Update on Benthic Scyphozoans from the Brazilian Coast
(Cnidaria: Scyphozoa: Coronatae)

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RESUMO
Uma atualização sobre cifozoários bentônicos da costa brasileira (Cnidaria: Scyphozoa: Coronatae). A ordem Coronatae é considerada o grupo basal de Scyphozoa, contendo aproximadamente 60 espécies. Observar do ciclo de vida é fundamental para desvendar a sistemática e a taxonomia da ordem. Entretanto, estudos recientes relacionados apenas ao estágio de pólipo foram capazes de promover progresso usando, exclusivamente, caracteres morfológicos do tubo peridérmico. A falta de conhecimento sobre o número real de espécies de coronados ocorrentes no Brasil e sua distribuição ao longo da faixa costeira é um fator que limita abordagens mais avançadas para interpretar a biogeografia desses animais. Nosso objetivo foi identificar e descrever esses pólipos do Norte, Sudeste e Sul do Brasil, levando em consideração a distribuição bathimétrica e longitudinal das espécies. As medidas do tubo peridérmico obtidas por meio de microscopia de luz e a organização e morfologia dos espinhos internos, observadas por meio de microscopia eletrônica de varredura, permitiram o reconhecimento de 3 morfotipos, identificados apenas ao nível de gênero: dois morfotipos de Nausithoe (oito e 16 espinhos) e um de Atorella.

Palavras-chave: Atorella, Cifostoma, Microscopia Eletrônica de Varredura (MEV), Nausithoe, Pólipo.

ABSTRACT
Members of the order Coronatae are considered the basal group of Scyphozoa, containing approximately 60 species. Observation of life cycle is critical to unravel the systematics and taxonomy of the order. However, recent studies related only to the polyp stage were able to promote progress using solely morphological characters of the periderm tube. The lack of knowledge about the actual number of coronate species occurring in Brazil and their distribution along the coast is a factor that limits more advanced approaches to interpret the biogeography of these animals. Our goal was to identify and describe the Coronatae polyps from N, SE and S Brazil, taking into account the bathymetric and longitudinal distribution of species. Measurements of the periderm tube under light microscopy and the organization and morphology of the internal cusps observed through Scanning Electron Microscopy allowed the recognition of three morphotypes, recognized only at the genus level: two morphotypes of Nausithoe (eight and 16 cusps) and one form of Atorella.

Keywords: Atorella, Nausithoe, Polyp, Scanning Electron Microscopy (SEM), Scyphistoma.
INTRODUCTION

The order Coronatae Vanhöffen, 1892 is considered the basal group of the class Scyphozoa Goette, 1887 (viz Marques & Collins, 2004; Collins, 2009). Members of this order have a polyp stage with a firm periderm tube that fully surrounds the soft parts (Werner, 1970; Arai, 1997; Mendoza-Becerril et al., 2016), distinguishing them from other Scyphozoa, the subclass Discomedusae Haeckel, 1880, that have only reduced exoskeleton at the base of the polyp stalk or at podocysts.

The diversity of coronates is estimated to be around 60 species (Morandini & Jarms, 2012; Jarms & Morandini, 2019) distributed all over the world. The group is widely known and represented in many general texts as being composed by deep-water medusae (Kramp, 1961). But since the mid 1960’s the number of polyp species recognized for the group grew (e.g. Werner, 1966; Werner, 1973; Jarms, 1990), and also several shallow water forms were found (e.g. Silveira & Morandini, 1997).

Along the Brazilian coast and territorial waters, eight coronate species were described/recorded: the medusae Atolla wyvillei Haeckel, 1880; Nausithoe atlantica Broch, 1914; Nausithoe punctata Kölliker, 1853; Periphylla periphylla (Péron & Lesueur, 1810); and the polyps Linuche unguiculata (Swartz, 1788); Nausithoe aurea Silveira & Morandini, 1997; Stephanoscyphistoma corniformis (Komai, 1936); and Stephanoscyphistoma simplex (Kirkpatrick, 1890) (Goy, 1979; Silveira & Morandini, 1997; Morandini, 2003; Oliveira et al., 2016). In addition, four more polyp forms occur in the Brazilian coast, but only identified to the generic level as Nausithoe sp. or Atorella sp. (Jarms et al., 2002a).

The study of the life cycle, emphasizing both the benthic polyp and the pelagic medusa, is critical in addressing the systematics of the order (Werner, 1973; Silveira & Morandini, 1997) and understanding aspects of the group’s evolution (Jarms, 2010). This statement is a consequence of the traditional systematics of coronates, which is mainly dependent on observation of adult and mature forms, i.e. the medusoid stage. In the past, many preserved polyp specimens were identified only as Coronatae polyps (see Jarms, 1990, 1991) thus creating some instability in the systematics and taxonomy of the order. In general, there were two groups of species (Werner, 1973) mainly distinguished based on bathymetry: a shallow water form (Stephanoscyphus corniformis), and a deepwater species (Stephanoscyphus simplex) (Kramp, 1959). Jarms (1990) proposed to use a taxonomic resource to accommodate species with unknown medusa, creating the genus Stephanoscyphistoma. However, recent studies analyzing only the polyp stage promoted progress using morphological characters of the periderm tube for differentiating some species (Morandini & Jarms, 2005, 2010, 2012). These characters were available in the literature (Kramp, 1959; Naumov, 1959, 1961), but their use for differentiating species were only proposed by Jarms.
(1990, 1991) and highlighted by Jarms et al. (2002b). Thus, the goal of this study was to identify and describe samples of Coronatae polyps available from different parts along the Brazilian coast, based on morphometric measurements of the periderm tubes.

**MATERIAL AND METHODS**

Coronate polyps from different projects along the Brazilian coast were available. The material was collected from 4º27'54"N to 29º12'S and 43º51'12"W to 49º58'05"W, with dept varying from 84 m to 2,064 m (Table 1, Figure 1). The projects referred to BFZ (Project on Amazon Basin) - 21 stations (Amapá State), REVIZEE (Programa de Avaliação do Potencial Sustentável de Recursos Vivos da Zona Econômica Exclusiva) Score Sul - 6 stations (Paraná and Santa Catarina States) and Ecology Project - 14 stations (Rio de Janeiro State). The samples were collected using different devices (dredge, van Veen, box corer), and preserved in 70 - 90% ethanol.

**Figura 1.** Map of Brazilian coast showing collection stations of studied coronate polyps. In green the Project on Amazon Basin; in yellow the Ecology Project in the coast of Rio de Janeiro; and in red the REVIZEE Project in the coast of Paraná and Santa Catarina.
All periderm tubes were measured to check the total length. For standardization, only the tubes longer than 5 mm were measured in detail, because all measurements and relationships available in the literature address animals over this size (5 mm; Jarms, 1990, 1991). Polyps were measured according to the standards presented by Jarms et al. (2002b): total length of tube, diameter at 2 mm above the base, diameter at 5 mm above the base, diameter of the basal disk, diameter immediately above the basal disk and the diameter of the tube opening. Additionally, the external arrangement of the periderm tube was noticed (considering the number of transverse rings in each 0.4 mm). To avoid variations in the number of transverse rings along the tube, two measurements were conducted for each tube: one at 2 mm and another at 5 mm above the base.

Table 1. Summary of data from studied samples. SP = São Paulo State, PR = Paraná State, SC = Santa Catarina State; RJ = Rio de Janeiro State; AP = Amapá State. REVIZEE = Programa de Avaliação do Potencial Sustentável de Recursos Vivos da Zona Econômica Exclusiva, Ministério do Meio Ambiente (Environmental ministry program for evaluation of the sustainable use of the living resources of the economic exclusive zone). BFZ = Project on Amazon Basin by Exxon and PEG (Petroleum and Environmental Geoservices Ltda). NIA = No information available.
| Project / Station | Date   | Latitude       | Longitude      | State | Depth (m) | Collection Method | # of polyps          |
|-------------------|--------|----------------|----------------|-------|-----------|-------------------|----------------------|
| Ecology / BMS-04 P4 (MZUSP 8480) | 19i2005 | 24º19'18"S | 43º52'11"W | RJ | 384 | NIA | 9 Nausithoe - 8 cusps |
|                   |        |                |                |      |           |                   | 2 Nausithoe - 16 cusps |
|                   |        |                |                |      |           |                   | 3 Nausithoe - 8 or 16 cusps |
| Ecology / BMS-04 P5 (MZUSP 8481) | 18i2005 | 24º19'25"S | 43º52'17"W | RJ | 390 | NIA | 5 Nausithoe - 8 cusps |
|                   |        |                |                |      |           |                   | 2 Nausithoe - 16 cusps |
|                   |        |                |                |      |           |                   | 8 Nausithoe - 8 or 16 cusps |
| Ecology / BMS-04 P6 (MZUSP 8482) | 19i2005 | 24º19'28"S | 43º52'05"W | RJ | 396 | NIA | 3 Nausithoe - 8 cusps |
|                   |        |                |                |      |           |                   | 3 Nausithoe - 8 or 16 cusps |
| Ecology / BMS-04 P7 (MZUSP 8483) | 19i2005 | 24º19'17"S | 43º52'01"W | RJ | 384 | NIA | 3 Nausithoe - 8 cusps |
|                   |        |                |                |      |           |                   | 3 Nausithoe - 8 or 16 cusps |
| Ecology / BMS-04 P8 (MZUSP 8484 e 8485) | | 24º19'14"S | 43º52'14"W | RJ | 395 | NIA | 3 Nausithoe - 8 cusps |
|                   |        |                |                |      |           |                   | 3 Nausithoe - 8 or 16 cusps |
| Ecology / BMS-04 P9 (MZUSP 8486) | 18i2005 | 24º19'29"S | 43º52'25"W | RJ | 397 | NIA | 2 Nausithoe - 8 cusps |
|                   |        |                |                |      |           |                   | 5 Nausithoe - 8 or 16 cusps |
| Ecology / BMS-04 P10 (MZUSP 8487) | 19i2005 | 24º19'35"S | 43º52'01"W | RJ | 422 | NIA | 6 Nausithoe - 8 cusps |
|                   |        |                |                |      |           |                   | 1 Nausithoe - 16 cusps |
| Ecology / BMS-04 P11 (MZUSP 8488) | 19i2005 | 24º19'13"S | 43º51'54"W | RJ | 393 | NIA | 17 Nausithoe - 8 cusps |
|                   |        |                |                |      |           |                   | 4 Nausithoe - 8 or 16 cusps |
| Ecology / BMS-04 P12 (MZUSP 8489) | 19i2005 | 24º19'07.3"S | 43º52'18"W | RJ | 371 | NIA | 5 Nausithoe - 8 cusps |
|                   |        |                |                |      |           |                   | 4 Nausithoe - 16 cusps |
|                   |        |                |                |      |           |                   | 9 Nausithoe - 8 or 16 cusps |
| Ecology / BMS-04 P13 (MZUSP 8490) | 18i2005 | 24º19'52"S | 43º53'06"W | RJ | 431 | NIA | 1 Nausithoe - 8 cusps |
|                   |        |                |                |      |           |                   | 4 Nausithoe - 8 or 16 cusps |
| Ecology / BMS-04 P14 (MZUSP 8491) | 19i2005 | 24º18'50"S | 43º51'12"W | RJ | 363 | NIA | 12 Nausithoe - 8 cusps |
|                   |        |                |                |      |           |                   | 2 Nausithoe - 16 cusps |
|                   |        |                |                |      |           |                   | 8 Nausithoe - 8 or 16 cusps |
| BFZ 1/1           | 13x2000 | 4º27'54"N  | 49º58'05"W  | AP | 160 | box-corer | 1 Atorella |
|                   |        |                |                |      |           |                   | 1 Nausithoe - 8 or 16 cusps |
| BFZ 1/5           | 13x2000 | 4º21'28"N  | 49º40'59"W  | AP | 1233 | box-corer | 3 Atorella |
|                   |        |                |                |      |           |                   | 7 Nausithoe - 8 or 16 cusps |
| BFZ 1/6           | 12x2000 | 4º21'13"N  | 49º49'20"W  | AP | 408 | box-corer | 3 Atorella |
|                   |        |                |                |      |           |                   | 1 Nausithoe - 8 or 16 cusps |
|                   |        |                |                |      |           |                   | 4 Nausithoe - 16 cusps |
|                   |        |                |                |      |           |                   | 3 Nausithoe - 8 or 16 cusps |
| BFZ 1/7           | 12x2000 | 4º14'00"N  | 49º32'15"W  | AP | 580 | box-corer | 4 Atorella |
|                   |        |                |                |      |           |                   | 6 Nausithoe - 8 or 16 cusps |
| BFZ 1/8           | 14x2000 | 4º07'34"N  | 49º44'08"W  | AP | 84  | box-corer | 3 Nausithoe - 8 or 16 cusps |

Continua.
Another important feature of the coronate polyps periderm tube is the presence and arrangement of internal cusps. Thus, 16 tubes of the different morphotypes were sectioned transversally, prepared for Scanning Electron Microscopy (SEM) (according to Jarms et al., 2002a, b) and observed. Features observed were: shape of cusps, presence and shape of additional cusps, number of cusps per whorl and the number of whorls per tube. As the observation of all samples by SEM was not feasible, we estimated the number of internal cusps of the rest of the polyps through light microscopy (whenever possible).

After analyses, material was deposited in the Museu de Zoologia da Universidade de São Paulo (MZUSP). Reference numbers: MZUSP 8477 – 8500.
RESULTS

From the 323 available polyps (41 from the REVIZEE Project, 179 from the Ecology Project, and 103 from the BFZ Project) only 170 were longer than 5 mm. Those were used for comparisons and detailed measurements. Moreover, among them only 157 had intact structure of the basal disk, and 145 had enough transparency in the tube to verify the number of internal cusps. For species descriptions we considered only the 145 tubes in which internal cusps could be counted.

Polyps were sorted in two categories: one with more prominent transversal rings (genus *Atorella*) and other with a smoother tube surface (genus *Nausithoe*). Such difference was found both at 2 mm as well as at 5 mm above the base. Differences in the number of internal cusps at each whorl and the contour of the cusp base were also observed (seen through the tubes and SEM). Based on this feature, we managed to distinguish two different morphotypes of *Nausithoe*.

*Atorella* sp.: Solitary polyps (27 of 145 specimens) growing on calcareous substrate. Conical periderm tubes with light to dark brown color; varying in length from 3.28 - 7.18 mm; basal disc 0.361 - 0.573 mm wide; diameter above the basal disc from 0.1 - 0.195 mm; tube aperture diameter from 0.604 - 0.882 mm. Number of transversal rings at tube surface from 6 - 8 in an interval of 0.4 mm measured 2 mm above the base (Figure 2B). The number of whorls of cusps varies from four - six and each whorl has eight cusps. The contour of the attachment of the cusp into tube wall is broader than higher when seen through the tube wall. Internally, cusps are arranged as four larger perradial and four smaller interradial ones, with additional cusps at the free margin (Figure 3E, F). From the 27 *Atorella* specimens observed, 23 were collected off the Amapá State.

Figura 2. Scanning Electron Micrography of members of the genera *Nausithoe* (A) and *Atorella* (B), showing the transversal rings; note rings closer to each other on the *Atorella* specimen when compared to *Nausithoe*. 
**Figura 3.** Scanning Electron Micrographies of internal cusps of studied specimens. **A/B:** *Nausithoe* sp. (morphotype with eight cusps) – 4 larger cusps and 4 smaller ones without additional cusps (A), and basal whorl with additional cusps at the free margin (B). **C/D:** *Nausithoe* sp. (morphotype with 16 cusps) – four large cusps, four intermediate and eight smaller ones; free margin with more additional cusps at the basal whorls (D) than upper part of the tube (C). **E/F:** *Atorella* sp. – four larger cusps and four smaller ones with, additional cusps at the free margin, both at the basal (F) and upper whorls (E).

*Nausithoe* sp. (morphotype with eight cusps): Solitary polyps (74 of 145 specimens) growing on calcareous substrate. Conical periderm tubes with light to dark brown color, varying in length from 1.191 - 30.216 mm; basal disc 0.247 - 0.809 mm wide; diameter above the basal disc from 0.089 - 0.375 mm; tube aperture diameter from 0.309 - 1.906 mm. Number of transversal rings at tube surface from 2 - 6 in
an interval of 0.4 mm, measured 2 mm above the base (Figure 2A). The number of whorls of cusps varies from 1 - 11, and each whorl has eight spines. The contour of the attachment of the cusp into the tube wall is higher than broader when seen through the tube wall. Internally, cusps are arranged as four larger perradial and four smaller interradial ones, with smooth surface and no further ornamentation. At the most basal whorls, additional cusps can be observed at the free margin (Figure 3A, B).

**Nausithoe sp. (morphotype with 16 cusps):** Solitary polyps (44 of 145 specimens) growing on calcareous substrate. Conical periderm tubes with light to dark brown color; varying in length from 2.182 - 11.343 mm; basal disc 0.362 - 0.823 mm wide; diameter above the basal disc from 0.103 - 0.192 mm; tube aperture diameter from 0.251 - 1.195 mm. Number of transversal rings at tube surface from 2 - 5 in an interval of 0.4 mm, measured 2 mm above the base (Figure 2A). The number of whorls of cusps varies from 1 - 11, and each whorl has 16 spines. The contour of the attachment of the cusp into tube wall is higher than broader when seen through the tube wall. Internally, cusps are arranged as 4 larger perradial, 4 intermediate interradial, and eight smaller adradial ones between the others. At the most basal whorls, additional cusps can be observed at the free margin (Figure 3C, D).

**DISCUSSION**

Up to now, eight species of coronates were reported along the Brazilian coast (Oliveira et al., 2016). The medusae: *Atolla wyvillei, Nausithoe atlantica, Nausithoe punctata* and *Periphylla periphylla*; and the polyps: *Linuche unguiculata, Nausithoe aurea, Stephanoscyphistoma corniformis* and *Stephanoscyphistoma simplex*. There are still four polypoid forms without specific identification; two belonging to the genus *Atorella* and two belonging to the genus *Nausithoe* (Jarms et al., 2002a). The exact number of coronate species on the Brazilian coast cannot be assured because of these unidentified polypoid forms, but also due to our widespread ignorance about the deep-water fauna (Morandin, 2003).

Considering the *Atorella* specimens, there is no record of any species of this genus along the Brazilian coast. Additionally, our knowledge of the diversity of species based on polyp forms is not satisfactory to precisely identify the present form, as happened in the past (Jarms et al., 2002a). The literature regarding the genus for the Atlantic Ocean reported only the medusa stage of *Atorella octogonos* Mills, Larson & Youngbluth, 1987 restricted to the region of the Bahamas (Mills et al., 1987; Morandini & Jarms, 2005) and two forms of polyps found on the Brazilian coast (Jarms et al., 2002a) – one with larger cusps presenting additional cusps and the other without further ornamentation on the internal cusps. Taking into account members of the genus *Nausithoe*, the feature “presence of additional cusps” is clearly indicative of distinction between species. Unfortunately, there is no comprehensive study on the genus
Atorella to evaluate the validity of this feature, partly due to the difficulties in collecting both medusa and polyp forms, partly for distinguishing the polypoid stage among polychaetes, anemones and other coronate tubes. Moreover, the polypoid form of A. octogonos is not known until now.

The studied specimens of the genus Nausithoe were also not possible to be identified to the species level. Although there are much more knowledge concerning the polyp forms of the genus (Morandini & Jarms 2005, 2010, 2012), most of the identification still relies on the medusa stage. Considering the records and occurrence data of Nausithoe medusae along the Brazilian coast, there are only a few reports (Goy, 1979; Neumann-Leitão et al., 2008; Nogueira Jr. et al., 2014, 2015; Oliveira et al., 2016). The listed species are Nausithoe punctata (Goy, 1979; Neumann-Leitão et al., 2008; Nogueira Jr. et al., 2014, 2015) and Nausithoe atlantica (Correia, 1983; Oliveira et al., 2016). However, those reports were made by non-specialists on scyphomedusae and due to the difficulty in distinguishing species, we consider them doubtful. The record of Nausithoe atlantica was based on plankton samples along southern states coast (Paraná and Santa Catarina), and included in a MSc thesis; the record was considered in the South American census of medusozoans published by Oliveira et al. (2016), but there is no picture or any voucher specimen to check the identity. The records of Nausithoe punctata were based on specimens from the northeast (Goy, 1979; Neumann-Leitão et al., 2008) and southern coasts (Nogueira Jr. et al., 2014, 2015). The traditional available descriptions of Nausithoe punctata (Mayer, 1910; Kramp, 1961) mention features that are so general that any Nausithoe species can fit in them. This makes the identification of the species extremely difficult and dependent on knowledge about the life cycle. The medusa of Nausithoe punctata comes from colonial polyps (Werner, 1973), and such polyps were never found in the Brazilian coast. The polyps of the species Nausithoe aurea were already found in the south (Santa Catarina), southeastern (Espírito Santo, Rio de Janeiro, and São Paulo) and northeastern (Bahia) regions (Morandini & Jarms, 2005). The polyps found in this study, presented eight and 16 internal cusps. Based on the literature (Morandini & Jarms, 2012: 65, Table 2) only three solitary species have eight cusps in all series: N. werneri (North Atlantic: Morocco, Greenland), N. marginata (Mediterranean), and N. globifera (North Atlantic: between Greenland and the British Isles). Considering these three species, only N. werneri has additional cusps, similar to our samples. However, the known distribution of the species is not consistent with the area of occurrence of the polyps observed in this study. Further data from the literature (Morandini & Jarms 2012: 65, Table 2) show that three solitary species present 16 spines in all transversal series: N. aurea (Brazil), N. maculata (Puerto Rico), and N. hagenbecki (only known from a Zoo aquarium; see Jarms, 2001). N. aurea and N. maculata have very similar features both as polyp and medusa stages, the only distinction between them, so far, is related to the pattern of asexual reproduction (Silveira & Morandini,
Although the literature on systematics and taxonomy of Coronatae rely mostly on life cycle observations, a few works stated that the polyp stage of families Nausithoidae and Atorellidae could be sufficient for identification of species. Unfortunately, the animals herein studied by us could only be identified up to genus level.

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REFERENCES

Arai, M.N. 1997. A functional biology of Scyphozoa. London: Chapman & Hall. 316p.

Collins, A.G. 2009. Recent insights into cnidarian phylogeny. Smithsonian Contributions to the Marine Sciences 38: 139-149.

Correia, K.V. 1983. As Medusas da Plataforma dos Estados do Paraná e Santa Catarina (Operação CONVERSUT III) Sistemática e Distribuição. Dissertação (Mestrado em Zoologia). Setor de Ciências Biológicas, Universidade Federal do Paraná. Curitiba, PR. 221p.

Goy, J. 1979. Campagne de la Calypso au large des côtes atlantiques de l'Amérique du Sud (1961-1962) - 35. Méduses. Resultats Scientifiques des Campagnes de la Calypso 11: 263-296.

Jarms, G. 1990. Neubeschreibung dreier Arten der Gattung Nausithoe (Coronata, Scyphozoa) sowie Wiederbeschreibung der Art Nausithoe marginata Kölliker, 1853. Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut 87: 7-39.

Jarms, G. 1991. Taxonomic characters from the polyp tubes of coronate medusae (Scyphozoa, Coronatae).
Hydrobiologia 216/217: 463-470.

Jarms, G. 2001. The life cycle of Nausithoe hagenbecki sp. nov. (Scyphozoa, Coronatae). Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut 98: 13-22.

Jarms, G. 2010. The early life history of Scyphozoa with emphasis on Coronatae. A review with a list of described life cycles. Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg 45: 17-31.

Jarms, G. & Morandini, A.C. 2019. World Atlas of Jellyfish. Hamburg: Dölling und Galitz Verlag. 816p.

Jarms, G.; Morandini, A.C. & Silveira, F.L. 2002a. Polyps of the families Atorellidae and Nausithoidae (Scyphozoa: Coronatae) new to the Brazilian fauna. Biota Neotropica 2(1): 11.

Jarms, G.; Morandini, A.C. & Silveira, F.L. 2002b. Cultivation of polyps and medusae of Coronatae (Cnidaria, Scyphozoa) with a brief review of important characters. Helgoland Marine Research 56(3): 203-210.

Kramp, P.L. 1959. Stephanoscyphus (Scyphozoa). Galathea Report 1: 173-187.

Kramp, P.L. 1961. Synopsis of the medusae of the world. Journal of the Marine Biological Association of the United Kingdom 40: 7-469.

Marques, A.C. & Collins, A.G. 2004. Cladistic analysis of Medusozoa and cnidarian evolution. Invertebrate Biology 123(1): 23-42.

Mayer, A.G. 1910. The medusae of the world. Volume III. The Scyphomedusae. Carnegie Institution of Washington, Publication 109(3): 499-735.

Mendoza-Becerril, M.A.; Maronna, M.M.; Pacheco, M.L.A.F.; Simões, M.G.; Leme, J.M.; Miranda, L.S.; Morandini, A.C. & Marques, A.C. 2016. An evolutionary comparative analysis of the medusozooan (Cnidaria) exoskeleton. Zoological Journal of the Linnean Society 178: 206-225.

Mills, C.E.; Larson, R.J. & Youngbluth, M.J. 1987. A new species of coronate scyphomedusa from the Bahamas, Atorella octogonos. Bulletin of Marine Science 40: 423-427.

Morandini, A.C. 2003. Deep-sea medusae (Cnidaria: Cubozoa, Hydrozoa and Scyphozoa) from the coast of Bahia (western South Atlantic, Brazil). Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut 100: 13-25.

Morandini, A.C. & Jarms, G. 2005. New combinations for two coronate polyp species (Atorellidae and Nausithoidae, Coronatae, Scyphozoa, Cnidaria). Contributions to Zoology 74(1/2): 117-123.

Morandini, A.C. & Jarms, G. 2010. The identification of the coronate polyp from the Arctic Ocean: Nausithoe werneri Jarms, 1990 (Cnidaria, Scyphozoa, Coronatae), with notes on the biology. Steenstrupia
32(1): 69-77.

Morandini, A.C. & Jarms, G. 2012. Discovery and redescription of type material of Nausithoe simplex (Kirkpatrick, 1890), comb. nov. (Cnidaria: Scyphozoa: Coronatae: Nausithoidae) from the North Atlantic. Zootaxa 3320: 61-68.

Morandini, A.C. & da Silveira, F.L. 2001. New observations and new record of Nausithoe aurea (Scyphozoa, Coronatae). Papéis Avulsos de Zoologia 41: 519-527.

Naumov, D.V. 1959. Vidovye razlichiya polipoidnogo pokoleniya Coronomeduz [Generic classification of polypoid generations of Coronomedusae] [in Russian]. Doklady Akademii Nauk SSSR 126(4): 902-904.

Naumov, D.V. 1961. Stsifoidnye meduzy morei SSSR [Scyphoid medusae of the seas of SSSR] [in Russian]. Opredeliteli po Faune S.S.S.R. [Fauna S.S.S.R.] 75: 1-98.

Neumann-Leitão, S.; Sant’anna, E.M.E.; Gusmão, L.M.O.; Nascimento-Oliveira, D.A.; Paranaguá, M.N. & Schwamborn, R. 2008. Diversity and distribution of the mesozooplankton in the tropical Southwestern Atlantic. Journal of Plankton Research 30: 795-805.

Nogueira Jr, M.; Brandini, F.P. & Codina, J.C.U. 2014. Distribution of planktonic cnidarians in response to South Atlantic Central Water intrusion in the South Brazilian Bight. Continental Shelf Research 89: 93-102.

Nogueira Jr., M.; Brandini, F.P. & Codina, J.C.U. 2015. Diel vertical dynamics of gelatinous zooplankton (Cnidaria, Ctenophora and Thaliacea) in a subtropical stratified ecosystem (South Brazilian Bight). PLoS ONE 10(12): e0144161.

Oliveira, O.M.P.; Miranda, T.P.; Araújo, E.M.; Ayón, P.; Cedeño-Posso, C.; Cepeda-Mercado, A.A.; Códova, P.; Cunha, A.F.; Genzano, G.; Haddad, M.A.; Mianzan, H.W.; Migotto, A.E.; Miranda, L.S.; Morandini, A.C.; Nagata, R.M.; Nascimento, K.B.; Nogueira JR, M.; Palma, S.; Quiñones, J.; Rodrigo, C.S.; Scarabino, F.; Schiariti, A.; Stampar, S.N.; Tronolone, V.B. & Marques, A.C. 2016. Census of Cnidaria (Medusozoa) and Ctenophora from South American marine waters. Zootaxa 4194: 1-256.

Silveira, F.L. & Morandini A.C. 1997. Nausithoe aurea n. sp. (Scyphozoa, Coronatae, Nausithoidae), a species with two pathways of reproduction after strobilation: sexual and asexual. Contributions to Zoology 66(4): 235-246.

Werner, B. 1966. Stephanoscyphus (Scyphozoa, Coronatae) und seine direkte Abstammung von den fossilen Conulata. Helgoländer Wissenschaftliche Meeresuntersuchungen 15: 317-347.

Werner, B. 1970. Contribution to the evolution in the genus Stephanoscyphus (Scyphozoa Coronatae) and ecology and regeneration qualities of Stephanoscyphus racemosus Komai. Publications of the Seto
Marine Biological Laboratory 18(1): 1-20.

Werner, B. 1973. New investigations on systematics and evolution of the class Scyphozoa and the phylum Cnidaria. Publications of the Seto Marine Biological Laboratory 20: 35-61.