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Diversity of freshwater hydrozoans from Neotropical region: an annotated inventory of species

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ABSTRACT

Introduction: Worldwide, six genera of the class Hydrozoa are recognized in continental waters: the cosmopolitan *Hydra*, the colonial *Cordylophora* and *Pachycordyle*, the medusae *Craspedacusta* and *Limnocnida* and the little polyp *Calpasoma*. Even though interest in cnidarians has grown in recent years, those restricted to freshwater continue to be relegated and there is even little published information on the ubiquity of certain species. In the Neotropical region, knowledge about its distribution is still very scarce.

Methods: We reviewed the global literature on the subject and different online database platforms, presenting in this work a nomenclator, including discussions of the status of some species and provide the most recent identification key.

Results: This analysis reveals that in 15 countries corresponding to the Neotropical region, the finding of freshwater hydrozoans has been reported. Panama, Brazil and Argentina are the countries with the highest number of reports.

Conclusions: The heterogeneity of environments where these genera have been found (from the Strait of Magellan to Mexico) offers a clear vision of their wide distribution and great adaptability to different environments. This study evidence the knowledge gap that still exists about the Neotropical freshwater hydrozoans and the importance of systematizing the current information about their distribution, biology and ecology, especially for those species considered invasive.

Key words: Cnidaria; inland waters; Neotropical region; freshwater species.

RESUMEN

Diversidad de hidrozoos de agua dulce de la región Neotropical: un inventario comentado de especies

Introducción: A nivel mundial, se reconocen seis géneros de hidrozoos de agua dulce: la cosmopolita *Hydra*, los pólipos coloniales *Cordylophora* y *Pachycordyle*, las medusas *Craspedacusta* y *Limnocnida* y el pequeño pólipo *Calpasoma*. A pesar de que el interés por los cnidarios ha crecido en los últimos años, los grupos restringidos a agua dulce siguen relegados, hay poca información sobre la ubicuidad de ciertas especies, o los datos no han sido publicados oficialmente. En la región Neotropical el conocimiento de la distribución de este grupo zoológico aún continúa siendo escaso.



Métodos: Analizamos la literatura mundial específica y diferentes bases de datos en línea, presentando en este trabajo un nomenclador, las claves de identificación más recientes, incluyendo, además, discusiones sobre el estado de algunas especies.

Resultados: Este análisis revela que al menos 15 países pertenecientes a la región Neotropical contienen reportes de hidrozoos dulceacuícolas. Panamá, Brasil y Argentina son los países con mayor número de hallazgos.

Conclusiones: La disparidad de ambientes donde estos géneros han sido hallados (desde el Estrecho de Magallanes hasta México) ofrece una clara visión de su amplia distribución y su gran adaptabilidad a diferentes ambientes. Revela el vacío de información que aún existe sobre estos organismos dulceacuícolas, y la importancia de retomar esta línea de investigación, para ampliar el conocimiento sobre su distribución, biología y ecología, especialmente para aquellas especies consideradas invasoras.

Palabras clave: Cnidarios; aguas continentales; región Neotropical; especies de agua dulce.

INTRODUCTION

Global diversity of inland waters cnidarians, excepting for Endocnidozoa, is low. It is comprised for less than 40 species from phylogenetically distinct groups. These organisms live in nearly all types of freshwater environments and are distributed in all continents, except Antarctica, but only few species are cosmopolitan (Jankowski et al., 2008). The freshwater species from the class Hydrozoa fall into phylogenetically disparate groups: the cosmopolitan *Hydra* sp., the simple and solitary polyps without medusae; Cordylophorinae, the colonial hydroids *Cordylophora* sp. and *Pachycordyle* sp.; the freshwater medusae *Craspedacusta* sp. and *Limnognathia* sp. and the enigmatic polyp *Calpasoma* sp. (Bouillon & Boero, 2000; Collins, 2002). The genera *Pachycordyle* sp. and *Limnognathia* sp. are not represented in the Neotropical region (Dumont, 1994).

Freshwater hydrozoans in the Neotropical region, have been known from 1858 with one record of *Cordylophora* sp, from Brazil made by Van Beneden. The works of Burger (1906), Smith (1925) and Froehlich (1963) cited for the first time specimens of *Hydra* sp., *Craspedacusta* sp. and *Calpasoma* sp., respectively. However, there is still a significant knowledge gap about the distribution of these genera.

In this review, the specific bibliography of *Calpasoma* sp., *Cordylophora* sp., *Craspedacusta*

sp. and *Hydra* sp. corresponding to the Neotropical region was analyzed, including the entire South American continent, Central America, the Antilles and Mexico. The main information extracted was geographic distribution and diagnostic characteristics. As a result of this review, we present a checklist's classification following the last update of WoRMS of the taxonomic classification, the most recent identification keys and discussions of the status of some species.

The main objective of this review is to identify the existing knowledge in the genera of freshwater hydrozoans, analyze and synthesize them, establishing a solid base for future research.

The compiled information comes from scientific literature and the online databases GBIF (Global Biodiversity Information Facility: <http://www.gbif.org>), THL (The Hydra Library: <http://www.biology.pomona.edu/martinez/library.html>), BHL (Biodiversity Heritage Library: www.biodiversitylibrary.org), SNRD (Sistema Nacional de Repositorios Digitales: <https://repositoriosdigitales.mincyt.gob.ar/vufind/>), WoRMS (World Hydrozoa Databases belonging to World Register of Marine Species: www.marinespecies.org/hydrozoa) (Schuchert, 2022) and observations from iNaturalist (www.inaturalist.org).

Classification and checklist of freshwater hydrozoans from the Neotropical region

Phylum Cnidaria Hatschek, 1888**Class** Hydrozoa Owen 1843**Subclass** Trachylinae Haeckel, 1879**Order** Limnomedusae Kramp, 1938**Family** Olindiidae Haeckel, 1879**Genus** *Calpasoma* Fuhrmann, 1939*Calpasoma dactylopterum* Fuhrmann, 1939**Genus** *Craspedacusta* Lankester, 1880*Craspedacusta sowerbii* Lankester, 1880**Subclass** Hydroidolina Collins, 2000**Order** Anthoathecata Cornelius, 1992**Suborder** Filifera Kühn, 1913**Family** Cordylophoridae von Lendenfeld, 1885**Genus** *Cordylophora* Allman, 1844*Cordylophora caspia* Pallas, 1771**Suborder** Aplanulata Collins, Winkelman, Hadrys & Schierwater, 2005**Family** Hydridae Dana, 1846**Genus** *Hydra* Linnaeus, 1758*Hydra viridissima* Pallas, 1766*Hydra vulgaris* Pallas, 1766*Hydra magellanica* Schulze, 1927*Hydra pseudoligactis* Hyman, 1931*Hydra paranensis* Cernovitov, 1935*Hydra iheringi* Cordero, 1939*Hydra thomsoni* Cordero, 1941*Hydra plagiodesmica*, Dioni 1968*Hydra intermedia* Carvalho-Whole, 1978*Hydra salmacidis* Lang da Silveira, 1996*H. vulgaris pedunculata* Deserti, Zamponi & Escalante, 2011**Remarks of *Calpasoma dactylopterum***

Fuhrmann, 1939: It has been referred in some reviews as a tentaculate form of *Craspedacusta* sp., some authors have even observed the transformation of the *Craspedacusta* sp. polypoid into a *Calpasoma*-like polyp (Holstein & Emschermann, 1995). The reproductive experiments developed by Spira (1964) and Matthews (1966), led them to believe that they were different species. However, Jankowski (2001) considered at least one form of *Calpasoma* sp. to be congeneric with *Craspedacusta* sp., besides in all other studies where *Craspedacusta* sp. polyps have been cultured, this conversion has never been observed (Kuhl, 1947; Lytle, 1961; McClary, 1959; Reisinger, 1957). This species

lives attached to plant substrates in natural or artificial ponds. These small tentaculate polyps, which rarely exceed a millimeter in length, are solitary and reproduce asexually originating propangles from their tentacles (Buchert, 1960; Dioni, 1974; Matthews, 1966; Rahat & Campbell, 1974).

The genus *Calpasoma* sp. has only been found so far in three countries: Argentina, Brazil and Uruguay (Table 1). All these observations are longstanding, the most recent dates from 1983 from Brazil, however-morphological descriptions are quite accurate.

Remarks of *Cordylophora caspia* Pallas, 1771: Clonal and athecate hydroid with medusa



Table 1

Calposoma dactylopterum Fhurmann, 1939 from Argentina, Uruguay and Brazil. (*) No information.

Country	Region	Morphological description	Author
Argentina	University of Buenos Aires (vegetation from Corrientes)	Small polyps (0,4 mm in length). Hyaline tentacles. Basitrich eurytele. Small propangles	Dioni (1974)
Uruguay	Rodó Park (artificial pond) Montevideo	Same characteristics as Argentine polyps.	Dioni (1974)
Brazil	University City of Sao Pablo	Light grey polyps (0.5 mm in length). Hyaline tentacles. Consider the polypoid form of <i>Craspedacusta</i>	Froehlich (1963)
	Southeast of Sao Paulo state	(*)	Domaneschi & Coneglian (1983)

stage lacking (Pennak, 1989). Reproduces sexually by new free-swimming planula larvae. It is dioecious—with gonophores containing eggs or sperm (Folino, 2000). Colonies are polymorphic and grow by adding hydrants to hydrocauli on the upright branches and extending the stolon or hydrorhiza (Jormalainen et al., 1994). This organism is able to survive unfavorable environmental conditions via spheres of coenosarcs tissue, called menonts, which regenerate when conditions are restored (Roos, 1979). This survival strategy and the ability to adapt to a wide salinity range contribute to its current large distribution, considered in many regions as an invasive species (CABI Digital Library, 2016).

There are eleven records of *C. caspia* from Argentina, Chile, Uruguay and Brazil (Table 2). According to Roch (1924) the first record of *C. caspia* from Brazil was made by van Beneden in 1858. Therefore, Silveira & Boscolo (1996) considered it doubtful, then Haddad & Nakatani (1996) made the first official record 133 years later.

In Panama *C. caspia* was reported in different regions of the Panama Canal (Folino-Rorem et al., 2009; Hildebrand, 1939; Jones & Rützler, 1975). However, none of the records provide morphological information associated with the specimens.

The oldest report of *C. caspia*, from 1925, is in the database GBIF, it was collected by Hildebrand in Gatun locks of the Panama Bay and deposited in the Smithsonian National Museum of Natural History (NMNH) (Orrell, 2022). The specimens officially cited in Hildebrand (1939)

correspond to samples collected ten years later, during 1935 and 1937. Other 20 records correspond to specimens collected in the lower east chamber of Gatun locks, one from Gatun Lake, At Air Strip NW of Gamboa, and another ten from Panama Bay, Pedro Miguel locks. The specimens of these 31 records are deposited in NMNH (Orrell, 2022). These records do not include morphological information. The references of the seven records corresponding to Mexico (six of them without morphological information) and the only one from Colombia are included in Table 2.

Remarks of *Craspedacusta sowerbii* Lankester, 1880 [= *Limnocodium Allman, 1880* = *Mycrohydra Potts, 1885*, according to Schuchert (2022)]: Freshwater hydrozoan commonly observed in the medusa stage. The species blooms seasonally, having mainly a subtropical to temperate distribution (Gasith et al., 2011; Jakovčev-Todorović et al., 2010; Jankowski, 2001; Jankowski et al., 2008; Karaouzas et al., 2015). Its life cycle includes both polyp (assuming asexual reproduction) and free-swimming stages (involved in sexual reproduction) (Gasith et al., 2011). The free swimming-pelagic stage is sporadic, lasting only few weeks, usually during the late summer and autumn (Minchin et al., 2016). The polyp stage is often overlooked because of its small size (usually less than one millimeter) and both stages are rarely reported together (Failla et al., 2017).

The polyp form, previously described as *Microhydra ryderi* (Potts, 1885), are cylindrical, without tentacles. They are commonly solitary

Table 2
Cordylophora caspia Pallas, 1771 from Argentina, Uruguay, Chile, Brazil, Colombia and Mexico. (*) No information.

Country	Region	Morphological description	Author
Argentina	Río Santiago (tributary of Río de la Plata estuary)	Slightly and whitish colony. Hydrants 11-17 mm length. 8 to 28 fine and filiform tentacles. Hydrocauli base with rings. Abundant oval female gonophores	Gaggero (1923)
	Chascomús lake (Río Salado basin)	<i>Albicola</i> form. Slightly and yellowish hydrocauli (0.18 mm diameter). Stenoteles and desmonemes.	Ringuélet & Olivier (1954)
	Lobos Lake (Río Salado basin)	<i>Lacustris</i> form. Dark brown hydrocauli and stolons (0.155 mm diameter). 15-20 tentacles. Abundant round and oval gonophores (one to eight embryos)	Ringuélet & Olivier (1954)
	Puerto Yerúa (Entre Ríos)	(*)	Liotta & Wagner (2003)
	Nahuel Rucá lagoon (Buenos Aires)	<i>Albicola</i> form. Gastrozooids 1.21 to 3.95 mm length. Four to seven fine and filiform tentacles. Cylindrical stolons. Hydrocauli base with rings. Desmonemes and heterotrichous microbasic eurytele. Menont (12.5 µm in diameter).	Deserti et al. (2015)
Uruguay	Las Brujas stream, tributary of the Santa Lucia River (Montevideo)	<i>Albicola</i> form. Dark, brown and cylindrical stolons. Fusiform gastrozooids with 15 tentacles.	Cordero (1941b)
Chile	Fjord Comau (Los Lagos region)	(*)	Galea (2007)
Brazil	Paraná river, Foz do Iguaçu (Paraná)	Hydrocauli 0.3 to 2 cm length. Abundant male and female gonophores	Haddad & Nakatani (1996)
	Estuary of Rio Ubatuba (Sao Paulo)	Male and female colonies. Hydrocauli up to 3.5 cm length. 9 to 16 tentacles. Elliptical gonophores.	Silveira & Boscolo (1996)
	Funil Plant, Itatiaia (Rio de Janeiro)	Regularly branched colonies. Hydrocauli base with rings. 16-20 tentacles. Gonophores ovate invested in a gonangium-like extension of perisarc.	Grohmann (2008)
	Reservoir Governador José Richa (Paraná)	(*)	Borges (2008) & da Silva (2021)
Colombia	Santa Marta	Branched colonies. 12-16 tentacles per hydrant. Oval gonophores	Wedler (2017)
Mexico	Mandinga lagoon (Veracruz)	(*)	Rioja (1959)
	San Juan river (Nuevo León)	(*)	Guajardo et al. (1987)
	Mandinga Estuary (Veracruz)	(*)	López-Ochoterena & Madrazo-Garibay (1989)
	Gulf of Mexico, Veracruz and Campeche	(*)	Okolodkov et al. (2007)
	Gulf of Mexico	(*) Authors consider a nonindigenous species	Calder & Cairns (2009)
	Veracruz Reef System National Protected Area (Gulf of Mexico)	Monopodial colony. Pale pink or yellowish hydrants. 14-27 scattered filiform tentacles. Eurytele and desmoneme.	Jerónimo (2013)
	Cayo Arenas Reef (Gulf of Mexico)	(*)	Mendoza-Becerril et al. (2020)



or form small colonies of two to four polyps (Russell, 1953). As explained above, *Calpasoma* sp. is usually considered to be the polypoid tentacular form of *Craspedacusta* sp.

The species *C. sowerbii* develops a resting stage under unfavorable environmental conditions, an adaptation that confers it high survival potential and enhances its dispersal capacity. There is a consensus about its human mediated

introduction through fish and aquatic plants and it is considered globally as an invasive species of lakes (Dumont, 1994; Fritz et al., 2009; Marsden & Hauser, 2009).-

In South America, this genus has been found in Argentina, Brazil, Uruguay, Chile and Venezuela (Table 3). Brazil and Chile, respectively, contain the greatest number of records, however nine of the 13 total citations from

Table 3

Craspedacusta sowerbii Lankester, 1880 from Argentina, Uruguay, Chile, Brazil, Venezuela, Mexico, Panama, Belize and Costa Rica. (*) No information.

Country	Region	Morphological description	Author
Argentina	Lake of General San Martin Park (Mendoza)	Female adults. 11 mm umbrellar diameter. Mouth with four lips. Four perradial channels. Four larger perradial tentacles. First, second and third order tentacles. Velum. Heterotrichous microbasic eurytele. Oval gonads.	Ringuelet (1950)
	Lake of General San Martin Park (Mendoza)	Reexamination of material deposited by Ringuelet (1950) in La Plata Museum	Vannucci & Tundisi (1962)
	La Florida (San Luis) and Horco Molle reserve (Tucumán)	(*)	Richard (1990)
	Rio III Reservoir (Córdoba)	Female specimens. Medusae 7-16 mm diameter. Gonads with <i>pistolera</i> form.	Boltovskoy & Battistoni (1981)
	Valle Medio (Rio Negro)	(*) Validated by GBIF	Tormo (2014)
Uruguay	Artigas and Durazno departments	Female medusae 8-10 mm diameter and 4-5 mm high	Mañé Garzón & Carbonell (1971)
	Del Medio Lagoon (upper basin of the Santa Lucía river) (Florida department)	Live colony (666.5-1 152.2 µm length). Solitary polyps (450-663 µm length). Transparent hydroids without tentacles. Nematocysts surrounding the hypostome forming a spherical capitulum. Frustules elongated and rod-like	Failla Siquier et al. (2017)
Chile	Tranque Marga-Marga (Valparaiso)	Medusae 5-10 mm diameter. Four to seven series of tentacles	Porter & Schmitt (1942)
	Valparaiso	(*)	Vannucci & Tundisi (1962)
	Laguna Grande de San Pedro (Concepción)	Adult female medusae 10.21 diameter. Velum and manubrium. Four perradial channels. Oval gonads. First, second and third order tentacles. Oval and elongated nematocysts	Quezada (1969)
	Playa Tranquila, Lanalhue lake, Contulmo (Arauco)	Medusae 8-15 mm diameter	Quezada & Aurora (1973)
	Peñuelas reservoir (Valparaiso)	(*)	Schmid-Araya & Zúñiga (1992)
	Carilafquén lagoon (Araucania region)	(*)	Figueroa & de los Ríos (2010)
	Illahuapi lagoon, De Los Ríos (Ranco)	Medusae 4-20 mm diameter. Four types of tentacles. Four gonads.	Caputo Galarce et al. (2013, 2018)

Country	Region	Morphological description	Author
	Del Bío-Bío, De La Araucanía and De Los Ríos region	(*) Single haplotype.	Fuentes (2015)
	Santa Elena (Bío-Bío region)	Medusae 2.3 cm length. Four visible gonads	Fraire-Pacheco et al. (2017)
	Mediterranean and Valdivian ecoregion	(*) Single, unique <i>C. sowerbii</i> haplotype in both ecoregions.	Fuentes et al. (2019)
	Lake Illahuapi and San Pedro (Valdivian ecoregion)	Illahuapi medusae 1.6 and 2.2 cm ² umbrellar area, slightly brownish gonads. San Pedro medusae 1.4 and 3.2 cm ² umbrellar area, whitish gonads. Two studied lakes host clonal population	Caputo Galarce et al. (2021)
	Los Lagos region (Llanquihue)	(*) Collected in 2020. Validated by GBIF	iNaturalist
Brazil	Porto Alegre (Rio Grande do Sul)	(*) Polyps and medusae.	Gliesch (1930)
	Belo Horizonte (Minas Gerais)	(*) Only female medusae	Martins (1941)
	Belo Horizonte	(*)	Sawaya (1957)
	São Paulo	(*) Polypoid form	Froehlich (1963)
	Minas Gerais	(*)	Bandeira de Mello et al. (1971)
	Curitiba	(*)	Loyola e Silva & Oliveira (1988)
	Serra da Mesa HPP Reservoir (Goiás)	(*)	De Filippo et al. (1999)
	Lajeado UHE	(*)	Reis Pereira (2002)
	Lagoa Misteriosa (Mato Grosso do Sul)	Juvenile 7.8 mm diameter. Adults 25 mm diameter	Silva & Roche (2007)
	14 de Julho Plant, Cotiporã (Rio Grande do Sul)	Medusae 5- 3 mm diameter	Schwarzbold et al. (2010)
	Lagoa Azul, Prados (Minas Gerais state)	(*)	Souza & Ladeira (2011)
	Passo Fundo (Rio Grande do Sul)	Medusae 8.1-11.5 mm diameter. Nematocysts in groups on papillae. Marginal cnidocyst ring. Four simple radial channels. Hanging, pouchlike gonads on radial channels.	Savaris et al. (2013)
	São Valentim (Rio Grande do Sul)	Medusae 5-15 mm diameter	Restello et al. (2015)
Venezuela	Lagartijo Reservoir	(*)	Infante & Infante (1994)
	Lagartijo and Camatagua reservoir, Aragua and Guanapito (Guárico)	(*)	Guajardo et al. (1987)
Mexico	Rodrigo Gomerza reservoir (Nuevo León)	(*)	Guajardo et al. (1987)
	Adolfo López Mateos reservoir, Badiraguato (Sinaloa)	Female medusae 10-19 mm bell diameter. iNaturalist reports <i>C. sowerbii</i> also for this site. Validated by GBIF	Moreno-Leon & Ortega-Rubio (2009)
Panama	Gatun Lake, Panama Canal	Male medusae 9-19 mm diameter	Smith (1925)
	Gatun Lake, La Chorrera, Panama Oeste	(*) Collected in 2019. Validated by GBIF	iNaturalist
Belize	Green Hills Butterfly Ranch (Cayo District)	(*) Collected in 2124. Not yet validated.	iNaturalist
Costa Rica	Arenal reservoir (Guanacaste)	(*)	Murillo (1989)



Brazil, do not contain any type of morphological information. The second oldest record of *C. sowerbii* from Brazil was made for Martins (1941) and he was the first author to assume that this species has been introduced to the country through fish imported from Europe. The records from Brazil, Mexico, Panama, Belize and Costa Rica are listed in Table 3.

Remarks of *Hydra Linnaeus, 1758* [= *Pelmatohydra Schulze, 1914* = *Clorohydra Schulze, 1914* according to Schuchert (2022)]: Sessile and solitary polyps that occurs in all continents, except Antarctica (Jankowski et al., 2008; Kaliszewicz, 2013). This genus can be found in any reasonably unpolluted body of freshwater during any season (Bossert &

Galliot, 2012). It is usually more abundant in lentic waters, often attached to submerged and floating macrophytes (Elliot et al., 1997; Schwartz et al., 1983).

All *Hydra* sp. species constitute a monophyletic clade (Collins et al., 2006) and are clustered into four morphological groups: *viridissima*, *vulgaris*, *oligactis*, and *braueri*, corroborated by DNA analyses (Campbell, 1983; Martínez et al., 2010).

Table 4 lists the most relevant results for the genus *Hydra* in the mentioned study area. Additionally, for Argentina, another four records refer to *Hydra plagiodesmica*, but do not provide morphological details (Alzugaray et al., 2013, 2019, 2021; Poggio Herrero et al., 2014). Also, *Hydra* have been reported in tributaries

Table 4

Hydra Linnaeus, 1758 from Argentina, Uruguay, Chile, Brazil, Paraguay, Venezuela, Peru, Ecuador, Colombia, Panama, Mexico, Costa Rica and Trinidad and Tobago. (*) No information.

Country	Region	Specie	Morphological description	Author
Argentina	Río Salado (Santa Fé)	<i>Hydra plagiodesmica</i>	Green. Column 0-12 mm length. Six to eight fine and long tentacles with three distinctive growth patterns. Protandric hermaphrodite. Embryotheca with penta or hexagonal prisms. Pyriform stenoteles, oval desmonemes, oval and elongated holotrichous isorhiza	Dioni (1968)
	Los Padres lagoon (Buenos Aires)	<i>Hydra viridissima</i>	Green. Column 1.82-3.10 mm length. Five or six short, transparent and moniliform tentacles. Pyriform stenoteles, spherical desmonemes, seed-shaped atrichous isorhiza and two morphotypes of holotrichous isorhiza	Deserti (2016)
	Nahuel Rucá lagoon (Buenos Aires)	<i>Hydra viridissima</i>	Green. Column 0.60-2.89 mm length. Six to eight tentacles. Holotrichous isorhiza slightly larger than the stenoteles.	Deserti (2016)
	Los Padres lagoon (Buenos Aires)	<i>Hydra vulgaris</i>	Brown. Column 1.98-9.88 mm length. Six to nine moniliform large tentacles. Dioecious. Round embryotheca. Holotrichous isorhiza with paramecium shape	Deserti, & Zamponi (2011)
	La Brava (Buenos Aires)	<i>Hydra vulgaris</i>	Brown. Medium-sized. Five to eight large, transparent and moniliform tentacles with discontinuous pattern growth. Separate sexes.	Deserti, (2016)
	Nahuel Rucá (Buenos Aires)	<i>Hydra vulgaris</i>	Five to seven tentacles. Same characteristic observed in La Brava	Deserti, (2016)

Country	Region	Specie	Morphological description	Author
	Los Padres, Nahuel Rucá, La Brava lagoons (Buenos Aires)	<i>Hydra vulgaris pedunculata</i>	Brown. Stalk. Column 1.97-9.88 mm length. Six or seven transparent, moniliform large tentacles with growth pattern discontinuous.	Deserti et al. (2011) and Deserti, (2016)
	Nahuel Rucá (Buenos Aires)	<i>Hydra pseudoligactis</i>	Brown. Column 2.12-5.78 mm length. Stalk. Six to nine transparent, moniliform and large tentacles with pattern growth typical of <i>braueri</i> group.	Deserti et al. (2012)
Uruguay	Santiago Vasquez, Bellaca Canyon, stream Miguelete and Arrozal Treinta y Tres	<i>Chlorohydra viridissima</i>	Green. Columns 0.5-5.5 mm in length. Seven to ten tentacles. Some specimens had simultaneously testes and ovaries. Ootheca surrounded by a thin capsule and attached by a conical funiculus to a broad rim.	Cordero (1941b)
	Santiago Vasquez, Bellaca Canyon, stream Miguelete	<i>Hydra attenuata thomsoni</i>	Orange to red. Straight column 4-12 mm in length. Six to nine large tentacles with pattern growth discontinuous. Stenoteles with two measurements, pyriform desmonemes, elliptical holotrichous isorhiza and oval atrichous isorhiza. Dioecius. Embryotheca with spines	Cordero (1941b)
Chile	Santiago de Chile	<i>Hydra grisea</i>	Orange. Column 14 mm in length. Six to ten large tentacles. Unclear description of nematocysts (measurements refer to stenoteles, but drawings to atrichous isorhiza)	Burger (1906)
	Ñuñoa near Santiago de Chile	<i>Hydra viridis</i>	Green. Columns up to 6 mm in length. Eight to ten tentacles. Only highlights the longest stinging capsules (we assume that it refers to stenoteles)	Burger (1906)
	Strait of Magellan (Punta Arenas)	<i>Hydra magellanica</i>	Small stenoteles, oval holotrichous ishorhiza, elongated and oval atrichous isorhiza	Schulze (1927)
Brazil	Pernambuco state	<i>Hydra</i> sp.	(*)	Schubart (1938)
	Ceará state	<i>Hydra viridissima</i>	(*) Green	Cordero (1939)
	Alagôas, Paraíba and Ceará states	<i>Hydra iheringi</i>	Orange. Column 3-6 mm length. Four to six tentacles	Cordero (1939)
	São Paulo state	<i>Hydra viridissima</i>	Green. Column 1.55 mm length. Five to nine short tentacles. Separated sexes	Carvalho Whole (1978)
	São Paulo state	<i>Hydra intermedia</i>	Brown. Column 2-12 mm length. Five to nine short tentacles, arise on buds successively. Dioecius. Embryotheca with short spines	Carvalho Whole (1978)
	University of São Carlos, (São Paulo state)	<i>Hydra viridissima</i>	Green. Column 0.8-2 mm length	Massaro & Rocha (2008)



Country	Region	Specie	Morphological description	Author
	São Paulo state	<i>Hydra salmacidis</i>	Brown. Columns 8.6-12.5 mm length. Four to eight filiform tentacles. Pattern growth simultaneous. Monoecious, protandrous with sex reversal. Rounded embryotheca with small spines. Stenotele larger than other types	Silveira et al. (1997)
Paraguay	Río Paraná	<i>Hydra paranensis</i>	Light yellowish. Columns 4-5 mm length. Oval stenoteles, oval and elongated holotrichous isorhiza	Cernosvitov (1935)
	Hernandarias (Alto Paraná)	<i>Hydra</i> sp.	(*) Collected in 2016. Not yet validated	iNaturalist
Venezuela	Paraiso (Caracas)	<i>Hydra viridissima</i>	Green. Column 1-2 mm length. Monoecius	Cordero (1941b)
	Paraiso (Caracas)	<i>Hydra</i> sp.	Pale yellow. Column up to 5 mm length. Five to seven tentacles with simultaneous growth. Oval stenoteles, desmonemes and atrichous ishorhiza, oval and elongated holotrichous isorhiza. Dioecious	Cordero (1941b)
Peru	Ojo del Milagro, Characato district (Arequipa)	<i>Hydra vulgaris</i>	(*)	Huarachi & González (2012)
	ACTS Field Station and Canopy Walkway, Maynas (Loreto region)	<i>Hydra</i> sp.	(*) Brown. Collected in 2019. Validated by GBIF	iNaturalist
Ecuador	Cumbayá (Quito), Ibarra (Imbabura), Pedro Moncayo (Pichincha) and Calvario and Sendero Llaviucu (Azuay)	<i>Hydra</i> sp.	(*) Collected in 2005, 2009, 2017, 2019 and 2021 Not yet validated	iNaturalist
	Cumbayá and Huayna-Capac (Azuay)	<i>Hydra viridissima</i>	(*) Collected in 2019 and 2021. Validated GBIF	iNaturalist
Colombia	Bogotá (Cundinamarca) and Santa Marta (Magdalena)	<i>Hydra</i> sp.	(*) Brown. Collected in 2019 and 2022. Not yet validated	iNaturalist
	Bogotá	<i>Hydra viridissima</i>	(*) Collected in 2017 and 2022. Validated by GBIF	iNaturalist
Panama	Antón River, Antón Valley (Coclé)	<i>Hydra vulgaris</i>	(*)	Martinez et al. (2010)
	La Cabaña (Boca del Toro)	<i>Hydra</i> sp.	(*) Brown. Collected in 2017. Not yet validated	iNaturalist
Mexico	Lake Arereko (Chihuahua)	<i>Hydra vulgaris</i>	(*)	Martinez et al. (2010)
	La Luna and El Sol lakes (crater of the Nevado de Toluca) (State of Mexico)	<i>Hydra vulgaris</i>	(*) Part of the benthic fauna	Oseguera et al. (2016)

Country	Region	Specie	Morphological description	Author
	Dolores, Tepotzotlán (State of Mexico)	<i>Hydra</i> sp.	(*)	Rivera De la Parra et al. (2016)
	Santiago (Nuevo León), Lerma (State of México) and Coyoacán (Mexico City)	<i>Hydra viridissima</i>	(*) Collected in 2018 and 2020. Validated by GBIF	iNaturalist
	Presa del Llano, Villa del Carbón (State of Mexico)	<i>Hydra oligactis</i>	(*) Collected in 2021. Not yet validated. Only consider as brown hydras	iNaturalist
Costa Rica	Arenal lagoon, Piedras River, De Los Ahogados River and tiny brook near Limonal (Guanacaste)	<i>Hydra vulgaris</i>	(*)	Martinez et al. (2010)
Trinidad and Tobago	Dibe, Port of Spain (Diego Martin region)	<i>Hydra</i> sp.	(*) Brown. Collected in 2021. Not yet validated	iNaturalist

of the Río Paraná, however these works provide little information associated with the specimens, not even mention their colors (Marchese & Drago, 1983; Paporello de Amsler, 1987). The same happens with the records from Saucesito and Las Tunas rivers (Río Paraná) (Pavé & Marchese, 2005) and from Lake Nahuel Huapi, Rio Negro (Trochine et al., 2008, 2009). The same occurs with *H. vulgaris* which has been reported in Argentina in five locations: two from Córdoba province, one from Neuquén province and two from Buenos Aires (Martínez et al., 2010). These records do not include morphological information associated with the specimens. Finally, during 2019 and 2020, *H. viridissima* was reported in Argentina from the capital of Santa Fé province and specimens of brown hydras from the department of Punilla, Córdoba province, respectively and the data was validated by GBIF site (iNaturalist, 2022).

In Bolivia, there are records of hydras in the lagoons of the Trinidad flood zone (Pouilly et al., 2004). However, they are somewhat doubtful because do not provide additional data on these observations (such as coloration, size or number of specimens) on its own observations or those of other researchers, so we do not know if they have been omitted or if their occurrence is a mere assumption.

For Brazil, Cordero (1939) based the decision to name a new species for the genus *Hydra*

on the fact that the specimens differed from others described for South America on the dimensions of their nematocysts. Considering the coloration and the presence of peduncle, the species could belong to *H. oligactis* group or to *H. vulgaris pedunculata*, a subspecies of the *H. vulgaris* group.

In addition to the results listed in Table 4, there are four more records from Brazil: from Governador José Richa plant in southern, and brown polyps collected in Lago Sul in Brasilia, and Rio Paranaíba in Minas Gerais (Da Silva-Bertão et al., 2021; iNaturalist, 2022), all citations without morphological data of the specimens.

In the case of Chile and in addition to the records listed in Table 4, include the findings of *H. vulgaris* from Punta Arenas and *H. viridissima* from Puerto Guadal, all of them without morphological descriptions (Martínez et al., 2010).

The records of *Hydra* sp. listed in Table 4 from Colombia, Ecuador, Costa Rica, Mexico, Panamá, Perú and Trinidad and Tobago, do not contain morphological descriptions.

Summary on the state of the of freshwater hydrozoan in the Neotropical region

There are approximately 170 records of freshwater hydrozoans from fifteen countries of the Neotropical region. Panama has the greatest

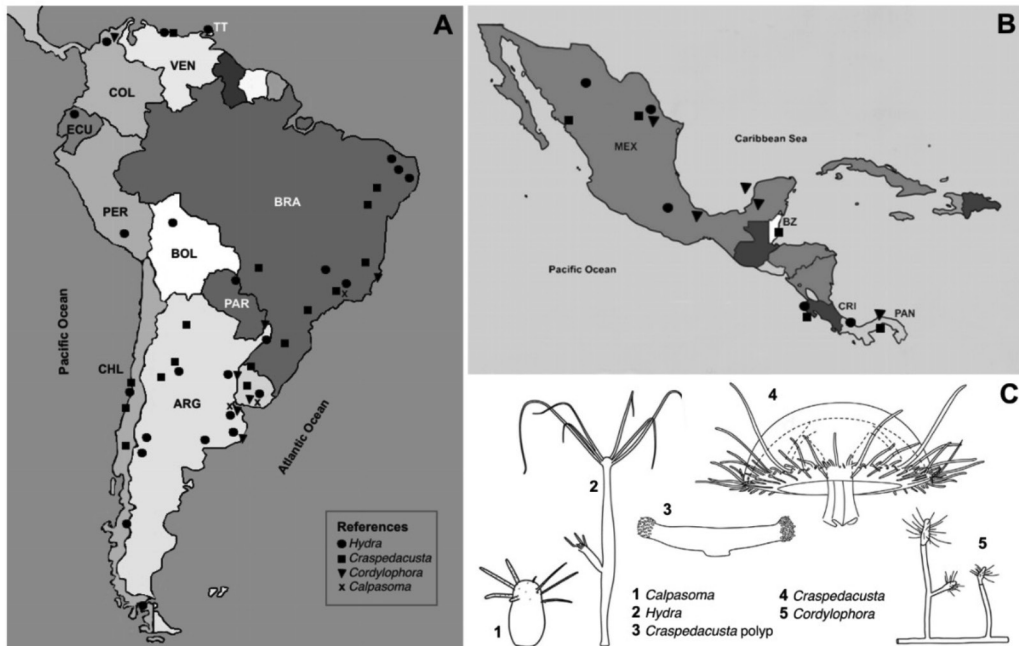


Fig. 1. Distribution and morphologies of the four genera of freshwater hydrozoans for the study area. **A.** South America. **B.** Central America, the Caribbean and Mexico and **C.** Morphologies of the four genera (modified from Campbell, 2016).

number of records, followed by Brazil, Argentina, Chile, Mexico, and Uruguay (Fig. 1). Most of the records from Panama are represented by preserved specimens of *C. caspia* deposited in NMNH, rather than bibliographic citations.

Among the various countries, *C. sowerbii* leads the records from Brazil and Chile, *Hydra* sp. from Argentina and Uruguay, and *Cordylophora* sp. from Mexico. The genus *Hydra* sp. is the most cited overall. For this genus, Argentina has the greatest number of records and diversity of species (four species and one subspecies), followed by Brazil with four species, three of which are endemic. Chile and Paraguay share the same situation as Brazil, with the endemics *H. magellanica* and *H. paranensis*, respectively, the latter species being the second oldest report of the genus for South America.

The first official record of freshwater hydrozoans in the Neotropical region was made with the discovery of *Hydra* sp. in Chile by Burger in 1906. However, the author does not guarantee the name of this species and only mentions the morphological similarities with

H. grisea Linnaeus, 1767, which was originally described only from North America and later considered synonymous with *H. vulgaris*. Consequently, these specimens are now cited as *Hydra* sp. officially.

Since this first record, many species have been described, leading to some limitations, for example, over the time many of these species have been rejected and accepted as synonyms, primarily for *H. vulgaris* Pallas, 1766. This species has nine synonyms: *H. grisea* Linnaeus, 1767; *H. vulgaris* var. *aurantiaca* Ehrenberg, 1838; *H. carnea* L. Agassiz, 1851; *H. trembleyi* Haacke, 1879; *H. americana* Hyman, 1931; *H. littoralis* Hyman, 1931; *Moerisia alberti* Leloup, 1938; *H. magnipapillata* Itô, 1947 and recently, *H. shenzhensis* Wang & Deng, 2012 (Schuchert, 2022).

A similar case occurs with *H. circumcincta* Schulze, 1914 of the *braueri* group, that has seven synonyms, of which *H. attenuata* Pallas, 1766 is the most cited in the literature (Schuchert, 2022). However, Lenhoff (1983), Campbell (1987) and Holstein et al.

(1990), considered *H. attenuata* as synonym of *H. vulgaris*. *H. littoralis*, *H. vulgaris* and *H. magnipapillata* are species restricted to North American territory, Europe, and Japan, respectively. Today, these three species are considered as *H. vulgaris*.

While Campbell (1987) and Holstein et al. (1990) consider *H. oligactis* as a cosmopolitan species, Jankowski et al. (2008) restricts the *oligactis* group to North America and Eurasia. In addition, they consider the species of the *vulgaris* group as cosmopolitan with slight differences between *H. vulgaris* from boreal and southern zones.

Such has been the confusion in this genus that even Wagner (1833) described the new species *Hydra aculeata*, a species later considered a basonym of *Hydractinia aculeata*, a marine colonial hydrozoan that belongs to the suborder Filifera.

Cordero (1941b) described the subspecies *H. attenuata thomsoni* from Uruguay, which was later rejected as a parent of *H. attenuata* = *H. circumcincta*. However, it was subsequently promoted to a species and renamed *H. thomsoni* by Schuchert in 2022. In addition, Cordero (1941b) reported on specimens found in Venezuela but did not assign them the species rank. The observed morphological characteristics of these specimens resemble those of the North American species *H. littoralis*, which is a synonym of *H. vulgaris*. Therefore, it is highly likely that Cordero's finding corresponds to the cosmopolitan *H. vulgaris*, as in the case of Burger (1906). The variety of reproductive strategies in this group reinforces the notion that Cordero's finding corresponds to *H. vulgaris* (Campbell, 1987; Lenhoff, 1983).

The records of *H. vulgaris* from other ten countries, expands knowledge about their distribution and reinforces the idea of Jankowski et al. (2008) that it is a cosmopolitan species. The records of Martínez et al. (2010) from Chile show that the species has reached the southernmost point of the American continent and could even validate the idea that the specimens found by Burger (1906) from Santiago de Chile corresponded to the species *H. vulgaris*.

The species *H. magellanica*, described by Schulze (1927) from the Strait of Magellan, could belong to the *vulgaris* group or even be a synonym of *H. vulgaris*. Although it currently retains its species status (Schuchert, 2022), a new review may be needed given the antiquity of its finding and the contributions made by Martínez et al. (2010).

The anatomical difference found in the subspecies *H. vulgaris pedunculata* is not manifested at the molecular level, since the conspicuous and translucent peduncle, is a variation that could respond solely to a phenotypic manifestation (Deserti, 2016). Martínez et al. (2010) and Schwentner & Bosch (2015) worked with *Hydra* sp. sequences of DNA from Chile and Argentina, which are available in GenBank, that showed clear differences in their mitochondrial and nuclear markers, despite occurring sympatrically. Schwentner & Bosch (2015) proposed that this difference may indicate that *H. vulgaris pedunculata* should be promoted in rank, declared as a new species. However, the results obtained in the study of biodiversity of the genus carried out by Deserti (2016), completely rule out this interpretation, but does not discard the possibility that other species exist. It is a clear example of the existence of intraspecific morphological variations that may have been, until today, one of the causes of misinterpretation in the naming of new species.

Other variations or subspecies have been reported in the literature, such as *H. vulgaris* var. *aurantiaca* Ehrenberg, 1838 and *H. attenuata thomsoni* for Uruguay (Cordero, 1941a). In WoRMS, the first one has been synonymized as *H. vulgaris* (Schuchert, 2020). The second one, as mentioned earlier, has been promoted to the rank of species.

The *viridissima* group have been reported in eight countries: Argentina, Brazil, Chile, Uruguay, Venezuela, Mexico, Ecuador and Colombia, represented by the species *H. viridissima*. Argentina is the only country with a second species of this group: *H. plagiodesmica*, but its description does not clearly distinguish it from the species *H. viridissima*, *H. sinensis* and *H. hadleyi*, so the validity of the species has



been questioned (Campbell, 1987; Grayson, 1971). However, in WoRMS it is considered as a valid report.

The genus *Calpasoma* sp. is the least represented and cited with only four records from South America. Given the difficulty of finding it, due to its small size and soft body, it is likely that its abundance is underestimated. In fact, if we consider this polyp as part of the life cycle of *Craspedacusta* sp., the records of *Calpasoma* sp. should coincide, at least asynchronously, with those of that jellyfish stage.

The case of invasive freshwater hydrozoans

The genus *Craspedacusta* sp. is the third one of freshwater hydrozoans with the largest number of records. The first report was made by Smith (1925) for Panama, but Chile is the country with more records of this genus and where the only molecular analysis on this genus until today has been done.

This genus includes a still uncertain number of hydromedusan species (Jankowski et al., 2008). The most reported around the world is *C. sowerbii* Lankester, 1880. As in the genus *Hydra* sp., the taxonomy of *Craspedacusta* sp. is unsettled because of the large morphological plasticity of the medusa stage (Lewis et al., 2012). Of the three species recognized as valid by the barcode of life database, *C. kiat-tingi*, *C. sowerbii* and *C. sinensis*, only *C. sowerbii* is recognized as a global invader of lakes (Fritz et al., 2009).

Although *C. sowerbii* is considered an invasive species, native of the Yangtze River basin in China, the type specimens described came from a water-lily tank in Regent's Park, London, England in 1880 (Kramp, 1961; Lankester, 1880). For Oualid et al. (2019) it is somewhat ironic that the type locality and the origin of this species are not the same, besides they point out that, in the type locality of *C. sowerbii*, the aquatic plants of the water-lily tank in Regent's Park (i.e., the potential dispersal vector) were imported from Brazil, and not from China, a fact that could complicate more the scenario about the true origin of this species.

Another problem related to the genus *Craspedacusta* sp. is the difficulty of finding its polyp form. For Duggan & Eastwood (2012), *C. sowerbii* is more common and widespread than it appears from jellyfish observations, making it difficult to estimate the timing of the introduction of this species to a given region using only the jellyfish findings.

As this species of hydromedusa is reported in lists of exotic species, the correct identification of the different lineages becomes an urgent challenge to correctly understand the number of invasion events and the species of the genus *Craspedacusta* that could be involved. (Oualid et al., 2019).

The colonial polyp *Cordylophora caspia* that has been reported in Argentina, Uruguay, Chile, Brazil, Colombia and Mexico, is also considered an alien species that besides causing ecological damage, adds an economic problem since it clogs the hydraulic and cooling systems of hydroelectric plants (Grohmann, 2008). This is one of the reasons for the considerable number of reports of this species for Panama in different sections of the Panama Canal, all of them without morphological information.

The citation of Gaggero (1923) of *C. lacustris* in Argentina, is the first mention of the genus *Cordylophora* from South America and the records of Hildebrand (1939) in Panama, the first one for Central America.

The taxonomy of this genus is characterized by the same interpretation problems as *Hydra* sp. and *Craspedacusta* sp., even some works have suggested that *C. caspia* may be a complex of species, because its high degree morphological plasticity (Folino-Rorem et al., 2005). These authors stated that at least *C. caspia* and *C. lacustris* are synonyms but suggested the integration of molecular and morphological analyses to clarify this question.

The analysis presented here demonstrates three important points: 1) freshwater hydrozoans are a frequent group in the Neotropical fauna; 2) given the appearance of the four genera in very dissimilar natural environments (even a point as southern as the Strait of Magellan), we can infer the existence of this group

of cnidarians in those territories for which there are still no official reports; and 3) a re-examination of the cited species is imperative, with solid molecular bases that clear up those

doubts about the really valid species, which would allow to establish the true geographic and phylogenetic distribution map, especially for those invasive species,

KEYS TO CNIDARIA (modified from Deserti et al. 2020)

CLASS HYDROZOA: Families

Note: *Cordylophora caspia* is a synonym of *C. lacustris* Allman, 1844.

- 1 Medusae or solitary polyps with or without buds 2
- 1' Branching colonies with polyps with several tentacles and a stolon attached to a substratum
Oceaniidae, one species: *Cordylophora caspia* Pallas, 1771 [Argentina, Brazil, Chile, Uruguay, Colombia, Mexico and Panama]
- 2(1) Medusa form or polyps < 1 mm in length **Olindiidae**
- 2' Single polyps >1 mm in length Hydridae, one genus: *Hydra* [Argentina, Brazil, Chile, Uruguay, Paraguay, Peru, Venezuela, Colombia, Mexico, Panama, Costa Rica, Bolivia, Ecuador and Trinidad and Tobago]

HYDROZOA: OLINDIIDAE: Genera

Note: these two forms may be conspecific.

- 1 Polypoid and medusoid forms; polyps colonial, lacking tentacles . . . *Craspedacusta sowerbii* Lankester, 1880 [Argentina, Brazil, Chile, Uruguay, Venezuela, Mexico, Panama, Belize and Costa Rica]
- 1' Only solitary polypoid forms with tentacles . . . *Calpasoma dactylopterum* Fhurmann, 1939 [Brazil, Argentina and Uruguay]

HYDROZOA: HYDRIDAE: HYDRA: Groups and species

- 1 Polyps not green; stenotele >11 mm in length; embryotheca either not piled or not roughly spherical 2
- 1' Green polyps due to endosymbiotic algae; nematocysts small; *viridissima* group 4
- 2(1) Holotrichous isorhiza narrowly oval or reniform, width <0.5 length; embryotheca not flattened 3
- 2' Holotrichous isorhiza broadly fusiform; embryotheca flattened against substratum .. *braueri* group
- 3(2) Young bud lateral tentacles arising conspicuously early; conspicuous peduncle; embryotheca smooth and thin *oligactis* group
- 3' Young bud tentacles arising in slightly staggered sequence or discontinuous; embryotheca thick with numerous radial spines *vulgaris* group [Cosmopolitan]
- 4(1) Holotrichous isorhiza reniform; embryotheca with one narrow chamber proximal to embryo
Hydra viridissima Pallas, 1766 [Cosmopolitan]
- 4' Holotrichous isorhiza stubby, not reniform; embryotheca with basal chambers in young embryos *Hydra plagiodesmica* Dioni, 1968 [Argentina]



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REFERENCES

- Alzugaray, M. E., Adami, M. L., Diambra, L. A., Hernández-Martínez, S., Damborenea, C., Noriega, F. G., & Rondero, J. R. (2013). Allatotropin: An Ancestral Myotrophic Neuropeptide Involved in Feeding. *PLoS ONE*, 8(10), e77520. <https://doi.org/10.1371/journal.pone.0077520>
- Alzugaray, M. E., Gavazzi, M. V., & Ronderos, J. R. (2019). Calcium signalling in early divergence of Metazoa: Mechanisms involved in the control of muscle-like cells contraction in *Hydra plagiodesmica*. *Canadian Journal of Zoology*, 824, 812–824. <https://doi.org/10.1139/cjz-2018-0295>
- Alzugaray, M. E., Gavazzi, M. V., & Ronderos, J. R. (2021). G protein-coupled receptor signal transduction and Ca²⁺ signaling pathways of the allatotropin/orexin system in *Hydra*. *General and Comparative Endocrinology*, 300, 113637. <https://doi.org/10.1016/j.ygcen.2020.113637>
- Bandeira De Mello, M. L. I., Melucci Cavenaghi, T. M. C., Melucci Cavenaghi & Resende, E. S. (1971). Nova ocorrência de medusa de água doce em Minas Gerais. *Ciência e Cultura*, São Paulo, 23, 265. <https://memoria.bn.br/docreader/DocReader.aspx?bib=003069&pagfis=9976>
- Boltovskoy, A., & Battistoni, P. A. (1981). La medusa *Craspedacusta sowerbyi* en el embalse Río Tercero, Córdoba, Argentina. *Physis*, 39(97), 78.
- Borges, P.D. (2008). *Aspectos do ciclo de vida da espécie invasora Cordylophora caspia (Cnidaria) no reservatório da Usina Hidrelétrica Governador José Richa, Rio Iguaçú, Paraná*. Universidade Federal do Paraná. <https://acervodigital.ufpr.br/bitstream/handle/1884/30409/Monografia%20Patricia%20Dammski%20Borges.pdf?sequence=1&isAllowed=y>
- Bossert, P., & Galliot, B. (2012). How to use *Hydra* as a model system to teach biology in a classroom. *International Journal of Developmental Biology*, 56, 637–652.
- Bouillon, J., & Boero, F. (2000). Synopsis of the families and genera of the Hydromedusae of the world, with a list of the worldwide species. *Thalassia Salentina*, 24, 47–296.
- Buchert, A. (1960). *Craspedacusta sowerbyi* Lank., eine Süßwasser Meduse und ihre beiden. Polyp-typen in der Ungarischen Fauna. *Acta Zoologica Hungary*, 6, 29–54.
- Burger, O. (1906). El género *Hydra* habitante de las aguas dulces de Chile. *Anales de la Universidad de Chile*, 119, 135–139.
- CABI Digital Library. (2023, March 28). *Cordylophora in Invasive Species Compendium*. CABI Digital Library. <https://www.cabidigitallibrary.org>
- Calder, D. R., & Cairns, S. D. (2009). Hydrozoa (Cnidaria: Hydrozoa) of the Gulf of Mexico. In D. L. Felder & D. K. Camp (Eds.), *Gulf of Mexico. Origin, waters, and biota* (Vol. 4. Biodiversity, pp. 381–394). Texas A&M University Press.
- Campbell, R. D. (1983). Identifying *Hydra* species. In H. M. Lenhoff (Ed.) *Hydra Research Methods* (pp. 19–28). Plenum Press.
- Campbell, R.D. (1987). A new species of *Hydra* (Cnidaria: Hydrozoa) from North America with comments on species clusters within the genus. *Zoological Journal of the Linnean Society*, 91, 253–263. <https://doi.org/10.1111/j.1096-3642.1987.tb01510a.x>
- Caputo-Galarce, L., Riquelme, K. V., Osman, D. Y., & Fuentes, R. A. (2013). A new record of the non-indigenous freshwater jellyfish *Craspedacusta sowerbii* Lankester, 1880 (Cnidaria) in Northern Patagonia (40° S, Chile). *BioInvasions Records*, 2, 263–270. <http://dx.doi.org/10.3391/bir.2013.2.4.01>
- Caputo-Galarce, L., Huovinen, P., Sommaruga, R., & Gómez, I. (2018). Water transparency affects the survival of the medusa stage of the invasive freshwater jellyfish *Craspedacusta sowerbii*. *Hydrobiologia*, 817, 179–191.
- Caputo-Galarce, L., Fuentes, R., Woelfl, S., Castañeda, L. E., & Cárdenas, L. (2021). Phenotypic plasticity of clonal populations of the freshwater jellyfish *Craspedacusta sowerbii* (Lankester, 1880) in Southern Hemisphere lakes (Chile) and the potential role of the zooplankton diet. *Austral Ecology*, 46, 1192–1197. <https://doi.org/10.1111/aec.13087>

- Carvalho-Wolle, L. (1978). *Hydra intermedia* sp. nov. and notes on *Chlorohydra viridissima* (Pallas) (Cnidaria). *Boletim de Zoologia*, 3, 143–152. <https://doi.org/10.11606/issn.2526-3358.bolzoo.1978.121657>
- Cernosvitov, L. (1935). Ueber zwei Hydren aus Paraguay. *Zoologischer Anzeiger*, 109(11–12), 307–311.
- Collins, A. G. (2002). Phylogeny of Medusozoa and the evolution of cnidarian life cycle. *Journal of Evolutionary Biology*, 15(3), 418–432. <https://doi.org/10.1046/j.1420-9101.2002.00403.x>
- Collins, A. G., Schuchert, P., Marques, A. C., Jankowski, T., Medina, M., & Schierwater, B. (2006). Medusozoan phylogeny and character evolution clarified by new large and small subunit rDNA data and an assessment of the utility of phylogenetic mixture models. *Systematic Biology*, 55, 97–115. <https://doi.org/10.1080/10635150500433615>
- Cordero, E. (1939). Observaciones sobre algunas especies sudamericanas del género *Hydra*. I. *Hydra* en el nordeste de Brasil. *Anais da Academia Brasileira de Ciências*, 11, 335–340.
- Cordero, E. (1941a). Observaciones sobre algunas especies sudamericanas del género *Hydra*. II. *Hydra* y *Cordylophora* en el Uruguay. *Anais da Academia Brasileira de Ciências*, 13(3), 173–183.
- Cordero, E. (1941b). Observaciones sobre algunas especies sudamericanas del género *Hydra*. III. (1) *Hydra* en Venezuela. (2) La acción de *Hydra iheringi* sobre las larvas de ciertos peces del nordeste de Brasil. *Anais da Academia Brasileira de Ciências*, 13(3), 195–201.
- Da Silva-Bertão, A. P., Leite, R. V. V., Horodesky, A., Pie, M. R., Zanin, T. L., Netto, O. S. M., & Ostrensky, A. (2021). Ecological interactions between invasive and native fouling species in the reservoir of a hydroelectric plant. *Hydrobiologia*, 848, 5169–5185.
- De Filippo, R., Batalha, F., & Nunes, A. J. B. (1999). *Primeira ocorrência de Craspedacusta sowerbyi* Lankester, 1880 (Cnidária, Limnomedusae) no Reservatório da UHE Serra da Mesa, Goiás, Brasil (Caderno de Resumos, VII Congresso Brasileiro de Limnologia, Vol. 2, pp. 487). Universidade Federal de Santa Catarina.
- Deserti, M. I. (2016). *Biodiversidad, biología y ecología del género Hydra* (Cnidaria: Hydrozoa) en ambientes acuáticos continentales del sudeste de la Provincia de Buenos Aires y algunos comentarios sobre el hidrozoo colonial *Cordylophora caspia* [Unpublished doctoral dissertation]. Universidad Nacional de Mar del Plata.
- Deserti, M. I., & Zamponi, M. O. (2011). *Hydra vulgaris* Pallas, 1766, (= *Hydra attenuata*) (Cnidaria; Hydrozoa) from the Los Padres Lagoon (Buenos Aires province, Argentina). *Revista Brasileira de Biociências*, 9(4), 82–87.
- Deserti, M. I., Zamponi, M. O., & Escalante, A. H. (2011). The genus *Hydra* from Argentina. I. *Hydra vulgaris pedunculata* subsp. nov. (Cnidaria, Hydrozoa). *Revista Real Academia Galega de Ciencias*, 30, 5–14.
- Deserti, M. I., Zamponi, M. O., & Escalante, A. H. (2012). The genus *Hydra* from Argentina. II. *Hydra pseudoligactis* Hyman, 1931 (Cnidaria; Hydrozoa), a new record. *Revista Real Academia Galega de Ciencias*, 31, 5–14.
- Deserti, M. I., Escalante, A. H., & Acuña, F. H. (2015). New record for the distribution of the colonial hydroid *Cordylophora caspia* (Pallas, 1771) (Cnidaria: Hydrozoa) in Argentina. *Check List*, 11(1), 1515. <https://doi.org/10.15560/11.1.1515>
- Deserti, M. I., Grohmann, P., & Stampar, S. N. (2020). Phylum Cnidaria. In C. Damborenea, D. C. Rogers & J. H. Thorp (Eds.), *Thorp and Covich's Freshwater Invertebrates (Fourth Edition) Volume 5: Keys to Neotropical and Antarctic Fauna* (pp. 93–99). Academic Press.
- Dioni, W. (1968). *Hydra* (*Chlorohydra*) *plagiodesmica* sp. nov., una hidra verde del río Salado, República Argentina (Cnidaria, Hydrozoa). *Physis*, 28(76), 203–210.
- Dioni, W. (1974). Noticia sobre un raro hidroide de agua dulce de la Argentina y Uruguay, *Calpasoma dactyloptera*. *Physis*, 33(86), 147–150.
- Domaneschi, O., & Coneglian, A. M. (1983, february 5). *Observações sobre o ciclo de vida de Calpasoma dactyloptera e Mycrohydra ryderi* (Cnidaria, Hydrozoa, Limnomedusae) do Estado de São Paulo [Paper presentation]. X Congresso Brasileiro de Zoologia, Belo Horizonte, Brazil.
- Duggan, I. C., & Eastwood, K. R. (2012). Detection and distribution of *Craspedacusta sowerbii*: observations of medusae are not enough. *Aquatic Invasions*, 7, 271–275.
- Dumont, H. J. (1994). The distribution and ecology of the fresh- and brackish-water medusae of the world. *Hydrobiologia*, 272, 1–12.
- Failla, M. G., Serra, W. S., & Martínez, C. (2017). First record of *Craspedacusta sowerbii* lankester, 1880 (Hydrozoa, Limnomedusae) in a natural freshwater lagoon of Uruguay, with notes on polyp stage in captivity. *Brazilian Journal of Biology*, 77(4), 665–672.
- Figueroa, D., & de los Ríos, P. (2010) First report of *Craspedacusta sowerbii* (Cnidaria) (Lankester, 1880) for Patagonian waters (38° S, Chile): a possible presence of invasive species and its potential ecological implications. *Brazilian Journal Biology*, 70(1), 227–228. <https://doi.org/10.1590/S1519-69842010000100032>
- Folino, N. C. (2000). The freshwater expansion and classification of the colonial hydroid *Cordylophora* (Phylum Cnidaria, Class Hydrozoa). In J. Pederson (Ed.),



- Marine Bioinvasions: Proceedings of the First National Conference* (pp. 139–144). Massachusetts Institute of Technology Sea Grant College Program.
- Folino-Rorem, N. C., Darling, J. A., & D'Ausilio, C. A. 2009. Genetic analysis reveals multiple cryptic invasive species of the hydrozoan genus *Cordylophora*. *Biological Invasions*, 11, 1869–1882.
- Fraire-Pacheco, K., Arancibia-Avila, P., Concha, J., Echeverría, F., Salazar, M. L., Figueroa, C., Espinoza, M., Sepúlveda, J., Jara-Zapata, P., Jeldres-Urra, J., & Vega-Román, E. (2017). A new report of *Craspedacusta sowerbii* (Lankester, 1880) in southern Chile. *BioInvasions Records*, 6(1), 25–31.
- Froehlich, C. G. (1963). Ocorrência de forma polipóide de *Craspedacusta sowerbii* Lankester. (Limnomedusae) em São Paulo. *Anais da Academia Brasileira de Ciências*, 35(3), 21–422.
- Fuentes, R., Cárdenas, L., Abarzua, A., & Caputo, L. (2019). Southward invasion of *Craspedacusta sowerbii* across mesotrophic lakes in Chile: geographical distribution and genetic diversity of the medusa phase. *Freshwater Science*, 38, 193–202.
- Fritz, G. B., Pfannkuchen, M., Reuner, A., Schill, R. O., & Brümmer, F. (2009). *Craspedacusta sowerbii*, Lankester 1880 – Population dispersal analysis using COI and ITS sequences. *Journal of Limnology*, 68, 46–52.
- Gaggero, P. (1923). *Cordylophora lacustris* Allman en el Río de la Plata. *Annales de la Sociedad Científica Argentina*, 96, 264–268.
- Galea, H. R. (2007). Cnidaria, Hydrozoa: latitudinal distribution of hydroids along the fjords region of southern Chile, with notes on the world distribution of some species. *Check List*, 3(4), 308–320.
- Gasith, A., Gafny, F., Hershkovitz, Y., Goldstein, H., & Galil, B. S. (2011). The invasive freshwater medusa *Craspedacusta sowerbii* Lankester, 1880 (Hydrozoa: Olinidiidae) in Israel. *Aquatic Invasions*, 6(1), S147–S152.
- Gliesch, R. (1930). A medusa de água doce *Microhydra* spec. *Egatea*, 15, 145–148.
- Grayson, R. F. (1971). The freshwater hydras of Europe. I. A review of the European species. *Archiv für Hydrobiologie*, 68, 436–449.
- Grohmann, P. (2008). Bioincrustation caused by a hydroid species in the turbine cooling system at the funil hydroelectric power plant, Itatiaia, Rio de Janeiro, Brazil. *Naturalia, Rio Claro*, 31, 16–21.
- Guajardo, M. G., Sanchez, H. V., & Salvador Contreras, Y. (1987) The cnidarians *Craspedacusta sowerbyi* new-record and *Cordylophora lacustris* new-record Hydrozoa for the Mexican fauna in Nuevo León. *Publicaciones Biológicas del Instituto de Investigaciones Científicas*, 2(2), 51–54.
- Haddad, M. A., & Nakatani, K. (1996). *Primeiro registro de Cordylophora caspia* (Pallas, 1771) (Cnidaria, Hydrozoa) em águas continentais brasileiras [Paper presentation]. XIV Congresso Brasileiro de Zoologia, Porto Alegre, Brazil.
- Hildebrand, S. F. (1939). The Panama Canal as a passageway for fishes, with lists and remarks on the fishes and invertebrates observed. *Zoologica*, 24(3), 15–45.
- Holstein, T. & Emschermann, P. (1995). *Cnidaria: Hydrozoa. Kamptozoa* (Süßwasserfauna von Mitteleuropa 1/2,3). Gustav Fischer Verlag.
- Holstein, T., Campbell, R., & Tardant, P. (1990). Identity crisis. *Nature*, 346, 21–22.
- Huarachi, R., & González, R. (2012). *Hydra vulgaris* Pallas, 1766 (Hydrozoa: Hydridae) como bioindicador de la calidad de aguas del río Chili, Arequipa, Perú. *The Biologist*, 10(2), 125–137.
- iNaturalist. (2022, October 30). *Comisión Nacional para el Conocimiento y Uso de la Biodiversidad*. <http://www.naturalista.mx>
- Infante, A., & Infante, O. (1994). Limnological Studies in a Tropical Man-Made lake (Lagartijo Reservoir) Venezuela. *Internationale Revue Der Gesamten Hydrobiologie Und Hydrographie*, 79, 17–25. <https://doi.org/10.1002/iroh.19940790105>
- Jakovčev-Todorović D., Dikanović V., Skorić S., & Cakić, P. (2010). Freshwater jellyfish *Craspedacusta sowerbyi* Lankester, 1880 (Hydrozoa, Olinidiidae)– 50 years'observations in Serbia. *Archive of Biological Sciences*, 62(1), 123–127.
- Jankowski, T. (2001). The freshwater medusae of the world– a taxonomic and systematic literature study with some remarks on other inland water jellyfish. *Hydrobiologia*, 462, 91–113.
- Jankowski, T., Collins, A. G., & Campbell, R. (2008). Global diversity of inland water cnidarians. *Hydrobiologia*, 595, 35–40.
- Jerónimo-Aguilar, S. (2013). *Hidroides (Cnidaria: Hydrozoa) del Sistema Arrecifal Veracruzano, México* [Doctoral dissertation, *Universidad Nacional Autónoma de México*]. Repositorio Institucional de la UNAM. <https://repositorio.unam.mx/contenidos/334518>
- Jones, M. L., & Rützler, K. (1975). Invertebrates of the upper chamber, Gatún Locks, Panama Canal, with emphasis on *Trochospongilla leidii* (Porifera). *Marine Biology*, 33, 57–66.
- Jormalainen, V., Honkanen, T., Vuorisalo, T., & Laihonon, P. (1994). Growth and reproduction of an estuarine population of the colonial hydroid *Cordylophora caspia* (Pallas) in the northern Baltic Sea. *Helgoländer Meeresuntersuchungen*, 48, 407–418.

- Kaliszewicz, A. (2013). Is larger better in sit-and-wait predators? Competitive superiority in *Hydra*. *Hydrobiologia*, 714(1), 105–114.
- Karaouzas, I., Zogaris, S., Lopes-Lima, M., Froufe, E., Varandas, S., Teixeira, A., & Sousa, R. (2015). First record of the freshwater jellyfish *Craspedacusta sowerbii* Lankester, 1880 in Greece suggests distinct European invasion events. *Limnology*, 16, 171–177.
- Kramp, P. L. (1961). Synopsis of the medusae of the world. *Journal of the Marine Biological Association of the United Kingdom*, 40, 7–382.
- Kuhl, G. (1947). Zeitrafferfilm-Untersuchungen tiber den Polypen von *Craspedacusta sowerbyi* (ungeschlechtliche Fortpflanzung, Okologie, und Regeneration). *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft*, 473, 1–72.
- Lankester, E. R. (1880). On a new jelly-fish of the order Trachomedusae, living in fresh water. *Science*, os-1(3), 34. <https://doi.org/10.1126/science.os-1.3.34>
- Lenhoff, H. M. (1983). *Hydra: Research methods*. Plenum Press.
- Lewis, C., Migita, M., Hashimoto, H., & Collins, A. G. (2012). On the occurrence of freshwater jellyfish in Japan 1928–2011: eighty-three years of records of *mamizu kurage* (Limnomedusae, Olindiidae). *Proceedings of the Biological Society of Washington*, 125, 165–179. <https://doi.org/10.2988/11-31.1>
- Liotta J., & Wagner M. (2003). Actualización del diagnóstico de estado ambiental: Aspectos físicos y bioecológicos (Proyecto n° ASR/B7-3100/IB/98/0143). MA BIO.
- López-Ochoterena, E., & Madrazo-Garibay, M. (1989). Protozoarios ciliados de México XXXIII. Estudio biológico de algunas especies de las subclases Suctorina y Peritrichia, asociados al hidrozooario *Cordylophora caspia* (Pallas) en la Laguna de Mandinga, Veracruz. *Revista de la Sociedad Mexicana de Historia Natural*, 40, 65–70.
- Loyola e Silva, J., & Oliveira, S. (1988). O surto de Medusa de água doce. *Ciência Hoje*, 7, 50–51.
- Lytel, C. F. (1961). Patterns of budding in the freshwater hydroid *Craspedacusta*. In H. M. Lenhoff & W. F. Loomis (Eds.), *Biology of Hydra and Some Other Coelenterates* (pp. 317–336). University of Miami Press.
- Mañé Garzón, F., & Carbonell, C. S. (1971). Sobre la medusa de agua dulce *Craspedacusta sowerbyi* Rey-Lank, 1880, en el Uruguay. *Boletín de la Sociedad Zoológica del Uruguay*, 1, 10.
- Marchese, M., & Drago, I. E. (1983). Zoobentos de los principales tributarios del río Paraná medio en el tramo Goya-Diamante: Su relación con el cauce principal y cauces secundarios. *Revista de la Asociación de Ciencias Naturales del Litoral*, 14(2), 95–109.
- Marsden, J. E., & Hauser, M. (2009). Exotic Species in Lake Champlain. *Journal of Great Lakes Research*, 35(2), 250–265. <https://doi.org/10.1016/j.jglr.2009.01.006>
- Martínez, D. E., Iñiguez, A. R., Percell, K. M., Willner, J. B., Signorovitch, J., & Campbell, R. D. (2010). Phylogeny and biogeography of *Hydra* (Cnidaria: Hydridae) using mitochondrial and nuclear DNA sequences. *Molecular Phylogenetics and Evolution*, 57(1), 403–410. <https://doi.org/10.1016/j.ympev.2010.06.016>
- Martins, A.V. (1941). Sobre a ocorrência da medusa de água doce *Craspedacusta sowerbyi* Lankester, 1880, em Minas Gerais. *Revista Brasileira de Biologia*, 1(2), 227–230.
- Massaro, F. C., & Rocha, O. (2008). Development and population growth of *Hydra viridissima* Pallas, 1766 (Cnidaria, Hydrozoa) in the laboratory. *Brazilian Journal of Biology*, 68(2), 379–383.
- Matthews, D. C. (1966). A comparative study of *Craspedacusta sowerbyi* and *Calposoma dactyloptera* life cycles. *Pacific Sciences*, 20, 246–259.
- McClary, A. (1959). The effect of temperature on growth and reproduction in *Craspedacusta sowerbii*. *Ecology*, 40, 158–162. <https://doi.org/10.2307/1929945>
- Mendoza-Becerril, M. A., González-Muñoz, R., Jerónimo-Aguilar, S., Tello-Musi, J. L., Genzano, G., Marques, C., Melo-Merino, S. M., Mendoza, T., Castillo-Cupul, R. E., Homá-Canche, P., Ugalde, D. & Simões, N. (2022, September 21). *Cnidarians from the Gulf of Mexico and Mexican Caribbean at the "Colección de Cnidarios del Golfo de México y Caribe Mexicano" at the UMDI-Sisal, Facultad de Ciencias, UNAM, México*. GBIF. <https://doi.org/10.15468/787j5n>.
- Minchin, D., Caffrey, J. M., Haberlin, D., Germaine, D., Walsh, C., Boelens, R., & Doyle, T. K. (2016). First observations of the freshwater jellyfish *Craspedacusta sowerbii* Lankester, 1880 in Ireland coincides with unusually high water temperatures. *BiolInvasions Records*, 5(2), 67–74.
- Moreno-Leon, M. A., & Ortega-Rubio, A. (2009). First record of *Craspedacusta sowerbyi* Lankester, 1880 (Cnidaria: Limnomedusae: Olindiidae) in Mexico (Adolfo Lopez Mateos reservoir), with notes on their feeding habits and limnological dates. *Biological Invasions*, 11, 1827–1834.
- Murillo, R. (1989). Presencia de *Craspedacusta Sowerbyi* en el embalse de Arenal provincia de Guanacaste, Costa Rica. *Uniciencia*, 6(1-2), 113–114.
- Okolodkov, Y. B., Bastida-Zavala, R., Ibáñez, A. L., Chapman, J. W., Suárez-Morales, E., Pedroche, F., & Gutiérrez-Mendieta, F. J. (2007). Especies acuáticas no indígenas en México. *Ciencia y Mar*, 11(32), 29–67.
- Orrell, T. (2022, September 20). National Museum of Natural History Extant



- Specimen Records. GBIF. <https://www.gbif.org/dataset/821cc27a-e3bb-4bc5-ac34-89ada245069d>
- Oseguera, L. A., Alcocer, J., & Escobar, E. (2016). Macroinvertebrados bentónicos de dos lagos tropicales de alta montaña en el volcán Nevado de Toluca, en la región central de México. *Hidrobiológica*, 26(3), 419–432.
- Oualid, J. A., Iazza, B., Tamsouri, N. M., El Aamri, F., Moukrim, A., & López González, P. J. (2019). Hidden diversity under morphology-based identifications of widespread invasive species: The case of the well-known hydromedusa *Craspedacusta sowerbii* Lankester 1880. *Animal Biodiversity and Conservation*, 42(2), 301–316. <https://doi.org/10.32800/abc.2019.42.0301>
- Paporello de Amsler, G. (1987). Fauna asociada a las raíces de *Eichhornia crassipes* en una laguna del valle aluvial del río Paraná (“Los Matadores”, Santa Fe, Argentina). *Revista de La Asociación de Ciencias Naturales Del Litoral*, 181, 93–103.
- Pavé, P. J., & Marchese, M. (2005). Benthic invertebrates as indicators of water quality in urban rivers (Paraná-Entre Ríos, Argentina). *Ecología Austral*, 15(2), 183–197.
- Pennak, R. W. (1989). *Fresh-water Invertebrates of the United States: Protozoa to Mollusca* (3rd ed.). John Wiley & Sons.
- Poggio Herrero, I. V., Mariame, M. P., Rodríguez, C., Fanelli, S. L., Porta, A., Fort, M., & Mastrantonio Garrigo, G. (2014). Aplicación de bioensayos a la evaluación ecotoxicológica de efluentes de tamba. *Publicación técnica - Estación Experimental Agropecuaria Anguil*, 97, 8-2014, 64–66
- Porter, C. E., & Schmitt, W. L. (1942). The first free-living freshwater jellyfish from South America. *Science*, 96(2501), 515.
- Potts, E. (1885). First use of name *Microhydra ryderi*. *Science*, 5, 123.
- Pouilly, M., Beek, S. G., Moraes M. R., & Ibañez, C. (2004). *Diversidad biológica en la llanura de inundación del Río Mamoré. Importancia ecológica de la dinámica fluvial*. Centro de Ecología Simón I.
- Quezada, A. E. (1969) Hallazgo de *Craspedacusta sowerbii* Lankester, 1880 (Coelenterata, Hydrozoa), en Concepción, Chile. *Boletín de la Sociedad de Biología de Chile*, 45, 31–35.
- Quezada, Q. & Aurora, E. (1973). Nueva localidad para Chile de *Craspedacusta sowerbyi* Lankester, 1880 (Coelenterata, Hydrozoa). *Boletín de la Sociedad de Biología de Concepción*, 46, 227.
- Rahat, M., & Campbell, R. D. (1974). Nematocyte migration in the polyp and one-celled tentacles of the minute fresh-water coelenterate *Calpasoma dactyloptera*. *Transactions of the American Microscopical Society*, 93(3), 379–385. <https://doi.org/10.2307/3225438>
- Reis Pereira, V. L. (2002). *A limnologia e o gerenciamento integrado do reservatório da usina hidrelétrica Lusi Eduardo Magalhães- UHE Lajeado, Tocantins* [Doctoral dissertation, Universidade de São Paulo]. Biblioteca Digital USP. <https://teses.usp.br/teses/disponiveis/18/18139/tde-25012017-151631/pt-br.php>
- Reisinger, E. (1957). Zur Entwicklungsgeschichte und Entwicklungsmechanik von *Craspedacusta* (Hydrozoa, Limnotrachelina). *Zeitschrift für Morphologie und Ökologie der Tiere*, 45(6), 656–698.
- Restello, R. M., Didone, M. A., & Carus, C. (2015). Medusa de água doce: *Craspedacusta sowerbii* (Lankester, 1880) (Hydrozoa, Limnomedusae) no Alto Uruguai do Rio Grande do Sul. *Perspectiva*, 39(145), 179–182.
- Richard, E. (1990). La curiosa medusita de agua dulce. *Subaquatica*, 2(6), 28–29.
- Ringuet, R. A. (1950). La medusa de agua dulce *Craspedacusta sowerbyi* Lank. en la Argentina. *Notas del Museo de La Plata, Zoología*, 134(15), 133–150.
- Ringuet, R. A., & Olivier, S. (1954). Anotaciones sobre *Cordylophora caspia* (Pallas) en la Argentina (Hydrozoa). *Notas del Museo de La Plata, Zoología*, 147(17), 67–70.
- Rioja, E. (1959). Estudios hidrobiológicos. XII: Hallazgo de la *Cordylophora caspia* (Pallas) (hidroideo gimnoblástico) en la laguna de Mandinga, Veracruz. *Anales del Instituto de Biología, Universidad Nacional Autónoma de México*, 30(1–2), 151–157.
- Rivera De la Parra, L., Sarma, S. S. S., & Nandini, S. (2016). Effects of predation by *Hydra* (Cnidaria) on cladocerans (Crustacea: Cladocera). *Journal of Limnology*, 75(S1), 39–47.
- Roch, F. (1924). Experimentelle Untersuchungen an *Cordylophora caspia* (Pallas) [=lacustris Allman] über die Abhängigkeit ihrer geographischen Verbreitung und ihrer Wuchsformen von den physikalisch-chemischen Bedingungen des umgebenden Mediums. *Zeitschrift für Morphologie und Ökologie der Tiere*, 2, 350–426.
- Roos, P. J. (1979). Two-stage life cycle of a *Cordylophora* population in the Netherlands. *Hydrobiologia*, 62(3), 231–239.
- Russell, F. S. (1953). *The medusae of the British Isles II: Anthomedusae, Leptomedusae, Limnomedusae, Trachymedusae and Narcomedusae*. Cambridge University Press.
- Savaris, M., Lampert, S., & Haddad, M. A. (2013). *Craspedacusta cf. sowerbii* Lankester, 1880 (Cnidaria: Hydrozoa: Limnomedusae): New record for the middle

- plateau region of the state of Rio Grande do Sul, Brazil. *Check List*, 9(44), 906–908.
- Sawaya, M. P. (1957). Ocorrência de *Craspedacusta sowerbyi* (medusa de água doce) no Estado do Rio de Janeiro. *Ciência e Cultura*, 9(2), 77.
- Schmid-Araya, J. M. & Zúñiga L. R. (1992). Zooplankton community structure in two Chilean reservoirs. *Archiv für Hydrobiologie*, 123, 305–335.
- Schubart, O. (1938). Considerações sobre as investigações nas águas de Pernambuco. *Arquivos do Instituto de Pesquisas Agronômicas Pernambuco*, 1, 26–57.
- Schulze, P. (1927). Zur Kenntnis und geographischen Verbreitung der Süßwasserpolypen. *Zoologischer Anzeiger*, 74, 129–140.
- Schuchert, P. (2022). *World Hydrozoa Database*. Retrieved March 11, 2023, from <https://www.marinespecies.org/hydrozoa>
- Schwartz, S., Hann, B. J., & Hebert, P. D. (1983). The feeding ecology of *Hydra* and possible implications in the structuring of pond zooplankton communities. *Biological Bulletin*, 164, 136–142.
- Schwarzbold, A., Volkmer-Ribeiro, C., Vasconcelos, M. C., Schneck, F., & Sponchiado, M. (2010). Ocorrência de *Craspedacusta sowerbyi* (Hydrozoa: Limnomedusae) (Lankester, 1880) no reservatório da Usina Hidrelétrica 14 de Julho, Rio Grande do Sul, Brasil. *Revista Brasileira de Biociências*, 8(3), 305–307.
- Schwentner, M., & Bosch, T. C. (2015). Revisiting the age, evolutionary history and species level diversity of the genus *Hydra* (Cnidaria: Hydrozoa). *Molecular Phylogenetics and Evolution*, 91, 41–55.
- Silva, W. M., & Roche, K. F. (2007). Occurrence of the freshwater jellyfish *Craspedacusta sowerbyi* (Lankester, 1880) (Hydrozoa, Limnomedusae) in a calcareous lake in Mato Grosso do Sul, Brazil. *Biota Neotropica*, 7(1), 173–176. <https://doi.org/10.1590/S1676-06032007000100028>
- Silveira, F., & Boscolo, H. K. (1996). *Primeira ocorrência de Cordylophora caspia* (Pallas, 1771) (Hydrozoa, Clavidae) para o Estado de São Paulo [Paper presentation].
- XIV Congresso Brasileiro de Zoologia, Porto Alegre, Brazil.
- Silveira, F., Gómez, C. S., & Silva, Z. D. (1997). New species of *Hydra* Linnaeus, 1758 (Cnidaria, Hydrozoa) from Southeastern Brazil. *Boletim do Museu Nacional*, 373, 1–15.
- Smith, F. (1925). Fresh-water medusae in the Panama Canal zone. *Science*, 61, 588–589.
- Souza, M., & Ladeira, M. (2011). *Craspedacusta sowerbyi* Lankester, 1880 (Cnidaria: Hydrozoa: Olindiidae): New record in Minas Gerais state, Brazil. *Check List*, 7(5), 610–611. <https://doi.org/10.15560/7.5.610>
- Spira, M. (1964). Observations of *Calpasoma dactyloptera* (Trachylina). *Israel Journal of Zoology*, 13(3), 134.
- Trochine, C., Balseiro, E. G., & Modenutti, B. E. (2008). Zooplankton of fishless ponds of Northern Patagonia: insights into predation effects of *Mesostoma ehrenbergii*. *International Review of Hydrobiology*, 93(3), 312–327. <https://doi.org/10.1002/iroh.200711011>
- Trochine, C., Modenutti, B. E., & Balseiro, E. G. (2009). Chemical signals and habitat selection by three zooplankters in Andean Patagonian ponds. *Freshwater Biology*, 54, 480–494. <https://doi.org/10.1111/j.1365-2427.2008.02125.x>
- Vannucci, M., & Tundisi, J. (1962). Las medusas existentes en los museos de La Plata y Buenos Aires. *Comunicaciones del Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Ciencias Zoológicas*, 3(8), 203–215.
- Wagner, R. (1833). Ueber eine neue im adriatischen Meere gefundene Art von nackten Armpolypen und seine eigenthümliche Fortpflanzungsweise. *Isis*, 1833, 256–260.
- Wedler, E. (2017). *Hidroides del Mar Caribe con énfasis en la región de Santa Marta, Colombia*. Instituto de Investigaciones Marinas y Costeras (Serie de Publicaciones generales del INVEMAR).