

First record of *Protohydra cf. leuckarti* (Cnidaria, Hydrozoa) from South America, in the Campos Basin, Rio de Janeiro, Brazil, with comments on its taxonomy and a brief review of its bio-ecology and distribution

Priscila A. Grohmann*

Abstract

Research on deep-sea benthic environments off the coast of Brazil started in the late 20th century. Sponsored by PETROBRAS, the Brazilian oil company, studies were undertaken to characterize these environments prior to exploitation of petroleum discoveries on the continental shelf. Samples of soft-bottom benthos were collected in the Campos Basin, site of one of the largest known oil deposits in the country, during a study known as Projeto HABITATS (2008/2009). Macrofauna extracted from these samples included small pelecypod molluscs (*Ledella* spp.) that provided substrate for associated hydroids, including *Protohydra cf. leuckarti*. This report constitutes the first records of a species of *Protohydra* from Brazil, from South America, and from the deep sea.

Key words: meiofauna, soft bottom, deep sea, canyon of the Brazilian slope, epibiosis of hydroids on Mollusca

Introduction

Biological exploration of the seabed on the Brazilian continental shelf began in the 1970s. Studies were prompted by the potential for commercial production of oil from newly discovered petroleum resources in the region. A discovery in the Campos Basin off the southeastern coast of Brazil is believed to harbor one of the largest oil reserves in the country, with the potential to be one of the largest in the world.

During the HABITATS Project, carried out with the supervision and financial support of CENPES/PETROBRAS, protobranchiate pelecypod molluscs (*Ledella* spp.) having the small hydroid *Protohydra cf. leuckarti* Greeff, 1869 on their shells were found in benthic samples collected at 1030 m from the Campos Basin. Previously, *Protohydra* had been reported in the literature as hydrozoans mostly inhabiting anoxic sediments of shallow brackish-water habitats in temperate regions, principally in the northern hemisphere

* Universidade Federal do Rio de Janeiro, Instituto de Biologia, Departamento de Zoologia, Laboratório de Taxonomia e Bioecologia de Cnidaria, CCS – Bloco A – Ilha do Fundão, Rio de Janeiro, RJ CEP 21941-590; e-mail: grohmann@biologia.ufrj.br

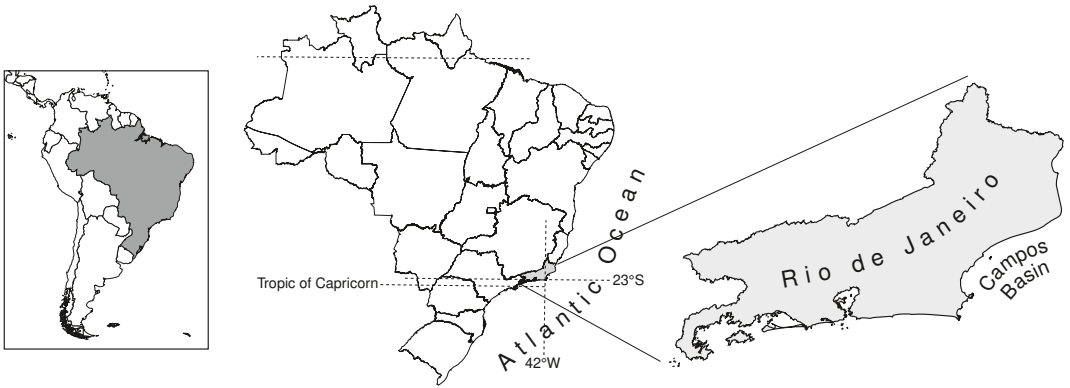


Fig. 1. Location of the Campos Basin, seaward of the state of Rio de Janeiro.

(Schuchert 2006a). *P. leuckarti* has so far never been found in the deep sea.

Among hydroids, a new record of a species regarded as cosmopolitan is hardly remarkable. However, this is the first record of a species of *Protohydra* from South America and from the deep sea. Moreover, no cnidarian had been known until recently to exist beyond the inner continental shelf of Brazil. The purpose of this paper is to report *P. cf. leuckarti* from the Campos Basin, Brazil, and to briefly review the taxonomy, bio-ecology and distribution of the species.

Material and methods

Study area. The Campos Basin, occupying an area of about 100 000 km², occurs on the continental shelf and slope off the states of Espírito Santo (from 20.5°S) and Rio de Janeiro (to 24°S), Brazil (Fig. 1). The continental shelf in this region is 100 km wide, and the slope ranges from 110 m to 3000 m in depth. Bottom features vary all along the Campos Basin. To the north the slope is steeper, with canyons and greater rates of sedimentation due to proximity of discharge from the Paraíba do Sul River (Viana et al. 1998, 2002). According to Viana et al. (1998), more than 70 % of the Campos Basin lies at depths greater than 200 m. Samples of benthos from the Brazilian slope, at depths from 700 to 1900 m, were collected as part of the HABITATS (Heterogeneidade Ambiental da Baía de Campos) Project, coordinated by

CENPES/PETROBRAS (Centro de Pesquisas da PETROBRAS). The sample containing *Protohydra*, reported herein, was collected in the Almirante Câmara Canyon (Lat 21.7 SGS 84, Long 39.9 WGS 84) at a depth of 1030 m (further details were provided by Lavrado et al. 2010).

Sampling. Samples were obtained using a box corer (USNEL Spade Corer MK 1) modified to collect 0.25 m² of sediment ("vegematic" as in Hessler & Jumars 1974 apud Lavrado et al. 2010), and fixed in buffered 4 % formaldehyde solution. In the laboratory, sediment was washed through sieves of 500 µm mesh and sorted under magnification (Lavrado et al. 2010).

Results

Specimens of *Protohydra cf. leuckarti* were found on valves of the pelecypod *Ledella* spp. Study of these molluscs continues because there are four closely related and still undescribed species of the genus in the Campos Basin (Viegas 2012).

Station where the bivalve-hydroid pair was obtained. Hab 9, #Canac 8, R1 (Lat 21.7 SGS 84, Long 39.9 WGS 84), on 6/Feb/2009, 1030 m depth, depth in sediment 0–2 cm, T = 10 °C.

Abbreviations: Hab, Project HABITATS; Canac, Canyon Almirante Câmara; R1, Replicate 1; T, temperature.

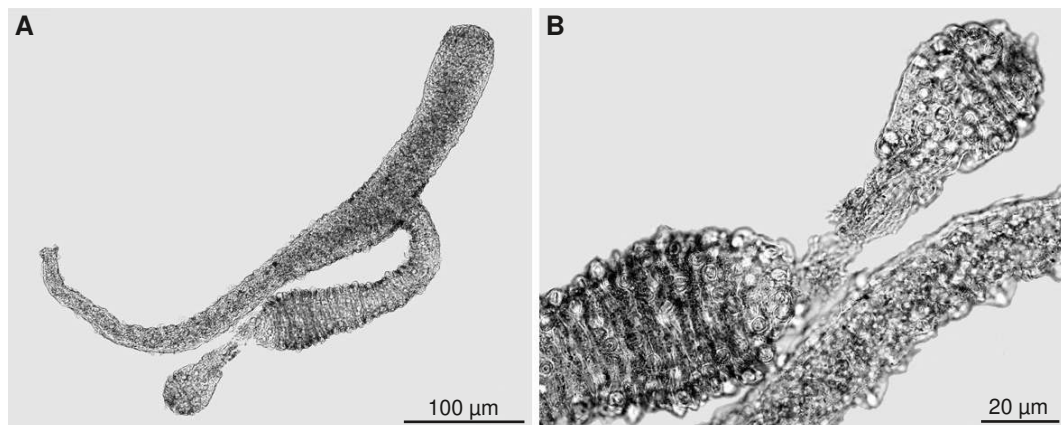


Fig. 2. *Protohydra* cf. *leuckarti* Greeff, 1869. A. two specimens found on a pelecypod shell; B. detail of one of the specimens in the process of transverse fission.

Taxonomic account

Phylum Cnidaria Verrill, 1865
 Class Hydrozoa Owen, 1843
 Order Anthoathecata Cornelius, 1992
 Suborder Capitata Kühn, 1913
 Family Protohydridae Allman, 1888
 Genus *Protohydra* Greeff, 1869

Protohydra cf. *leuckarti* Greeff, 1869 (Fig. 2)

Protohydra leuckarti Greeff, 1869: 37, pls. 4–5.
 Hickson, 1920: 419–424.
 Luther, 1923: 1–23, figs. 1–11.
 Koller, 1927: 97–100, figs. 1–2.
 Westblad, 1935: 152–158, figs. 1–4.
 Weill, 1935: 84–86, fig. V.
 Madsen, 1939: 551–557, fig. 1.
 Ruebush, 1939: 617–618.
 Hyman, 1940: 440, fig. 133A.
 Schulz, 1950a: 53–57.
 Teissier, 1950: 8–43.
 Nyholm, 1951a: 529–530, figs. 1–4.
 Omer-Cooper, 1957: 486.
 Wieser, 1958: 106–108, figs. 1–2.
 Delamare-Deboutteville, 1960: 166–167.
 Omer-Cooper, 1964: 145–150.
 Muus, 1966: 141–160, figs. 1–2.
 Naumov, 1969: 593, fig. 439.
 Clausen, 1971: 1–2.
 Clausen & Salvini-Plawen 1986: 34.
 Thiel, 1988: 267.
 Stepanjants et al., 2000: 155–162.

Bouillon et al., 2004: 84, fig. 47 A–E.
 Schuchert, 2006a: 338–340, fig. 6.
 Kilvington et al., 2008: 1555–1557.
 Piraino et al., 2008: 1640.
 Siebert et al., 2009: 552.
 Giere, 2009: 116.

Type locality. Oostende, Belgium, in tidal pools covered by muddy bottom, with a thin layer of diatoms and debris over it.

Description of the material. Small-sized solitary specimens, with elongate body, length varying from 170 µm to 1.2 mm. Found aggregated, apparently contracted, pale brownish-yellow in color; tentacles and gonophores absent; peristomial edge hemispheroidal; fertile specimens not seen. Nematocysts are stenoteles of two sizes, distributed along the entire body, the largest ones of 15 × 12.5 µm; no isorhizas observed on the material. Under higher magnification the specimens present a clear pseudo-segmentation along the body.

Discussion

Taxonomy. Three species have been assigned in the past to *Protohydra*: *P. leuckarti* Greeff, 1869; *P. caulleryi* Dawydoff, 1930, and *P. psamathe* Omer-Cooper, 1964. Described from specimens collected in Indochina, *P. caulleryi* was recently referred to family Olindiidae (Schuchert 2006a). Moreover *Protohydra psamathe*, discovered in coastal sedi-

ments of south and southeast Africa, has been regarded as a synonym of *P. leuckarti* (Bouillon et al. 2006 apud Piraino et al. 2008). As for the date of Greeff's original description of *P. leuckarti*, authors including Hickson (1920) Luther (1923), Westblad (1930), Madsen (1939), Schulz (1950a), Nyholm (1951a), and Muus (1966), have cited it as 1870. Omer-Cooper (1964) referred to Greeff's paper with a doubtful date, as "1869(1870)". In fact, Greeff's paper was published on 1 December 1869.

In the present study, "cf." is used to designate the hydroid resembling *Protohydra leuckarti* that occurs in the Campos Basin, considering the extensive lacuna existing between this and other *Protohydra* populations in the world. The Brazilian material is morphologically identical to *P. leuckarti* found in the northern hemisphere (Greeff 1869, Hickson 1920, Luther 1923, Westblad, 1935, Madsen 1939, and others). However, there is no definitive proof that the Brazilian species is the same as that from other localities. Populations in Atlantic waters of Europe and North America have mostly been reported from intertidal zones, whereas those from Brazil were found on the continental slope at a depth of 1030 m. While alike morphologically, such a great difference in habitat is probably too wide for a single species. Nevertheless, *P. leuckarti* appears to have a possible cosmopolitan distribution; moreover, as with *Monobrachium parasitum* Mereschkowsky, 1877, recently found in the Campos Basin (Grohmann et al. in press), *P. cf. leuckarti* could have migrated, in this case from the north, via the North Atlantic Deep Water (NADW), a water mass that flows southward and reaches the Campos Basin in deep regions (Viana et al. 1998).

The specimens found in Campos Basin, off the coast of Rio de Janeiro State, apparently only presented stenotele nematocysts but, according to the literature, even when present the isorhiza type is rare. For instance, Omer-Cooper (1964) found only one of these nematocysts on his material. On the other hand, Stepanjants et al. (2000) and Anokhin et al. (2001) (both apud Piraino et al. 2008) found a third type of nematocyst, a macrobasic mastigophore, in live material.

While studying the fauna of sandy beaches and muddy sublittoral zones in the vicinity of the White Sea Biological Station in Russia, Pyataeva et al. (2011) showed the preliminary results of SEM, TEM and sequence information from mitochondrial 16S rDNA of *Protohydra leuckarti* (and

Boreohydra simplex) aligned with a large data set representing many other hydrozoans. These data could, in the future, be used for a detailed comparison of the geographical distributions between northern and southern populations, and could be essential in shedding light on this question.

Bio-ecology. *Protohydra leuckarti* Greeff is one of the best-known cnidarians of the marine meiofauna (Wieser 1958, Delamare-Deboutteville 1960, Higgins & Thiel 1988, Giere 2009). Its life style allows great flexibility in the colonization of habitats.

First found in muddy bottoms of tidal pools, *P. leuckarti* has also been collected in coarse and/or fine sand, with or without a mud fraction (Hickson 1920, Luther 1923, Schulz 1950a), and even on algae (Warwick et al. 1981, Schuchert 2006a, Kilvington et al. 2008). Apparently it is tolerant of wide variations of environmental factors such as salinity, temperature, oxygen content and pollution (Luther 1923, Schultz 1950a, Kilvington et al. 2008). Up to now the species has not been considered specifically depth-restricted, since all bathymetric records were in the range of 0–35 m depth (Purasjoki 1945 apud Muus 1966). In any event, the occurrence of *P. leuckarti* in a canyon at depths of more than 1000 m is surprising. But, the discovery of an unexpected abundance and diversity of planktonic species present in deep-water canyons of the Mediterranean Sea (Gili et al. 1999, Gili et al. 2000), caused by the accumulation of organic matter from the continental shelf and carried by bottom currents, suggests that the benthic fauna of canyons is generally much richer and more abundant than previously thought.

Protohydra leuckarti can adhere to organic or gravel particles by a small basal disc (Luther 1923, Westblad 1935, Madsen 1939), can move freely on the sediment surface, crawling with typical larvae-like movements called "caterpillar movements" (Omer-Cooper 1957, Clausen 1971), or move freely among the grains using movements of the "euglenoid" type (Omer-Cooper 1964). In Campos Basin *Protohydra* was found attached to shells of 2 mm length, sieved from the bottom sediment, by a typical basal disc.

Early investigators considered *Protohydra leuckarti* as an archaic cnidarian, referring to the species as a "Stammform" (Greeff 1869, Hickson 1920, Ruebush 1939 and others) because of its wormlike shape, lack of tentacles and gonophores, and its great plasticity. The small size of the spe-

cies allied to these convergent trends conferring a homogeneous appearance on the interstitial fauna, make it difficult for sorters to recognize the species. It must be remembered that, in broad benthic research projects, most of the fixed samples sorting works are done by technicians and/or by students, that probably don't recognize *Protohydra* as a cnidarian because of its appearance. On the other hand, live specimens crawl on the sediment surface in a manner similar to that of a kinorhynch (Omer-Cooper 1957), which may also confuse the observer. But the presence of nematocysts (the diagnostic characteristic of the phylum Cnidaria) is fundamental in recognizing it (Figs. 2a,b).

Records of *P. leuckarti* tend to be sporadic: from time to time the species may not be found in the same locations where it had been collected previously (Hickson 1920, Omer-Cooper 1964). Its presence in or absence from these sites may be associated with more or fewer predators in the environment (Herman & Heip 1988). At the same time, the species may significantly reduce the numbers of other groups of meiofauna such as nematodes and harpacticoid copepods, especially if these components share the same food items. Besides these groups, its basic diet usually consists of oligochaetes, ostracodes and, in tidal zones, chironomid insects (Hickson 1920, Schulz 1950a, Omer-Cooper 1957). The impact caused by *Protohydra* can be very high, mainly in the summer, when the predation rate has profound consequences for trophic relationships in these communities (Muus 1966, Heip & Smol 1976).

The species is often portrayed in its distended and contracted forms. Feeding behavior, types of nematocysts, histology, and methods of reproduction have also been addressed (Luther 1923, Muus 1966).

In *Protohydra* the rare gonads mature within the body. According to Bouillon & Grohmann (1994), this character is uncommon among the Hydroidomedusae (= Hydroidolina) but is known in some Narcomedusae and is characteristic of the order Actinulida. A gonochoristic species, *P. leuckarti* produces gametes in its epidermis, which then migrate to the interior of the gastrovascular cavity (Hyman 1940). Although Koller (1927) was the first to observe an oocyte within its body, it was Westblad (1935) who documented the process of reproduction involving a fertile female, a mature male, and the first stages of development. Nyholm (1951a) associated the fertile phase of

the species with high temperatures, but Muus (1966) obtained fertile specimens in both summer and winter. Considering the lack of a flagellate planula larval stage in the life cycle of *P. leuckarti* (characteristic of hydrozoans of Aplanulata clade) Pyataeva et al. (2011) proposed the hypothesis of a paedomorphic origin through progenesis.

But, the most common reproductive process in *Protohydra* is by transverse fission (Hickson 1920). Investigators including Thiel (1988) and Schuchert (2006a) suggested that it also reproduces by budding, but Muus (1966) believed that "budding" may be the result of abnormal regeneration following rupture of the body wall after release of an oocyte.

It is common to see aggregating behavior (Westblad 1935: 154), suggesting a "probable copulation". In the present study (Figure 2a), two individuals were observed in contact, but this was interpreted simply as one specimen using the other as a substrate.

Distribution. Considered circumglobal in the temperate zone of the northern hemisphere, on the eastern Atlantic *Protohydra leuckarti* has been reported from Norway, Sweden, Finland, Denmark, Germany, The Netherlands, Scotland, England, the English Channel, and France (Atlantic and Mediterranean coasts). It has also been reported from the Black Sea, the Sea of Azov, the Aral Sea and the White Sea. On the western Pacific it was described from Sea of Japan; on the east Pacific, from North America. It is also known from the Atlantic coast of North America. Up to the present, the species has been mentioned from the southern hemisphere only twice, both times from Africa (see details in Hickson 1920, Luther 1923, Koller 1927, Westblad 1929, Westblad 1935, Madsen 1939, Ruebush 1939, Teissier 1950, Schulz 1950a, Nyholm 1951a, Omer-Cooper 1957, 1964, Wieser 1958, Muus 1966, Naumov 1969, Boaden 1976, Schuchert 2006a, Kilvington et al. 2008, Pyataeva et al. 2011, and others).

Acknowledgements

Thanks are due to MSc Cléo D. C. Oliveira, MSc Natalia P. Benaim and Biol. Diniz C.P. Viegas (Laboratório de Malacologia, Departamento de Zoologia, Instituto de Biologia, UFRJ) for calling our attention to the hydroids associated with Pelecypoda; to Dr Ricardo S. Absalão, MSc Vera M. A. P. da Silva and Dr Janet W. Reid for suggestions; to MSc Alessandra P. Botelho (Instituto de

Biologia, UFPE) and Biol. Valéria L Marques (Museu Nacional, UFRJ) for taking the photographs, and to MSc Rafael B. de Moura for mounting the figures. Miss Daniele Masterson helped with searching for references from some other information sources. The Supervisor of the HABITATS Project, Dr Helena P. Lavrado (Departamento de Biologia Marinha, IB, UFRJ) kindly invited us to study this material. The project as a whole was sponsored by PETROBRAS. Dr. Dale R. Calder (Royal Ontario Museum, Toronto, Canada) critically read the manuscript, helped with valuable suggestions and improved the English. The referees Dr Peter Schuchert and Dr Celia Besteiro also contributed with helpful suggestions.

References

- Boaden, P. J. S. (1976). Soft meiofauna of sand from the delta region of the Rhine, Meuse and Scheldt. *Neth. J. Sea Res.* 10: 461–471.
- Bouillon, J. & P. A. Grohmann (1994). A new interstitial stolonoid hydroid: *Nannocoryne* gen. nov. *mammillia* sp. nov. (Hydrodromedusae, Anthomedusae, Corynidae). *Cah. Biol. mar.* 35: 431–439.
- Bouillon, J., M. D. Medel, F. Pagès, J.-M. Gili, F. Boero & C. Gravili (2004). Fauna of the Mediterranean. Hydrozoa. *Sci. Mar.* 68(Suppl. 2): 5–438.
- Clausen, C. (1971). Interstitial Cnidaria: Present status of their systematics and ecology. *Smithson. Contr. Zool.* 76: 1–8.
- Clausen, C. & L. von Salvini-Plawen (1986). A faunistic, distributional, and ecological synthesis of the world fauna inhabiting subterranean waters. E. J. Brill/Dr. W. Backhuys, Leiden: 34–42.
- Delamare-Deboutteville, C. (1960). Biologie des eaux souterraines littorales et continentales. Herman, Paris (Vie et Milieu Suppl. 9): 740 pp.
- Giere, O. (2009). Meiobenthology. The Microscopic Motile Fauna in Aquatic Sediments. 2nd ed. Springer-Verlag, Berlin: 527 pp.
- Gili, J.-M., J. Bouillon, F. Pagès, A. Palanques & P. Puig (1999). Submarine canyons as habitats of prolific plankton populations: three new deep-sea Hydrodromedusae in the western Mediterranean. *Zool. J. Linn. Soc. Lond.* 125: 313–329.
- Gili, J.-M., F. Pagès, J. Bouillon, A. Palanques, P. Puig, S. Heussner, A. Calafat, M. Canals & A. Monaco (2000). A multidisciplinary approach to the understanding of hydromedusan populations inhabiting Mediterranean submarine canyons. *Deep-Sea Res.* 47: 1513–1533.
- Greiff, R. (1869). *Protohydra leuckarti*. Eine marine Stammform der Coelenteraten. *Z. Wiss. Zool.* 20: 37–54.
- Grohmann, P. A., R. S. Absalão & V. M. A. P. da Silva (in press). First record of *Monobrachium parasitum* Mereschkowsky, 1877 (Cnidaria, Hydrozoa) from Brazil, in the tropical southwestern Atlantic, and its implication for bipolarity concepts. *Journ. Nat. Hist.* (Special Issue).
- Heip, C. & N. Smol (1976). On the importance of *Protohydra leuckarti* as a predator of meiobenthic populations. Pp. 285–296 in Persoone, F. & E. Jaspers (eds.): *Proceedings of the 10th European Marine Biology Symposium vol. 2, Population dynamics of marine organisms in relation with nutrient cycling in shallow waters.* Universa Press, Wetteren.
- Herman, P. M. J. & C. Heip (1988). On the use of meiofauna in ecological monitoring: Who needs taxonomy? *Mar. Pollut. Bull.* 19: 665–668.
- Hickson, S. J. (1920). On the occurrence of *Protohydra* in England. *Q. Jl microsc. Soc.* 64: 419–424.
- Higgins, R. P. & H. Thiel (eds.) (1988). *Introduction to the Study of Meiofauna.* Smithsonian Inst. Press, Washington, D.C.: 488 pp.
- Hyman, L. H. (1940). *The Invertebrates: Protozoa through Ctenophora.* 1st ed. McGraw-Hill Company, New York: 726 pp.
- Kilvington, C. C., A. G. Collins, I. A. Kosevich, S. V. Pyataeva & E. A. Robson (2008). *Protohydra leuckarti* near Plymouth. *J. mar. biol. Ass. U.K.* 88 (8S1): 1555–1557.
- Koller, G. (1927). Geschlechtliche Fortpflanzung der *Protohydra*. *Zool. Anz.* 73(5/8): 97–100.
- Lavrado, H. P., A. C. dos S. Brasil, M. P. C. Fernandez & L. de S. Campos (2010). Aspectos gerais da macrofauna bentônica da Bacia de Campos. Pp. 17–27 in: Lavrado, H. P. & A. C. dos S. Brasil (orgs.): *Biodiversidade da Região Oceânica Profunda da Bacia de Campos*, 1st ed., Rio de Janeiro, SAGServ ISBN 978-85-6352-300-6.
- Luther, A. (1923). Ueber das Vorkommen von *Protohydra leuckarti* Greeff bei Tvärminne nebst komplettierenden Bemerkungen über den Bau dieses Polypen. *Acta Soc. Fauna Flora fenn.* 52(3): 1–23.
- Madsen, H. (1939). *Protohydra leuckarti* Greeff, neu für Dänemark. *Vidensk. Medd. Naturh. Foren. Kbh.* 103: 551–557.
- Muus, K. (1966). Notes on the biology of *Protohydra leuckarti* Greeff (Hydroidea, Protohydridae). *Ophelia* 3: 141–150.
- Naumov, D. V. (1969). Hydroids and Hydromedusae of the USSR. *Zoological Institute of the Academy of Sciences of the USSR 70* (Translated from Russian by the Israel Program for Scientific Translations): 660 pp.
- Nyholm, K. G. (1951a). A contribution to study of the sexual phase of *Protohydra leuckarti*. *Ark. Zool.* 2(6): 529–530.
- Omer-Cooper, J. (1957). *Protohydra* and *Kinoryncha* in Africa. *Nature* 179: 486.
- (1964). On *Protohydra psamathe* n. sp. from South Africa. *J. Linn. Soc. (Zool.)* 45(304): 145–150.
- Pyataeva, S., A. Collins, T. Neretina, I. Kosevich & N. Muge. (2011). Meiobenthic cnidarians *Protohydra leuckarti* Greeff, 1870 and *Boreohydra simplex* Westblad, 1937 (Cnidaria, Hydrozoa): integrated

- approach based on fine morphology and molecular analysis. 14th International Meiofauna Conference. Ghent, Belgium. Abstract: 65.
- Piraino, S., B. A. Bluhm, R. Gradinger & F. Boero (2008). *Sympagohydra tuuli* gen. nov. and sp. nov. (Cnidaria, Hydrozoa), a cool hydroid from the Arctic sea ice. *J. Mar. Biol. Ass. U.K.* 88(8): 1637-1641.
- Ruebush, T. (1939). The occurrence of *Protohydra* on the east coast of North America. *Science* 90(2348): 617-618.
- Schuchert, P. (2006a). The European athecate hydroids and their medusae (Hydrozoa, Cnidaria): Capitata Part 1. *Rev. Suisse Zool.* 113(2): 325-410.
- Schulz, E. (1950a). Zur Oekologie von *Protohydra leuckarti* Greef. (Studien an Hydrozoa, I). *Kiel. Meeresforsch.* 7(1): 53-57.
- Siebert, S., F. Anton-Erxleben, R. Kiko & M. Kramer (2009). *Sympagohydra tuuli* (Cnidaria, Hydrozoa): first report from sea ice of the central Arctic Ocean and insights into histology, reproduction and locomotion. *Mar. Biol.* 156: 541-554.
- Stepanjants, S. D., B. A. Anokhin & V. G. Kuznetsova (2000). Hydrida composition and place in the system of Hydroidea (Cnidaria: Hydrozoa). *Trudi Zoologicheskogo Instituta RAN/Proc. Zool. Inst. Zool. Sess. Ann. Rep.* 286: 155-162.
- Teissier, G. (1950). Cnidaires et cténaires. *Inventaire de la Faune Marine de Roscoff I*: 8-43.
- Thiel, H. (1988). Cnidaria. In: Higgins, R. P. & H. Thiel (eds.): *Introduction to the Study of Meiofauna*. *Smiths. Inst. Press, Washington, D.C.*: 488 pp.
- Viana, A. R., W. Almeida Jr & C. W. Almeida (2002). Upper slope sands: Late Quaternary shallow-water sandy contourities of Campos Basin, SW Atlantic Margin. *Geol. Soc. Lond. Mem.* 22: 261-270.
- Viana, A. R., J. C. Faugères, R. O. Kowsmann, J. A. M. Lima, L. F. G. Caddah & J. G. Rizzo (1998). Hydrology, morphology and sedimentology of the Campos continental margin, offshore Brazil. *Sediment. Geol.* 115: 133-157.
- Viegas, D. C. P. (2012). Discriminação morfológica de quatro morfoespécies de *Ledella* Verrill & Bush, 1897 (Mollusca: Pelecypoda: Nuculanidae) do litoral brasileiro. Universidade Federal do Rio de Janeiro, Instituto de Biologia (Bachelor's Monograph): 48 pp.
- Warwick, R. M., J. T. Davey, J. M. Gee & C. L. George (1981). Faunistic control of *Enteromorpha* blooms: a field experiment. *J. Exp. Mar. Biol. Ecol.* 56(1): 23-31.
- Weill, R. (1935). *Halammohydra* Remane, genre d'hydrozoaires aberrant. Son cnidome et sa position taxonomique: Affinités avec les Siphonophores chondrophorides et avec *Protohydra Leuckarti* Greeff. *B. Soc. Zool. Fr.* 60: 73-87.
- Westblad, E. (1929). *Protohydra Leuckarti* Greeff, an der schwedischen Küste entdeckt. *Ark. Zool.* 21 B(4): 1-4.
- (1935). Neue Beobachtungen über *Protohydra*. *Zool. Anz.* 111: 152-158.
- Wieser, W. (1958). Occurrence of *Protohydra leuckarti* in Puget Sound. *Pac. Sci.* 12(1): 106-108.

