height of hydrothecal cusps, length of hydrothecae	Obeliidae, except for *O. longissima* (length of hydrothecae)
Family Clytiidae Cockerell, 1911		**no**		
Genus *Clytia* Lamouroux, 1812		**no**		
Clytia elsaeoswaldae Stechow, 1914	MZUSP2762-65; USNM 1078725, 1078728	yes	Diameter of hydrotheca, thickness of diaphragm	*Clytia* cf. *gracilis* and *Clytia* cf. *hemisphaerica* (diameter); Clytiidae (diaphragm)
Clytia cf. *gracilis* sp.1	MZUSP 2768-70, 2772, 2773	yes	Length and diameter of hydrotheca and pedicel, number and height of	*Clytia* cf. *gracilis* sp.3 and sp.4

Taxon	Specimen(s) (see Table S1)	Monophyletic? (Cunha *et al.*, 2017)	Morphometric diagnostic characters	Morphometric characters are distinctive when compared to
			hydrothecal cusps	
Clytia cf. *gracilis* sp.2	MZUSP 2785; *Clytia gracilis* sp.D (USNM 1106152)	yes	Length and diameter of hydrotheca and pedicel, number and height of hydrothecal cusps	*Clytia* cf. *gracilis* sp.3 and sp.4
Clytia cf. *gracilis* sp.3	MZUSP 2766, 2767, 2771[1]	yes	Length and diameter of hydrotheca and pedicel, number and height of hydrothecal cusps	*Clytia* cf. *gracilis* sp.1, sp.2 and sp.B
Clytia cf. *gracilis* sp.4	USNM 1420648, 1420655, 1420660	yes	Length and diameter of hydrotheca and pedicel, number and height of hydrothecal cusps, length:diameter ratio of hydrotheca	*Clytia* cf. *gracilis* sp.1, sp.2 and sp.B (length, diameter, number and height of cusps); Clytiidae, except for remaining *C.* cf. *gracilis* and *C.* cf. *hemisphaerica* (ratio)
Clytia cf. *gracilis* sp.5	MZUSP 2774-84[2]	yes	Distinctive morphometric characters not	-

Taxon	**Specimen(s) (see Table S1)**	**Monophyletic? (Cunha *et al.*, 2017)**	**Morphometric diagnostic characters**	**Morphometric characters are distinctive when compared to**
			found	
Clytia cf. *gracilis* sp.B	USNM 1078730	yes	Length and diameter of hydrotheca and pedicel, number and height of hydrothecal cusps	*Clytia* cf. *gracilis* sp.3 and sp.4
Clytia cf. *hemisphaerica* sp.1	MZUSP 2786-89[3]	yes	Distinctive morphometric characters not found	-
Clytia cf. *hemisphaerica* sp.2	MZUSP 2790-95; USNM 1106186	yes	Distinctive morphometric characters not found	-
Clytia cf. *hemisphaerica* sp.3	USNM 1420636, 1420659, 1420673	yes	Distinctive morphometric characters not found	-
Clytia linearis	MZUSP 2796; USNM 1078729	yes	Length of hydrotheca	Clytiidae
Clytia noliformis	MZUSP 2797-98; USNM 1078720	yes	Perisarc thickness	Clytiidae, except for *Clytia* sp.2

Taxon	Specimen(s) (see Table S1)	Monophyletic? (Cunha *et al.*, 2017)	Morphometric diagnostic characters	Morphometric characters are distinctive when compared to
Clytia paulensis	USNM 1106158	yes	Length:diameter ratio of hydrotheca	Clytiidae, except for *C.* cf. *gracilis*
Clytia sp.1	MZUSP 2799	yes	Length:diameter ratio of hydrotheca	Clytiidae, except for *C.* cf. *gracilis* and *C.* cf. *hemisphaerica*
Clytia sp.2	MZUSP 2800	yes	Perisarc thickness	Clytiidae, except for *C. noliformis*
Clytia sp.3	MZUSP 2801	yes	Length of pedicel, number of pedicel annuli at base	Clytiidae, except for *C.* cf. *gracilis* and *C.* cf. *hemisphaerica*
Family Obeliidae Haeckel, 1879		yes		
Genus *Gonothyraea* Allman, 1864		yes*		
Gonothyraea loveni (Allman, 1859)	MZUSP 2802-03; USNM 1106154	yes	Branching of erect colonies, length:diameter ratio of hydrotheca, height of hydrothecal cusps	Obeliidae, except for *Obelia* (branching); *O. bidentata* (ratio and cusps)
Genus *Hartlaubella* Poche,		yes*		

Taxon	**Specimen(s) (see Table S1)**	**Monophyletic? (Cunha *et al.*, 2017)**	**Morphometric diagnostic characters**	**Morphometric characters are distinctive when compared to**
1914				
Hartlaubella gelatinosa (Pallas, 1766)	MZUSP 2804-06	yes	Branching of erect colonies, length:diameter ratio of hydrotheca, height of hydrothecal cusps	Obeliidae, except for *Obelia* (branching); *O. bidentata* (ratio and cusps)
Genus *Laomedea* Lamouroux, 1812		**no**	Length of pedicel and gonotheca	*Obelia* (pedicel); Obeliidae (gonotheca)
Laomedea angulata Hincks, 1861	MZUSP 2807-08	yes	Distinctive morphometric characters not found	-
Laomedea calceolifera (Hincks, 1861)	MZUSP 2810, 2812-15; MHNG INVE 37296; USNM 1106177	yes	Distinctive morphometric characters not found	-
Laomedea flexuosa Alder, 1857	MZUSP 2816; USNM 1106190,	yes	Diameter of hydrotheca and pedicel	Obeliidae

Taxon	**Specimen(s) (see Table S1)**	**Monophyletic? (Cunha *et al.*, 2017)**	**Morphometric diagnostic characters**	**Morphometric characters are distinctive when compared to**
	1106192			
Genus *Obelia* Péron & Lesueur, 1810		**no**		
Obelia bidentata Clark, 1875	MZUSP 2817-2818; USNM 1106162, 1106185, 1420668	yes	Length:diameter ratio of hydrotheca, number and height of hydrothecal cusps	Obeliidae (ratio); *G. loveni* and *H. gelatinosa* (cusps)
Obelia cf. *dichotoma* sp.1	MZUSP 3336-40, 3344-45	yes	Distinctive morphometric characters not found	-
Obelia cf. *dichotoma* sp.2	MZUSP 3335, 3342-43; USNM 1106156	yes	Distinctive morphometric characters not found	-
Obelia cf. *dichotoma* sp.3	MZUSP 2819-20, 3334	yes	Branching of erect colonies, total length of trophosome	*Obelia* cf. *dichotoma* sp.1 and sp.2
Obelia cf. *dichotoma* sp.4	MZUSP 3341, 3346	yes	Branching of erect colonies, total length of trophosome	*Obelia* cf. *dichotoma* sp.1 and sp.2

Taxon	**Specimen(s) (see Table S1)**	**Monophyletic? (Cunha *et al.*, 2017)**	**Morphometric diagnostic characters**	**Morphometric characters are distinctive when compared to**
Obelia geniculata (Linnaeus, 1758)	MZUSP 3347-51; USNM 1106165, 1106176, 1106179	yes	Perisarc thickness	Obeliidae
Obelia longissima (Pallas, 1766)	MZUSP 3352-55; USNM 1106153, 1106173, 1106189, 1106191	yes	Branching of erect colonies, total length of trophosome, length of internodes and hydrotheca, height (shape) of hydrothecal cusps	Obeliidae, except some specimens of *Obelia* cf. *dichotoma* (branching, total length); some specimens of *O.* cf. *dichotoma* (all remaining characters)
Obelia sp.1	MZUSP 3356-57	yes	Length:diameter ratio of hydrotheca, length of hydrotheca, height of hydrothecal cusps	*O. bidentata* (ratio and length); Obeliidae, except for *O. bidentata* and Obeliida indet. (cusps)

[1] Specimens identified as *Clytia sp.* from He *et al.* (2015) clustered with specimens of *Clytia* cf. *gracilis* sp.3 in the phylogeny of Cunha *et al.* (2017), and should be referred to that species. However, since we were not able to study the morphology of these specimens, they were not considered in the proposed reidentifications.

[2] Specimens identified as *Clytia gulangensis* from He *et al.* (2015) clustered with specimens of *Clytia* cf. *gracilis* sp.5 in the phylogeny of Cunha *et al.* (2017) (see discussion). Since we were not able to study the morphology of these specimens, they were not considered in the proposed reidentifications.

[3] Specimens identified as *Clytia gracilis* sp.A from Lindner *et al.* (2011) clustered with specimens of *Clytia* cf. *hemisphaerica* sp.1 in the phylogeny of Cunha *et al.* (2017), and should be referred to that species. Specimens identified as *Clytia xiamenensis* from Zhou *et al.* (2013) also clustered with *Clytia* cf. *hemisphaerica* sp.1, but these results are only based on 16S sequences (see Cunha *et al.*, 2017), and should be confirmed. Since we were not able to study the morphology of these specimens, they were not considered in the proposed reidentifications.

Table S1. Materials analyzed in this study. The symbol * indicates materials that were reidentified in this study (see Table 2). Specimens in bold indicate samples from which intracolony measurements were taken. Vouchers and specimen codes are in accordance with Cunha *et al.* (2017), unless not included in that study. USNM = National Museum of Natural History, Smithsonian Institution, USA; MZUSP = Museu de Zoologia da Universidade de São Paulo, Brazil; ZMUC = Zoological Museum, Natural History Museum of Denmark; MHNG INVE = Muséum d'Histoire Naturelle de Genève, Switzerland; BMNH = Natural History Museum, United Kingdom.

Species	**Locality**	**Voucher**	**Codes**	**References**
Bonneviella ingens	Simushir Island, Japan	USNM 34576 (type)	not included	Museum specimen
Bonneviella regia	Aleutians, USA	USNM 1106181	USA	Govindarajan *et al.*, 2006
Bonneviella regia	Prince William Sound, Alaska, USA	USNM 71390 (type)	not included	Museum specimen
Bonneviella superba	Bering Sea	USNM 3480	not included	Museum specimen
Bonneviella superba	Aleutians, USA	USNM 1106182	*Bonneviella* sp.2_USA*	Govindarajan *et al.*, 2006
Bonneviella ingens	Aleutians, USA	USNM 1106187	*Bonneviella* sp.4_USA*	Govindarajan *et al.*, 2006
Campanularia hincksii	Italy	MZUSP 2759, 2760	**IT10**, IT14_IT	Cunha *et al.*, 2017
Campanularia hincksii	Otranto, Italy	USNM 1106157	IT	Govindarajan *et al.*, 2006
Campanularia sp.	Punta Cuevas, San Juliàn, Argentina	MZUSP 2761	**PT10_ARG**	Cunha *et al.*, 2017
Campanularia sp.	La Mina, Puerto San Julián, Argentina	MZUSP 2641, 2642	SJ4, SJ5_ARG	Cunha *et al.*, 2015
Campanularia subantarctica	La Mina, Puerto San Julián, Argentina	MZUSP 2639, 2643	SJ2, SJ6_ARG	Cunha *et al.*, 2015
Campanularia volubilis	Monterey, USA	USNM 1106166	**USA**	Govindarajan *et al.*, 2006
Campanularia volubilis	Casco Bay, USA	USNM 29217	not included	Museum specimen
Campanularia volubilis	Greenland	ZMUC	not included	Museum specimen
Clytia elsaeoswaldae	Palmas Island, Brazil	MZUSP 2764, 2762	PM18, PM36_BRA	Cunha *et al.*, 2017
Clytia elsaeoswaldae	Mel Island, Brazil	MZUSP 2765	**Me26_BRA**	Cunha *et al.*, 2017
Clytia elsaeoswaldae	Cabras Island, Ilhabela, Brazil	MZUSP 2763	**CB19_BRA**	Cunha *et al.*, 2017
Clytia elsaeoswaldae	São Sebastião, Brazil	USNM 1078725, 1078728	1, 2_BRA	Govindarajan *et al.*, 2006; Lindner *et al.*, 2011

Species	Locality	Voucher	Codes	References
Clytia cf. *gracilis* sp.1	Strunjan, Piran, Slovenia	MZUSP 2768	EL15_SLV	Cunha *et al.*, 2017
Clytia cf. *gracilis* sp.1	Slovenia	MZUSP 2769, 2770	EL31, **EL32**_SLV	Cunha *et al.*, 2017
Clytia cf. *gracilis* sp.1	Italy	MZUSP 2772, 2773	IT12, **IT13**_IT	Cunha *et al.*, 2017
Clytia cf. *gracilis* sp.2	Punta Cuevas, San Julià n, Argentina	MZUSP 2785	**PT9_ARG**	Cunha *et al.*, 2017
Clytia cf. *gracilis* sp.2	Georges Bank, USA	USNM 1106152	sp.D_USA	Govindarajan *et al.*, 2006
Clytia cf. *gracilis* sp.3	Mund Bay, Piran, Slovenia	MZUSP 2766	**EL05_SLV**	Cunha *et al.*, 2017
Clytia cf. *gracilis* sp.3	Strunjan, Piran, Slovenia	MZUSP 2767	EL14_SLV	Cunha *et al.*, 2017
Clytia cf. *gracilis* sp.3	Piran, Slovenia	MZUSP 2771	EL38_SLV	Cunha *et al.*, 2017
Clytia cf. *gracilis* sp.4	Twin Cays, Belize	USNM 1420648	CBC13_BLZ	Cunha *et al.*, 2017
Clytia cf. *gracilis* sp.4	Carry Bow Cay, Belize	USNM 1420655	CBC20_BLZ	Cunha *et al.*, 2017
Clytia cf. *gracilis* sp.4	Twin Cay Fisheries Dock, Belize	USNM 1420660	**CBC26**_BLZ	Cunha *et al.*, 2017
Clytia cf. *gracilis* sp.5	Mel Island, Brazil	MZUSP 2784	Me24_BRA	Cunha *et al.*, 2017
Clytia cf. *gracilis* sp.5	Farol Velho, Salinópolis, Brazil	MZUSP 2776	PAF03_BRA	Cunha *et al.*, 2017
Clytia cf. *gracilis* sp.5	Panaquatira, São Luís do Maranhão, Brazil	MZUSP 2774, 2775	**MAP01**, MAP11_BRA	Cunha *et al.*, 2017
Clytia cf. *gracilis* sp.5	Flexeiras, Trairí, Brazil	MZUSP 2777, 2778, 2779	T1, T5, T6_BRA	Cunha *et al.*, 2017
Clytia cf. *gracilis* sp.5	Náutico, Fortaleza, Brazil	MZUSP 2780, 2782	CE1, **CE3**_BRA	Cunha *et al.*, 2017
Clytia cf. *gracilis* sp.5	Caponga, Cascavel, Brazil	MZUSP 2781, 2783	**CE2**, CE5_BRA	Cunha *et al.*, 2017
Clytia cf. *gracilis* sp.B	Beaufort, USA	USNM 1078730	**USA**	Govindarajan *et al.*, 2006; Lindner *et al.*, 2011
Clytia cf. *hemisphaerica* sp.1	Westport, USA	MZUSP 2786	**FLT03_USA**	Cunha *et al.*, 2017
Clytia cf. *hemisphaerica* sp.1	Salem, USA	MZUSP 2787	HCM04_USA	Cunha *et al.*, 2017
Clytia cf. *hemisphaerica* sp.1	Bourne, USA	MZUSP 2788	MMA05_USA	Cunha *et al.*, 2017
Clytia cf. *hemisphaerica* sp.1	Point Judith, Rhode Island, USA	MZUSP 2789	PTJ01_USA	Cunha *et al.*, 2017
Clytia cf. *hemisphaerica* sp.2	Mund Bay, Piran, Slovenia	MZUSP 2790, 2791	**EL06**, EL08_SLV	Cunha *et al.*, 2017
Clytia cf. *hemisphaerica* sp.2	Strunjan, Piran, Slovenia	MZUSP 2792, 2793	EL12, EL20_SLV	Cunha *et al.*, 2017
Clytia cf. *hemisphaerica* sp.2	Slovenia	MZUSP 2795	EL35_SLV	Cunha *et al.*, 2017

Species	**Locality**	**Voucher**	**Codes**	**References**
Clytia cf. *hemisphaerica* sp.2	Croacia	MZUSP 2794	EL28_CRO	Cunha *et al.*, 2017
Clytia cf. *hemisphaerica* sp.2	North Sea	USNM 1106186	*Clytia hemisphaerica*_NS*	Govindarajan *et al.*, 2006
Clytia cf. *hemisphaerica* sp.3	Carry Bow Cay, Belize	USNM 1420636	**CBC1_BLZ**	Cunha *et al.*, 2017
Clytia cf. *hemisphaerica* sp.3	Twin Cay Fisheries Dock, Belize	USNM 1420659	CBC25_BLZ	Cunha *et al.*, 2017
Clytia cf. *hemisphaerica* sp.3	Cuda Cut, Twin Cays, Belize	USNM 1420673	CBCB40.1_BLZ	Cunha *et al.*, 2017
Clytia hummelincki	Cuda Cut, Twin Cays, Belize	USNM 1420675	**CBC42_BLZ**	Cunha *et al.*, 2017
Clytia linearis	Paraty Brazil	MZUSP 2796	**PY10_BRA**	Cunha *et al.*, 2017
Clytia linearis	Beaufort, USA	USNM 1078729	USA	Govindarajan *et al.*, 2006; Lindner *et al.*, 2011
Clytia noliformis	Barão Tefé Island, São Pedro and São Paulo Archipelago, Brazil	MZUSP 2797, 2798	SP3, **SP9**_BRA	Cunha *et al.*, 2017
Clytia noliformis	São Sebastião, Brazil	USNM 1078720	1_BRA	Govindarajan *et al.*, 2006; Lindner *et al.*, 2011
Clytia paulensis	Otranto, Italy	USNM 1106158	IT	Govindarajan *et al.*, 2006
Clytia sp.1	Boca da Enseada, São Pedro and São Paulo Archipelago, Brazil	MZUSP 2799	**SP1_BRA**	Cunha *et al.*, 2017
Clytia sp.2	Caponga, Cascavel, Brazil	MZUSP 2800	**CE4_BRA**	Cunha *et al.*, 2017
Clytia sp.3	Natal, Brazil	MZUSP 2801	**NAT05_BRA**	Cunha *et al.*, 2017
Obeliida indet.	Cuda Cut, Twin Cays, Belize	USNM 1420685, 1420678	**CBC40.2**, CBC45_BLZ	Cunha *et al.*, 2017
Gonothyraea loveni	Dennis, USA	USNM 1106154	USA	Govindarajan *et al.*, 2006
Gonothyraea loveni	Plymouth, USA	MZUSP 2802	BPM03_USA	Govindarajan *et al.*, 2006
Gonothyraea loveni	Sandwich, USA	MZUSP 2803	**SWM03_USA**	Govindarajan *et al.*, 2006
Hartlaubella gelatinosa	Río Gallegos, Argentina	MZUSP 2804, 2805, 2806	PT13, PT14, PT16_ARG	Cunha *et al.*, 2017
Laomedea angulata	Piran, Slovenia	MZUSP 2807, 2808	**EL40**, EL50_SLV	Cunha *et al.*, 2017
Laomedea calceolifera	Bourne, USA	MZUSP 2814	MMA06_USA	Cunha *et al.*, 2017

Species	**Locality**	**Voucher**	**Codes**	**References**
Laomedea calceolifera	Boston, USA	MZUSP 2815	**ROW03_USA**	Cunha *et al.*, 2017
Laomedea calceolifera	Gloucester, USA	MZUSP 2812	GFP01_USA	Cunha *et al.*, 2017
Laomedea calceolifera	Hampton, USA	MZUSP 2813	HRM06_USA	Cunha *et al.*, 2017
Laomedea calceolifera	Newport, USA	MZUSP 2810	FTA01_USA	Cunha *et al.*, 2017
Laomedea calceolifera	Herquemoulin, Normandie, France	MHNG INVE 37296	FR	Leclère *et al.*, 2009
Laomedea calceolifera	Woods Hole, USA	USNM 1106177	USA	Govindarajan *et al.*, 2006
Laomedea flexuosa	Rye, USA	MZUSP 2816	RYE02_USA	Cunha *et al.*, 2017
Laomedea flexuosa	Sandgerdi, Iceland	USNM 1106190	IC	Govindarajan *et al.*, 2006
Laomedea flexuosa	White Sea, Russia	USNM 1106192	WS	Govindarajan *et al.*, 2006
Obelia bidentata	Cuda Cut, Twin Cays, Belize	USNM 1420668	**CBC35_BLZ**	Cunha *et al.*, 2017
Obelia bidentata	Raposa Channel, São Luís do Maranhão, Brazil	MZUSP 2817	MAR02_BRA	Cunha *et al.*, 2017
Obelia bidentata	Panaquatira, São Luís do Maranhão, Brazil	MZUSP 2818	MAP10_BRA	Cunha *et al.*, 2017
Obelia bidentata	North Sea, Denmark	USNM 1106185	NS	Govindarajan *et al.*, 2006
Obelia bidentata	Beaufort, USA	USNM 1106162	USA	Govindarajan *et al.*, 2006
Obelia cf. *dichotoma* sp.1	Westport, USA	MZUSP 3336	FLT04_USA	Cunha *et al.*, 2017
Obelia cf. *dichotoma* sp.1	New Bedfort, USA	MZUSP 3337, 3338	PIM01, **PIM02**_USA	Cunha *et al.*, 2017
Obelia cf. *dichotoma* sp.1	Boston, USA	MZUSP 3340	ROW04_USA	Cunha *et al.*, 2017
Obelia cf. *dichotoma* sp.1	Punta Cuevas, San Juliàn, Argentina	MZUSP 3344	PT3_USA	Cunha *et al.*, 2017
Obelia cf. *dichotoma* sp.1	Point Judith, Rhode Island, USA	MZUSP 3339	PTJ03_USA	Cunha *et al.*, 2017
Obelia cf. *dichotoma* sp.1	Rocha, Uruguay	MZUSP 3345	**UR1_URG**	Cunha *et al.*, 2017
Obelia cf. *dichotoma* sp.2	Slovenia	MZUSP 3342	EL30_SLV	Cunha *et al.*, 2017
Obelia cf. *dichotoma* sp.2	Bourne, USA	MZUSP 3335	MMA03_USA	Cunha *et al.*, 2017
Obelia cf. *dichotoma* sp.2	Punta Cuevas, San Juliàn, Argentina	MZUSP 3343	**PT2_USA**	Cunha *et al.*, 2017
Obelia cf. *dichotoma* sp.2	Otranto, Italy	USNM 1106156	*Obelia dichotoma*_IT*	Govindarajan *et al.*, 2006
Obelia cf. *dichotoma* sp.3	Farol Velho, Salinópolis, Brazil	MZUSP 3334, 2819	PAF07, **PAF09**_BRA	Cunha *et al.*, 2017

Species	**Locality**	**Voucher**	**Codes**	**References**
Obelia cf. *dichotoma* sp.3	Calhau, São Luís Maranhão, Brazil	MZUSP 2820	MA03_BRA	Cunha *et al.*, 2017
Obelia cf. *dichotoma* sp.4	Providence, USA	MZUSP 3341	**Site1.1_USA**	Cunha *et al.*, 2017
Obelia cf. *dichotoma* sp.4	Rocha, Uruguay	MZUSP 3346	**UR6_URG**	Cunha *et al.*, 2017
Obelia geniculata	South Freeport, USA	MZUSP 3347	BSF05_USA	Cunha *et al.*, 2017
Obelia geniculata	Punta Cuevas, San Juliàn, Argentina	MZUSP 3350	**PT5_ARG**	Cunha *et al.*, 2017
Obelia geniculata	New Castle, New Hampshire, USA	MZUSP 3351	**UNH01_USA**	Cunha *et al.*, 2017
Obelia geniculata	New Brunswick, Canada	USNM 1106176	NB_CAN	Govindarajan *et al.*, 2006
Obelia geniculata	João Gonçalves, Búzios, Brazil	MZUSP 3348	**BZ5_BRA**	Cunha *et al.*, 2017
Obelia geniculata	Mund Bay, Piran, Slovenia	MZUSP 3349	**EL23_SLV**	Cunha *et al.*, 2017
Obelia geniculata	Misaki, Sagami Bay, Japan	USNM 1106179	JP	Govindarajan *et al.*, 2006
Obelia geniculata	Wellington, New Zealand	USNM 1106165	NZ	Govindarajan *et al.*, 2006
Obelia longissima	Bourne, USA	MZUSP 3355	MMA04_USA	Cunha *et al.*, 2017
Obelia longissima	Gloucester, USA	MZUSP 3353	GFP04_USA	Cunha *et al.*, 2017
Obelia longissima	Hampton, USA	MZUSP 3354	HRM05_USA	Cunha *et al.*, 2017
Obelia longissima	San Julián, Argentina	MZUSP 3352	PT1_ARG	Cunha *et al.*, 2017
Obelia longissima	Antarctic Peninsula	USNM 1106173	AN	Govindarajan *et al.*, 2006
Obelia longissima	Sandgerdi, Iceland	USNM 1106189	IC	Govindarajan *et al.*, 2006
Obelia longissima	Ryders Cove, USA	USNM 1106153	USA	Govindarajan *et al.*, 2006
Obelia longissima	White Sea, Russia	USNM 1106191	WS	Govindarajan *et al.*, 2006
Obelia sp.1	Farol Velho, Salinópolis, Brazil	MZUSP 3357	PAF08_BRA	Cunha *et al.*, 2017
Obelia sp.1	Flexeiras, Trairí, Brazil	MZUSP 3356	**T2_BRA**	Cunha *et al.*, 2017
Orthopyxis caliculata	João Gonçalves, Búzios, Brazil	MZUSP 2612-15	JGB1-4_BRA	Cunha *et al.*, 2015
Orthopyxis caliculata	Paciência, Penha, Brazil	MZUSP 2563, 2565	AB, GB_BRA	Cunha *et al.*, 2015
Orthopyxis caliculata	Bombinhas, Brazil	MZUSP 4177, 4265	BB, COB_BRA	Cunha *et al.*, 2015
Orthopyxis caliculata	Paciência, Penha, Brazil	MZUSP 2550, 2552, 2554, 2556	PAB1, PAB3, PAB4, PAB5_BRA	Cunha *et al.*, 2015
Orthopyxis caliculata	Kinsale, Ireland	BMNH 1853.4.7.16 (type)	not included	Museum specimen

Species	Locality	Voucher	Codes	References
Orthopyxis compressa	Shumagin Islands, USA	USNM 4408 (type)	not included	Museum specimen
Orthopyxis crenata	Caponga, Cascavel, Brazil	MZUSP 2633	CB_BRA	Cunha *et al.*, 2015
Orthopyxis crenata	Paciência, Penha, Brazil	MZUSP 2551, 2560	PAB2, PAB7_BRA	Cunha *et al.*, 2015
Orthopyxis crenata	Lázaro, Ubatuba, Brazil	MZUSP 2598, 2601	LB5, LB8_BRA	Cunha *et al.*, 2015
Orthopyxis crenata	Comodoro Rivadavia, Argentina	MZUSP 3359	**PT19_ARG**	Cunha *et al.*, 2017
Orthopyxis crenata	Caleta Olivia, Argentina	MZUSP 2644	*Orthopyxis* sp._Co1_ARG*	Cunha *et al.*, 2017
Orthopyxis crenata	New Zealand	USNM 1106163	*Orthopyxis integra*_NZ*	Govindarajan *et al.*, 2006
Orthopyxis integra	La Mina, Puerto San Julián, Argentina	MZUSP 2638, 2640	Campanulariidae sp. indet._SJ1, SJ3_ARG*	Cunha *et al.*, 2015
Orthopyxis integra	San Julián, Argentina	MZUSP 3358	**PT20_ARG**	Cunha *et al.*, 2017
Orthopyxis integra	Aleutians, USA	USNM 1106184	1_USA	Govindarajan *et al.*, 2006
Orthopyxis mianzani	Mel Island, Brazil	MZUSP 2570-80, USNM 1259970	MB1-5, FOB1-7_BRA	Cunha *et al.*, 2015
Orthopyxis mianzani	Paciência, Penha, Brazil	MZUSP 2559	PAB6_BRA	Cunha *et al.*, 2015
Orthopyxis sargassicola	Aracruz, Brazil	MZUSP 2617-20, 2627-2630, 2632	FB1-2, PB2-7_BRA	Cunha *et al.*, 2015
Orthopyxis sargassicola	Paraty, Brazil	MZUSP 2605-09	PTY1-5_BRA	Cunha *et al.*, 2015
Orthopyxis sargassicola	Ratos Island, Paraty, Brazil	MZUSP 2610	RI_BRA	Cunha *et al.*, 2015
Orthopyxis sargassicola	Meros Island, Paraty, Brazil	MZUSP 2611	MI_BRA	Cunha *et al.*, 2015
Orthopyxis sargassicola	Lázaro, Ubatuba, Brazil	MZUSP 2594-97, 2599-2600, 2602-03	LB1-5, LB6-7, LB9-10_BRA	Cunha *et al.*, 2015
Orthopyxis sargassicola	São Sebastião, Brazil	MZUSP 2593	SS_BRA	Cunha *et al.*, 2015
Orthopyxis sargassicola	Campeche Island, Florianópolis, Brazil	MZUSP 4597	CI1_BRA	Cunha *et al.*, 2015
Orthopyxis asymmetrica	Piran, Slovenia	MZUSP 3360, 3361, 3362, 3363	*Orthopyxis* sp. 1_**EL02**, EL04, EL16, EL52_SLV*	Cunha *et al.*, 2017
Orthopyxis asymmetrica	Torre del Serpe, Italy	USNM 1106159	*Orthopyxis everta*_IT*	Govindarajan *et al.*, 2006
Orthopyxis asymmetrica	Italy	USNM 1106180	*Orthopyxis integra*_IT*	Govindarajan *et al.*, 2006

Species	**Locality**	**Voucher**	**Codes**	**References**
Rhizocaulus verticillatus	Aleutians, USA	USNM 1106183	**USA**	Govindarajan *et al.*, 2006
Silicularia rosea	San Julián, Argentina	MZUSP 3365, 3364	**PT8**, PT11_ARG	Cunha *et al.*, 2015, 2017
Silicularia rosea	Bay of Islands, New Zealand	USNM 1106164	1_NZ	Govindarajan *et al.*, 2006
Tulpa tulipifera	Patagonia, Argentina	MZUSP 3366	PT18_ARG	Cunha *et al.*, 2017

Table S2. Comparison among different species of *Bonneviella* [mean ± standard error (range)]. Specimens in bold indicate measurements taken from type materials deposited at the National Museum of Natural History, Smithsonian Institution. Numbers in brackets indicate total number of specimens examined. Morphometric data for *B. grandis* were based on the literature. The symbol “-” indicates lack of the structure to be measured (e.g., gonothecae, pedicel).

Measures (mm)	***Bonneviella regia*** **USNM 71390 [2]**	*Bonneviella regia* USNM 1106181 [4]	*Bonneviella* sp.4 USNM 1106182 [1]	*Bonneviella* sp.2 USNM 1106187 [1]	***Bonneviella ingens*** **USNM 34576 [2]**	***Bonneviella superba*** **USNM 3480 [1]**	*Bonneviella grandis* [Schuchert, 2001]
Total Length of Trophosome	-	4.8476±0.2956 (4.0132-5.3944)	35.4123	15.8825	10.1459±1.4820 (8.6638-11.6280)	24.4778	-
Hydrotheca							
Length	2.5790±0.4149 (2.1642-2.9939)	2.7700±0.1295 (2.4487-3.0061)	7.4064	5.6638	3.9850±0.8077 (3.1774-4.7927)	9.8829	7.0
Diameter at margin	0.8298±0.0677 (0.7621-0.8975)	0.5407±0.1182 (0.3300-0.8499)	4.7948	2.5493	2.3789±0.0975 (2.2814-2.4764)	2.8841	2.5
Length:Diameter Ratio	3.2729±0.0284 (3.2446-3.3013)	3.1023±0.1522 (2.8369-3.4191)	1.7263	2.3124	1.8832±0.3385 (1.5446-2.2217)	3.4267	2.8
Pedicel							
Length	-	2.0776±0.2428 (1.5646-2.7209)	28.0060	0.8149	6.1608±2.2897 (3.8711-8.4506)	14.5949	-
Diameter at Medial Portion	-	0.2574±0.0038 (0.2502-0.2650)	10.2187	0.4744	0.6383±0.0811 (0.5571-0.7194)	0.6796	-
Gonotheca							
Length	-	1.1538±0.0462 (1.0884-1.2192) [2]	-	-	-	5.9855	6.0-8.0
Maximum Diameter	-	0.7048±0.0057 (0.6967-0.7129) [2]	-	-	-	1.61487	2.5
Shape	-	Cylindrical, transversely ribbed	-	-	-	Cylindrical, transversely ribbed	Oblong ellipsoid, longitudinally ribbed

Table S3. Comparison among different species of *Orthopyxis* [mean±standard error (range)]. Specimens in bold indicate measurements taken from type materials deposited at the National Museum of Natural History, Smithsonian Institution (USNM), and the Natural History Museum, United Kingdom (BMNH). Number in brackets indicate total number of specimens examined. Morphometric data for the species *O. asymmetrica* and *O. angulata* are based on the literature. Symbol "-" indicates lack of the structure to be measured (e.g., gonotheca, pedicel), or lack of information from the literature.

Measures (μm)	*Orthopyxis* sp.1 (as in Cunha *et al.*, 2017) [6]	*Orthopyxis everta* USNM 1106159 [1]	*Orthopyxis integra*_IT USNM 1106180 [1]	*Orthopyxis asymmetrica* [Stechow, 1919; Peña-Cantero & Carcía-Carrascosa, 2002]	*Orthopyxis angulata* [Bale, 1914; Watson, 2005]	***Orthopyxis compressa* USNM 4408 [3]**	***Orthopyxis caliculata* NHM-UK 1853.4.7.16 [3]**
Total Length of Trophosome	1284.41±80.46 (1054.67-1573.61)	1038.97	886.58	1000-1200	-	2696.53±699.11 (1334.95-3652.68)	1001.65±34.66 (933.33-1045.92)
Hydrotheca							
Length	248.15±16.56 (184.77-296.94)	237.02	228.03	336	435-593	673.99±61.55 (551.26-743.59)	273.14±2.51 (268.31-276.76)
Diameter at margin	270.47±14.12 (213.15-314.34)	262.56	246.9	320	270-370	417.64±34.14 (362.07-479.79)	223.62±6.53 (215.09-236.45)
Length:Diameter Ratio	1.05±0.06 (0.8851-1.2739)	1.15	1.09	1.05	-	1.61±0.08 (1.52-1.77)	1.22±0.04 (1.16-1.29)
Maximum Perisarc Thickness at Medial Portion	12.84±2.44 (7.94-24.26)	15.36	4.96	-	-	24.12±10.62 (11.21-45.17)	29.03±1.72 (25.60-31.01)
Length:Diameter Ratio of the Basal Chamber	0.64±0.07 (0.5475-0.6739)	1.07	0.89	-	-	1.37±0.21 (0.95-1.63)	0.86±0.03 (0.80-0.90)
Pedicel							
Length	990.81±85.85 (721.10-1310.71)	762.73	615.55	-	686-2900	2050.28±686.95 (726.54-3030.73)	664.60±31.18 (603.53-706.04)

Measures (µm)	*Orthopyxis* sp.1 (as in Cunha *et al*., 2017) [6]	*Orthopyxis everta* USNM 1106159 [1]	*Orthopyxis integra*_IT USNM 1106180 [1]	*Orthopyxis asymmetrica* [Stechow, 1919; Peña-Cantero & Carcía-Carrascosa, 2002]	*Orthopyxis angulata* [Bale, 1914; Watson, 2005]	***Orthopyxis compressa* USNM 4408 [3]**	***Orthopyxis caliculata* NHM-UK 1853.4.7.16 [3]**
Diameter at Medial Portion	84.97±2.95 (73.53-94.79)	61.97	90.75	-		133.80±17.69 (107.88-167.63)	87.22±9.13 (69.69-100.42)
Maximum Perisarc Thickness at Medial Portion	10.71±1.18 (7.52-14.5)	6.09	14.42	-		14.84±5.46 (9.34-25.75)	18.46±5.80 (10.80-29.83)
Gonotheca							
Length	1242.49±218.36 (536.22-1912.54) [5]	1052.19	-	-	1176-1333	1528.11±58.32 (1411.90-1594.76)	-
Maximum Diameter	917.14±102.64 (681.94-1300.00) [5]	492.18	-	-	882-980	1312.18±5.86 (1300.84-1320.45)	-

Table S4. Comparison among lineages identified as *C*. cf. *gracilis* [mean±standard error (range)] and descriptions from the literature. Number in brackets indicates total number of specimens examined. The symbol “-” indicates lack of the structure to be measured (e.g., gonothecae, pedicel) or lack of information from the literature.

Measures (μm)	*Clytia gracilis*_sp.B_USA [3]	*Clytia* cf. *gracilis* sp.1 [8]	*Clytia* cf. *gracilis* sp.2 [4]	*Clytia* cf. *gracilis* sp.3 [5]	*Clytia* cf. *gracilis* sp.4 [5]	*Clytia* cf. *gracilis* sp.5 [19]	*Clytia gulangensis* [He *et al*., 2015]	*Clytia gracilis* [Calder, 1991]	*Clytia gracilis* [Cornelius, 1995]	*Clytia gracilis* [Schuchert, 2001]
Colony	Stolonal	Stolonal or erect	Erect or planktonic	Stolonal	Stolonal or erect	Stolonal	Stolonal or erect	Stolonal or erect	Erect	Erect
Total Length of Trophosome	2990.86±218.55 (2741.86-3426.48)	2500.15±361.81 (973.26-3864.64)	3695.33±504.25 (2315.12-4543.49)	1393.55±126.63 (1004.20-1721.53)	2423.75±211.27 (1866.44-2930.02)	2053.73±281.65 (1115.65-5187.18)	-	up to 11000	up to 20000	up to 2000
Hydrotheca										
Length	713.77±11.81 (690.36-728.16)	638.37±41.21 (487.44-791.12)	658.92±7.75 (648.72-681.58)	487.44±28.64 (443.85-558.93)	486.39±30.92 (369.70-547.92)	431.96±18.99 (320.56-729.91)	530-1020	736-932	500-900	1000-1200
Diameter (Maximum or at Margin)	284.51±2.64 (279.30-287.91)	284.53±9.76 (248.28-327.05)	301.53±17.63 (261.45-338.07)	210.43±21.82 (174.36-260.24)	218.70±9.31 (194.57-251.66)	244.56±11.54 (178.54-352.18)	180-330	391-522	300-400	400
Length:Diameter Ratio	2.83±0.02 (2.80-2.87)	2.5±0.09 (2.21-2.93)	2.40±0.15 (2.13-2.83)	2.58±0.08 (2.35-2.70)	2.51±0.14 (2.08-2.88)	2.14±0.08 (1.57-2.64)	2.94-3.09	-	-	2.5-3.0
Hydrothecal Cusps										
Number	11.66±0.33 (11-12)	10.25±0.45 (9-12)	10.25±0.48 (9-11)	9.2±0.48 (8-10)	8.8±0.49 (8-10)	9.63±0.37 (7-12)	8-12	12-15	8-12	10-12
Maximum Height of Cusps	83.61±1.54 (81.36-86.57)	67.16±3.70 (48.62-81.64)	39.65±5.99 (24.07-50.25)	38.02±4.56 (27.59-48.69)	59.75±4.72 (48.33-72.03)	49.01±2.46 (29.96-70.82)	-	-	-	-
Inclined	yes	yes, 1 specimen	no	yes, 1 specimen	yes	yes, 4 specimens	yes	no^{A}	yes	yes
Pedicel										
Length	2277.07±230.35 (2013.70-2736.11)	1500.11±237.12 (485.83-2466.46)	1307.50±121.55 (1071.29-1633.54)	906.11±137.21 (560.35-1162.59)	860.76±233.54 (344.24-1489.87)	1209.32±152.16 (613.03-3646.93)	up to 5900	500-3500	2000	-

Measures (μm)	*Clytia gracilis*_sp.B _USA [3]	*Clytia* cf. *gracilis* sp.1 [8]	*Clytia* cf. *gracilis* sp.2 [4]	*Clytia* cf. *gracilis* sp.3 [5]	*Clytia* cf. *gracilis* sp.4 [5]	*Clytia* cf. *gracilis* sp.5 [19]	*Clytia gulangensis* [He *et al*., 2015]	*Clytia gracilis* [Calder, 1991]	*Clytia gracilis* [Cornelius, 1995]	*Clytia gracilis* [Schuchert, 2001]
Diameter (Maximum or at Medial Portion)	70.52±1.40 (67.87-71.02)	85.27±3.41 (97.18-85.27)	82.00±1.96 (78.55-87.62)	58.24±2.48 (53.73-63.14)	55.21±3.60 (45.80-64.27)	69.33±3.17 (46.72-96.07)	60-100	103-145		-
Gonotheca		Smooth	Smooth			Smooth	Smooth	Smooth	Smooth	Smooth
Length	-	681.98±14.03 (625.85-681.98) [2]	1377.5 [1]	-	-	434.91±99.34 (268.86-612.43)	790-900	1000	1100-1800	1500
Maximum Diameter	-	262.46±7.49 (247.49-277.44) [2]	282.5 [1]	-	-	219.44±13.25 (203.60-245.75)	260-290	425	400-600	550
Growing from	-	Hydrorhiza	Branches	-	-	Hydrorhiza	Hydrorhiza, pedicels, branches	Hydrorhiza	-	-
Locality	United States	Italy, Slovenia	Argentina, United States	Slovenia	Belize	Brazil	Xiamen Bay, China	Bermuda	North-west Europe	Iceland

[A] Not mentioned in the text, but the cusps are not included in the illustrations (Vervoort, 1959, Fig. 55b, c; Calder, 1991, Fig. 31).

Table S5. Comparison among lineages identified as *Clytia* cf. *hemisphaerica* [mean±standard error (range)] and descriptions from the literature. Number in brackets indicate total number of specimens examined. The symbol "-" indicates lack of the structure to be measured (e.g., gonothecae, pedicel) or lack of information from the literature.

Measures (µm)	*Clytia* cf. *hemisphaerica* sp.1 [6]	*Clytia* cf. *hemisphaerica* sp.2 [11]	*Clytia* cf. *hemisphaerica* sp.3 [5]	*Clytia xiamenensis* [Zhou *et al.*, 2013]	*Clytia hemisphaerica* [Calder, 1991]	*Clytia hemisphaerica* [Cornelius, 1995]	*Clytia hemisphaerica* [Peña Cantero & García Carrascosa, 2002]
Colony	Stolonal or erect	Stolonal	Stolonal	Stolonal, rarely erect	Stolonal, ocasionally erect	Stolonal or erect	-
Total Length of Trophosome	4040.44±979.97 (1782.27-7734.57)	1698.03±210.02 (898.94-3375.35)	2071.67±220.30 (1569.02-2890.12)	-	-	20000	-
Hydrotheca							
Length	655.93±57.00 (474.90-861.70)	563.59±36.00 (440.56-814.05)	585.95±27.27 (521.40-660.51)	260-470	596-926	400-650	400-808
Diameter (Maximum or at Margin)	275.08±31.23 (186.30-404.28)	294.64±14.36 (193.17-346)	274.19±9.93 (244.83-305.49)	140-230	234-394	200-350	176-400
Length:Diameter Ratio	2.52±0.10 (2.17-2.85)	2.03±0.04 (1.70-2.20)	2.37±0.07 (2.18-2.59)	1.5-2.5	-	-	-
Hydrothecal Cusps							
Number	10.83±0.54 (9-13)	11.27±0.45 (10-15)	9.8±0.37 (9-11)	6-12	10-14	8-14	8-14
Maximum Height of Cusps	57.4±4.88 (39.85-70.26)	55.24±1.78 (43.29-66.00)	65.11±6.19 (46.10-81.38)	-	-	-	-
Inclined	no	no	no	yes	yes[A]	no[B]	no[B]
Pedicel							
Length	1583.02±357.03 (533.05-3122.36)	1134.47±176.17 (446.39-2561.30)	1485.72±203.81 (1047.62-2260.33)	260-1500	600-800	2200	-
Diameter (Maximum or at Medial Portion)	72.26±4.95 (59.43-93.91)	75.92±2.49 (60.43-93.38)	69.83±1.88 (64.26-73.90)	-	64-83	-	-
Gonotheca	Transversely ribbed	Transverselly ribbed	Transversely ribbed	Undulated walls	With distinct spiral ribs	Deeply concertinared walls, but smooth in some specimens	Transverselly ribbed[C]

Measures (μm)	*Clytia* cf. *hemisphaerica* sp.1 [6]	*Clytia* cf. *hemisphaerica* sp.2 [11]	*Clytia* cf. *hemisphaerica* sp.3 [5]	*Clytia xiamenensis* [Zhou *et al*., 2013]	*Clytia hemisphaerica* [Calder, 1991]	*Clytia hemisphaerica* [Cornelius, 1995]	*Clytia hemisphaerica* [Peña Cantero & García Carrascosa, 2002]
Length	796.85±54.77 (742.08-851.62) [2]	664.57±110.51 (422.88-901.12) [8]	669.98±24.26 (610.12-705.08)	890-1400	750	900-1200	-
Maximum Diameter	300.47±117.39 (183.08-417.86) [2]	281.34±33.59 (204.84-344.02) [8]	259.06±9.11 (240.87-284.35)	200-300	350	450-600	-
Growing from	Hydrorhiza	Hydrorhiza and pedicels	Hydrorhiza	Hydrorhiza, pedicels or branches	Hydrorhiza	-	-
Locality	United States	Slovenia, North Sea	Belize	Xiamen Bay, China	Bermuda	North-west Europe	Western Mediterranean

[A] According to Calder (1991), the cusps are “often somewhat skewed” (page 59, Fig. 32).

[B] Not mentioned in the text, but the cusps are not inclided in the illustrations (Cornelius, 1995, Fig. 57; Peña Cantero & García Carrascosa, 2002, Fig. 28C).

[C] As seen in the illustration (Peña Cantero & García Carrascosa, 2002, Fig. 28C, D).

Table S6. Comparison among lineages identified as *Obelia* cf. *dichotoma* and *O. longissima* [mean±standard error (range)], and literature descriptions. Number in brackets indicates total number of specimens examined. The symbol "-" indicates lack of the structure to be measured (e.g., gonothecae) or lack of information from the literature.

Measures (μm)	*Obelia* cf. *dichotoma* sp.1 [11]	*Obelia* cf. *dichotoma* sp.2 [5]	*Obelia* cf. *dichotoma* sp.3 [5]	*Obelia* cf. *dichotoma* sp.4 [6]	*Obelia longissima* [8]	*Obelia hyalina* [Vannucci, 1949; Calder, 2013]	*Obelia griffini* [Calkins, 1899]	*Obelia dichotoma* [Calder, 1991]	*Obelia dichotoma* [Cornelius, 1995]
Colony	Unbranched to 6th-order branched, monosiphonic	Unbranched to 3rd-order branched, monosiphonic	Unbranched to 1st-order branched, monosiphonic	Up to 2nd-order branched, monosiphonic	Up to 4th-order branched, monosiphonic	Monosiphonic	Branched, monosiphonic[B]	Unbranched to branched, monosiphonic	Mono to polysiphonic
Total Length of Trophosome (mm)	20.86±83.14 (35.70-90)	18.18±52.15 (8.69- 36.97)	7.81±1.18 (3.95-11.15)	9.89±1.38 (5.61-13.31)	41.66±10.84 (15.07-105)	15-20	25-50	21	50-350
Length of Internode of Main Stem	1129.80±233.73 (440.89-2709.04)	1261.81±208.01 (884.75-2066.44)	553.87±45.61 (445.98-718.64)	577.68±37.92 (464.04-715.20)	1725.41±237.24 (689.84-2549.04)		-	-	up to 2000
Hydrotheca									
Length	404.53±20.62 (331.48-542.29)	426.27±26.88 (359.92-517.745)	324.64±13.33 (294.42-372.82)	319.78±22.00 (253.15-390.78)	456.83±59.88 (338.17-844.59)	315-390	250-350	219-359	300-400
Diameter (Maximum or at Margin)	211.36±12.09 (164.01-286.37)	223.2182±5.60 (211.22-237.92)	191.22±11.02 (156.49-219.47)	187.44±8.08 (158.94-214.76)	261.41±26.25 (206.20-422.73)	190-270	-	210-317	200-250
Length:Diameter Ratio	1.93±0.06 (1.96-2.02)	1.91±0.12 (1.53-2.00)	1.71±0.05 (1.59-1.88)	1.71±0.12 (1.29-2.15)	1.73±0.07 (1.56-2.10)	-	-	-	-
Diaphragm	transverse to oblique	transverse to oblique	transverse to oblique	transverse to oblique	transverse to oblique	oblique[A]	transverse[B]	oblique	transverse to oblique
Hydrothecal Margin	even to crenate	even to crenate	even to crenate	even	sinuous	even	even	even	even to crenate
Number of cusps	5.27±1.84 (0-13)	2.80±2.80 (0-14)	2.80±2.80 (0-14)	-	13.12±0.51 (11-15)	-	-	-	-
Maximum Height of Cusps	5.05±1.81 (0-15.35)	3.48±3.48 (0-17.42)	2.76±2.76 (0-13.81)	-	11.05±1.45 (6.98-19.95)	-	-	-	-

Measures (μm)	*Obelia* cf. *dichotoma* sp.1 [11]	*Obelia* cf. *dichotoma* sp.2 [5]	*Obelia* cf. *dichotoma* sp.3 [5]	*Obelia* cf. *dichotoma* sp.4 [6]	*Obelia longissima* [8]	*Obelia hyalina* [Vannucci, 1949; Calder, 2013]	*Obelia griffini* [Calkins, 1899]	*Obelia dichotoma* [Calder, 1991]	*Obelia dichotoma* [Cornelius, 1995]
Pedicel									
Length	152.63±14.07 (101.60-241.03)	296.43±61.51 (128.65-457.85)	262.57±54.57 (122.08-445.59)	145.47±33.69 (71.54- 266.94)	227.17±38.97 (112.35-465.95)	160-900	-	-	200-400 (up to 700)
Diameter (Maximum or at Medial Portion)	89.3±4.08 (70.70-114.47)	88.65±3.10 (78.52-95.94)	81.52±1.72 (76.88-86.72)	76.17±2.55 (70.22-84.55)	95.76±5.20 (78.94-126.39)	-	-	-	-
Gonotheca									
Length	-	896.64±128.37 (666.02-1109.65) [3]	516.53±68.17 (448.36-584.70) [2]	711.39±93.68 (429.58-980.49)	-	390-430	800-1000	708-885	800-1050
Maximum Diameter	-	262.86±16.18 (233.53-289.35) [3]	157.66±9.41 (148.25-167.07) [2]	185.12±11.65 (148.20-231.27)	-	190-220	250-300	233-294	230-290
Locality	United States, Uruguay, Argentina	Italy, Slovenia, United States, Argentina	Brazil	United States, Argentina	Iceland, United States, White Sea, Argentina, Antarctica	Brazil, United States	Puget Sound, United States	Bermuda	North West Europe

[A] Not mentioned in the species description, taken from the illustrations (Clarke, 1879; Calder, 2013).

[B] Not clearly mentioned in the text, taken from the illustration (Calkins, 1899)