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Synopsis of the knowledge, zoogeography and an on-line interactive map of Brazilian marine gastrotrichs

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Information regarding the records of Brazilian marine gastrotrichs is presented. We systematize and organize the existing information associated with approximately 23 species (8 endemic species from the Brazilian coast) and their 1,581 records from 36 marine ecoregions of the world. A link is provided to an on-line interactive map where all occurrences for each species are shown, accompanied by geographic co-ordinates, oceans, country, cities, granulometric characteristics and ecoregions. Furthermore, a critical analysis of the geographical distributions of Brazilian marine gastrotrichs, an estimate of the number of undescribed species, a summary of the existence and status of taxonomical collections, and a list of the current specialists for this taxon are also presented



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Abstract

- 13 Information regarding the records of Brazilian marine gastrotrichs is presented. We systematize
- and organize the existing information associated with approximately 23 species 3 endemic
- species from the Brazilian coast) and their 1,581 records from 36 marine ecoregions of the
- world. A link is provided to an on-line interactive map where all occurrences for each species are
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- 18 characteristics and ecoregions. Furthermore, a critical analysis of the geographical distributions
- of Brazilian marine gastrotrichs, an estimate of the number of undescribed species, a summary of
- 20 the existence and status of taxonomical collections, and a list of the current specialists for this
- 21 taxon are also presented.

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- 23 **Subjects:** Marine Biology, Biodiversity, Taxonomy, Zoology
- 24 **Keywords:** Gastrotricha, Chaetonotida, Macrodasyida, biodiversity, species distribution.

2526

Introduction

- Organism diversity is a result of historical processes, and all extant species are
- 28 phylogenetically connected through time. Therefore, it is only possible to understand the
- 29 structural changes that we observe in the light of evolution (*Nunes & Christoffersen, 2009*).
- 30 Knowledge regarding biodiversity, history and interconnections is essential in understanding and



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anticipating the effects of disturbances, such as habitat destruction or the exchange of organisms
31
     between different localities, in this system (Andreas Schmidt-Rhaesa, 2002).
32
33
            In the last decade, more than 20,000 marine species (9% of those currently known) have
     been described (Appeltans et al., 2012). The number of marine species described per year
34
     reached an all-time high in the past decade, with over 2,000 species described in each of four
35
     different years. The statistical model predicted a total of 540,000 marine species, with a 95%
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     probability interval of 320,000 to 760,000. When stratified by the different taxonomic groups,
37
     the estimates were comparable to or less than the estimates. For taxonomic groups where the
38
     majority of species remain to be described, the rate of discovery is still rising; therefore, the
39
     model could not make a meaningful estimate of total species numbers, which was the case for
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     Gastrotricha. (Appeltans et al., 2012).
41
            Gastrotricha are microinvertebrates (from to 3,500 µm) commonly found in
42
     marine and freshwater habitats that are recognized for their complex anatomy and life cycle, with
43
     a predominance of hermaphroditism (Weiss 2001; Todaro & Hummon 2008; Balsamo et al.
44
     2014; Kånneby & Hochberg 2014). Although gastrotrichs can be considered a cosmopolitan
45
46
     taxon found on all major continents (Kånneby & Hockberg 2014), at least marine gastrotrichs
     show some level of endemism, mainly in the Northern Hemisphere (Garraffoni & Balsamo,
47
     2017)
48
            The taxon comprises approximately 825 pecies (Todaro, 2019a,b), traditionally divided
49
50
     into the two orders: Macrodasyida and Chaetonotida (see Kieneke et al. 2008). The first order
     comprises 5 Tamilies, 34 genera and more than 300 50 cies (Todaro, 2019a), with strap-shaped
51
     bodies, the presence of pharyngeal pores and, usually, numerous adhesive tubes present in the
52
     anterior, lateral and posterior regions (Todaro & Hummon 2008; Kånneby & Hockberg 2014).
53
54
     The majority of macrodasyids are marine species; only four species have been reported in
     freshwater from the Swiss Alps, Brazilian streams and a reservoir and aquifer from the USA
55
     (Ruttner-Kolisko 1955, Kisielewski 1987, Garraffoni et al. 2010, 2019; Todaro et al. 2012,
56
     Araújo et al. 2013, Kånneby & Wicksten 2014, Kånneby & Kirk, 2017). Within Chaetonotida, 7
57
    families, 30 nera and hearly 520 nero, 2019b) are interstitial or epibenthic in
58
     marine and brackish water, and 2/3 live in freshwater habitats (Balsamo et al. 2008; 2014). They
59
    are tenpin-shaped and have been reported to have one pair (rarely two) adhesive tubules,
60
     limited to the posterior end (Balsamo et al. 2008, Kånneby & Hochberg 2014). The taxon
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62	Chaetonotida is divided into two suborders: Multitubulatina (only one genus, Neodasys) and
63	Paucitubulatina. Within this order, the family Chaetonotidae is the most specious taxon among
64	the Gastrotricha, comprising approximately 1/3 of the species described for the whole group
65	(Kisielewski, 1991, 1997). =
66	Knowledge about marine gastrotrich biodiversity began to be discovered a few decades
67	ago in South America (Hochberg, 2014). The first two mentions of the taxon in Brazil occurred
68	when du Bois-Raymond Marcus (1952) reported an undescribed species of the genus
69	Thaumastoderma collected at a 3-5 m depth off the coast of Ilhabela Island (northern coast of
70	São Paulo state) and Forneris (1985) cited an undescribed species of the genus Macrodasys
71	sampled in the intertidal zone of Porchat Island (Santos region of São Paulo state). However, we
72	can consider that the gastrotrich fauna were not discovered until the pioneer taxonomical study
73	was carried out by Todaro & ha (2004) along the northern coasts of the state of São Paulo
74	(Ubatuba, Caragutatuba, Ilhabela and São Sebastião). In this first study, the authors described
75	one new species, Macrodasys fornerisae, and reported 42 other species (most of these species
76	were undescribed species belonging to Macrodasyida and Chaetonotida). One year later, Todaro
77	and Rocha (2005) reported results of a second study, mostly conducted on the northern coasts of
78	the state of São Paulo and, for the first time, in the southern part of the State of Rio de Janeiro
79	(Paraty). In this second study, the authors found 30 species, most of which were also found in the
80	first study, but they also reported some species not formally described and species recorded from
81	the first time in Brazil. After, rodaro (2012, 2013) described the new species <i>Pseudostomella</i>
82	dolichopoda and Ptychostomella lamelliphora, but they appeared as Pseudostomella sp. and
83	Ptychostomella sp., respectively, in Todaro cha (2004, 2005). All four of these studies
84	performed by Antonio Todaro were part of a larger research programme studying the diversity of
85	marine invertebrates of the northern coasts of the state of São Paulo (Migotto & Tiago 1999).
86	During the workshop "Taxonomy and Diversity of Marine Meiofauna" held in São
87	Sebastião, state of São Paulo. pnseca et al. 2014), Hochberg (2014) described the new species
88	Crasiella fonseci. Additionally, Araújo et al. (2014) described another species belonging to the
89	genus Pseudostomella (P. squamalongispinosa). Araújo et al. (2014), for the first time, found
90	and described a new species of Gastrotricha from Brazil outside of the state of São Paulo; the
91	new species was found on the south coast of the state of Bahia (Nova Viçosa).



Araújo et al. (2016) reported a new record of *Pseudostomella dolichopoda* Todaro, 2012, originally described from the northern coast of São Paulo, and now collected from the state of Espírito Santo. Garraffoni et al. (2016) analysed the patterns of diversity in marine Gastrotricha among benthic habitats and localities along with the southeastern Brazilian coast. The authors concluded that the diversity patterns of Brazilian marine gastrotrichs could be explained by differences in sediment textures, tidal zones, and localities. Garraffoni et al. (2017) reported new records of marine gastrotrichs from sublittoral sediments around São Sebastião Island (where the municipality of Ilhabela is housed). Among the findings, species belonging to the genus *Acanthodasys* (Macrodasyida) were reported for the first time in the Southern Hemisphere, and *Dactylopodola todaroi* was described as a new species. Recently, Todaro et al. (2019) described a new Macrodasyida genus (*Kryptodasys*) with 3 distinct species from Italy, Sweden and Brazil. The Brazilian species (*Kryptodasys carlosrochai*) appeared as "*nov. gen. nov. spec.*" in Todaro and Rocha (2004).

The aim of the present study was to systematize and organize the knowledge about Gastrotricha diversity on the Brazilian coast, with a species inventory, critical analysis of geographical distribution patterns of these species and some future perspectives about the study of these taxa in Brazil.

Materials and Methods

MARINE ECOREGIONS OF THE WORLD

We avoided using geopolitical boundaries to analyse gastrotrich distributions because the delimitation of such areas does not reflect natural units (*Nihei*, 2006). Thus, we used the biogeographic regionalization for coastal and shelf areas proposed by Spalding et al. (2007) to establish the distribution patterns of species. The hierarchical system proposed by these authors has three levels of inclusiveness: ecoregion (smallest-scale unit), province (nested within the realm) and realm (largest spatial unit). In the present study, we used the spatial unit ecoregion, as it is defined as "Areas of relatively homogeneous species composition, clearly distinct from adjacent systems. The species composition is likely to be determined by the predominance of a small number of ecosystems and/or a distinct suite of oceanographic or topographic features" (*Spalding et al.*, 2007).



122	The system proposed by Spalding et al. (2007) is composed of 232 ecoregions covering all
123	coastal and shelf waters of the world. Among them, 5 ecoregions occur in Brazil: Amazonia,
124	northeastern Brazil, eastern Brazil, southeastern Brazil and Rio Grande (Fig. 1).
125	
126	LITERATURE DATABASE
127	Distribution data on marine gastrotrichs up to 2010 were obtained from the "Global
128	distribution of marine Gastrotricha" compilation by Dr. William D. Hummon (Todaro 2017b),
129	and from 2011 to 2017, we gathered data directly from the literature (see complete list in
130	Garraffoni & Balsamo, 2017) (Fig. 1, Supplemental data 1). Furthermore, we also listed all
131	species collected t not yet described by Todaro and Rocha (2004; 2005) and Garraffoni et al.
132	(2017) and data obtained by ARSG and colaborators that is not yet published (Supplemental
133	data 2).
134	
135	BRAZILIAN SPECIES RECORDS
136	The species lists of Brazilian gastrotrichs followed the classification proposed by Todaro
137	(2019a,b).
138	Below the name of each species there is mention about the type locality, a summary of
139	records per country, and the total number of records in Brazil and the world. When possible, a
140	brief remark about the current species distribution and taxonomy status is noted. The list of the
141	geographic coordinates of the locality sites where each species was found are arranged following
142	the world bioregionalization framework of ecoregions (the ecoregions number are the same as
143	those reported by Spalding et al. [2007, 578]), countries and beaches.
144	
145	INTERACTIVE MAP
146	All species listed in this paper were entered into a spreadsheet, and an interactive map was
147	produced using My Maps in Google Drive. The map can be accessed at
148	https://drive.google.com/open?id=1OHFZF9r5PAR_WiNDLuR5209Z509_cfFk&usp=sharing.
149	Screenshots from the My Maps of Marine Gastrotrichs of Brazil are shown in Figure 2 for
150	instructional purposes. Three views are available: Cosmopolitan species in a first layer, with a
151	species distribution around the world (Fig. 2a), Endemic Brazilian species (Fig. 2b) and map
152	view with information of species (Fig. 2c). Names of species can be displayed using the filter



function, where species occurrences can be filtered (Figs. a,b). Each occurrence in the map is 153 clickable, resulting in a window showing an image of the species and information about the 154 record (Fig. 2c). 155 Schematic drawings of those species formally described in Brazil were redrawn from 156 original descriptions or redescriptions. Micrographs of specimen habitus were used to exemplify 157 the species collected by researchers from the Laboratory of the Meiofaunal Organisms Evolution 158 and yet not formally described. In this case, samples of the upper sediment layer were collected 159 with a manual corer, and in the laboratory, the specimens were sorted with a Zeiss DM2000, 160 mounted on glass slides, observed in vivo under a Zeiss Axioskop 2 plus equipped with 161 differential interference contrast (DIC) and AxioCam MRC5 digital video camera. 162 163 Results 164 To date, specimens of 23 species were collected from the Brazilian coast, and all of these 165 named taxa (at the species level) are considered valid according to modern standards. The order 166 Chaetonotida is the most speciose with 14 species (Chaetonotidae: Aspidiophorus mediterraneus: 167 168 Aspidiophorus paramediterraneus; Aspidiophorus tentaculatus; Chaetonotus ap chochaetus; Chaetonotus atrox; Chaetonotus dispar; Chaetonotus neptuni; Halichaetonotus decipiens; 169 Halichaetonotus marivagus; Halichaetonotus spinosus; Xenotrichulidae: Draculiciteria 170 tesselata; Heteroxenotrichula pygmaea; Heteroxenotrichula squamosa; Xenotrichula intermedia. 171 172 In contrast, 10 species are listed within the order Macrodasyida (Thaumastodermatidae: Pseudostomella dolichopoda, Pseudostomella squamalongispinosa, Ptychostomella 173 174 lamelliphora; Planodasyidae: Crasiella fonseci; Macrodasyidae: Macrodasys fornerise, 175 Urodasys viparus, Kryptodasys carlosrochai; Dactylopodolidae: Dactylopodola baltica, Dactylopodola todaroi). 176 Only 8 species (30%), all belonging to the order Macrodasyida (*Pseudostomella* 177 dolichopoda, Pseudostomella squamalongispinosa, Ptychostomella lamelliphora, Crasiella 178 fonseci, Macrodasys fornerise, Dactylopodola todaroi, Kryptodasys carlosrochai), were 179 originally described from samples collected in Brazil. Since the first marine gastrotrichs 180 originally described in Brazil were published in 2004 and the last one in 2019, the historical rates 181 of species description are 0.43/per year, much lower when compared, in the same period, with 182

183

the world historical rates of marine gastrotrich descriptions (8.93/per year).



184	The number of species registered from the Brazilian coast was only 25% of the total
185	marine gastrotrichs richness estimate, as 66 species were collected but not yet formally
186	(Supplemental data 2). Among these unpublished species, some of them, e.g., Xenodasys sp.
187	(Fig. 3) (Xenodasyidae), Acanthodasys sp., nd sp2 7 haumastodermatidae), Mesodasys sp.,
188	Dolichodasys sp. (Cephalodasyidae), Dendrodasys sp., Dendrodasys aff. rubomarinus
189	(Dactylopodolidae) are mentioned for the first time in the Southern Hemisphere.
190	Gastrotrichs samplings conducted on the Brazilian coastline were performed on at least
191	38 distinct beaches: 26 in the state of São Paulo (69%), 5 in the state of Rio de Janeiro (13%), 3
192	in the states of Bahia (7%) and Paraná (7%) and 1 in the state of Espírito Santo (4%).
193	Nominal species records of Brazilian marine gastrotrichs were present in 37 ecoregions,
194	covering 6.2% of the marine ecoregions of the world (total of 232 ecoregions). Among the 9
195	ecoregions found in the bioregionalization of the Brazilian coast, only 2 (22%) of them
196	registered the occurrence of species. Among these 2 ecoregions, another strong bias was
197	observed; one of them, Southeastern Brazil (which encompass the northern coast of São Paulo
198	State and southern coast of Rio de Janeiro), contained 97% of the sampling sites in Brazil.
199	Furthermore, the registered gastrotrich species appear to have a very heterogeneous geographic
200	distribution, with few restricted/endemic species (27%) or species with a relatively wide
201	distribution, such as Heteroxenotrichula pygmaea and Aspidiophorus paramediterraneus present
202	in 21 ecoregions, Heteroxenotrichula intermedia in 19 ecoregions, Aspidiophorus mediterraneus
203	and <i>Chaetonotus</i> rox in 17 ecoregions and <i>Halichaetonotus euromarinus, Draculiciteria</i>
204	tesselata and Urodasys viviparus in 13 ecoregions.

Discussion

HISTORICAL STUDY OF BRAZILIAN GASTROTRICHA

This is the first historical review on the gastrotrichs occurring along the Brazilian coast and the first synthesis of the available literature shown as an annotate species checklist. Although the obtained data showed scattered references from Brazilian literature, this panorama has started to change slowly. Historically, in Brazil (and in many other countries Southern Hemisphere, *e.g.*, *Hummon*, 1974; *Hochberg*, 2003, 2009; *Todaro et al.* 2015a,b, 2017), only sporadic collections were carried out by foreign researchers, and the involvement of Brazilian researchers could thus be considered incipient (*Balsamo et al.*, 2014; *Garraffoni & Balsamo*, 2017). Furthermore, any



215	research team dedicated to the study this group of animals was active, so the information about
216	diversity was poor and fragmented. However, this panorama started to change slowly when, a
217	few years ago, the senior author of the present study became the first active Brazilian researcher
218	in Brazil and started to coordinate a research group interested in uncovering the systematics,
219	evolution and biogeography of Brazilian gastrotrichs. Thus, tendency to organize and coordinate
220	the researchers who study gastrotrichs as their main or preferred working group seems positive.
221	As an exemplar of this new era in the gastrotricology in Brazil, at least 3 research projects are
222	currently being conducted on marine fauna (1 postdoctoral, 1 PhD and 2 MsC theses).
223	Garraffoni (2017) noted three major gaps in the current knowledge about Brazilian
224	freshwater Gastrotricha: a) large extensions of the Brazilian inland waters have never been
225	sampled before (records show a strong bias because most of the sampling sites were conducted
226	in the state of São Paulo, and only few samples were conducted in other states); b) identification
227	keys for a great number of genera are absent and there is difficulty in obtaining classic and old
228	literature from the end of century XIV and early century XX; and c) reference collections about
229	the taxon in Brazilian Museums are absent.
230	Unfortunately, most of these gaps are also observed for marine animals. Most of the
231	surveys are concentrated on the northern coast of São Paulo state and the southern coast of Rio
232	de Janeiro state (Todaro & Rocha 2004, 2005 7) daro 2012, 2013, Hochberg, 2014, Garraffoni
233	et al. 2017, Todaro et al. 2019), and only two studies were performed outside this area (Araújo et
234	al. 2014: Bahia State; Araújo et al. 2016: Espírito Santo st (see below section Brazilian
235	Gastrotricha distribution patterns). This panorama does not change even if we considered those
236	species that were not formally described (supplementary materia
237	The unique Brazilian collection, with adequate and permanent curatorial attention in
238	Brazil, which contains type material regarding marine Gastrotricha is located in the Zoological
239	Museum "Adão José Cardoso" (ZUEC) of the State University of Campinas. This museum
240	houses the type series for <i>Pseudostomella squamalongispinosa</i> Araújo, Balsamo & Traffoni
241	2014 (GCH 02-04), Dactylopodola todaroi Garraffoni, Di Domenico & Hochberg, 2016 (GCH
242	26-28) and Crasiella fonseci Hochberg, 2014. Regarding this last species, due to problems
243	sending back the type material to Brazil (pers. comm. R. Hochberg), in the original description, it
244	was only mentioned that the holotype was deposited at the ZUEC, but without an accession
245	number. However, we had the possibility to obtain the original type material and deposit it at the



246	ZUEC as GCH-51. Furthermore, additional material was deposited for <i>Pseudostomella</i>
247	dolichopoda Todaro, 2012 (GCH 29). The Zoological must um is housed in the same university
248	where the senior author of the present study conducts his sarch and supervision activities, and
249	it is possible that the number of deposited species will increase in a short period of tin
250	However, the representation of the Gastrotrich ecimens in collections razil (and also in
251	the world) is extremely poor.
252	The only significant difference between Brazilian marine and freshwater gastrotrichs is
253	related to the number of available identification keys; availability of identification keys is
254	much higher for the former than for the latter. In the last year, onomic keys for 6 genera
255	belonging to Gastrotricha were published, and many species of these taxa re recorded in
256	Brazil, e.g., Aspidiophorus (Todaro et al. 2009); Tetranchyroderma (Todaro 2002);
257	Pseudostomella (Clausen, 2004; Todaro 2012; Araújo et al. 2016); Paraturbanella (Todaro et
258	al. 2017); Dactylopodola (Von Und Zu Gilsa et al. 2014); Cephalodasys (Kieneke et al. 2015).
259	If the taxonomic knowledge of Brazilian gastrotrichs is far from appropriate, then studies
260	on other biological aspects, such as gastrotrich ecology or natural history, are totally absent.
261	
262	BRAZILIAN GASTROTRICHA DISTRIBUTION PATTERNS
263	In general, in recent years, researchers interested in better understanding the gastroundh
264	distribution have given more attention to geographic locations known for poor sampling (e.g.,
265	Todaro & Rocha, 2004, 2005; Todaro, 2012, 2013; Hochberg, 2003, 2009, 2014; Hochberg et
266	al. 2013; Todaro et al. 2014; 2015a,b, 2017, 2019; Kieneke et al. 2015; Garraffoni et al. 2016,
267	2017; Von Und Zu Gilsa et al. 2014; Araújo et al. 2014, 2016; Araújo & Hochberg, 2017;
268	Chatterjeeet al. 2019).
269	In this scenario, when compared to the other countries in South America (Colombia:
270	·
	Hummon, 1974; Ecuador, Galapagos Island: Schmidt 1974; and Uruguay: Dioni 1960)
271	
271 272	Hummon, 1974; Ecuador, Galapagos Island: Schmidt 1974; and Uruguay: Dioni 1960)
	Hummon, 1974; Ecuador, Galapagos Island: Schmidt 1974; and Uruguay: Dioni 1960) the information of the Gastrotricha fauna in Brazil can be considered to be incore complete. However, when only Brazil, with a coastline encompassing almost 7,500 km and varying between ~5° and ~25° of longitude, was analysed, it was found that more than 95% of the country was never
272	Hummon, 1974; Ecuador, Galapagos Island: Schmidt 1974; and Uruguay: Dioni 1960) the information of the Gastrotricha fauna in Brazil can be considered to be more complete. However, when only Brazil, with a coastline encompassing almost 7,500 km and varying between ~5° and
272 273	Hummon, 1974; Ecuador, Galapagos Island: Schmidt 1974; and Uruguay: Dioni 1960) the information of the Gastrotricha fauna in Brazil can be considered to be incore complete. However, when only Brazil, with a coastline encompassing almost 7,500 km and varying between ~5° and ~25° of longitude, was analysed, it was found that more than 95% of the country was never



277	highlight that these results in the state of São Paulo did not happen by accident because many
278	initiatives for funding studies that aimed to reveal the biodiversity of fauna and flora in the state
279	were supported the Virtual Institute of Biodiversity, BIOTA-FAPESP, organized by FAPESP,
280	the State of São Paulo Research Foundation (Migotto & Tiago 1999; Joly et al. 2010).
281	However, if we compared the number of sampled beaches along the São Paulo coastline
282	(26) with the total number beaches in continental and islands in the state (342), the sampling
283	effort very low, with a very limited number of sample sites (7% of the total beaches in the
284	state). With we considered the states of São Paulo and Rio de Janeiro, which together support
285	85% of the sampled sites located in Brazil, the sampling effort is even worse (4% of the total
286	beaches in both states). For comparison purposes, the Italian coastline encompasses almost 7,800
287	km and has the best data information about marine Gastrotricha fauna in the Mediterranean and
288	Black Sea countries (Todaro et al. 2003), if not one of the best in the work this country,
289	gastrotrichs were sampled in 246 localities and comprise 177 different species.
290	As noted above, this difference regarding the knowledge of gastrotrich biodiversity
291	between the Northern and Southern hemispheres occurs because historically, studies dedicated to
292	this group of animals were conducted by European or American Institutions (Balsamo et al.
293	2014; Garraffoni & Balsamo, 2017). Thus, this discrepancy in information between the two
294	hemispheres has some consequences; a) the first record and description of a marine gastrotrichs
295	in the Mediterranean was done by Claparède (1867). In contrast, the first mention of a Brazilian
296	gastrotrich was noted by Eveline du Bois-Raymond Marcus 85 years after the René-Édouard
297	Claparède publication (Bois-Raymond Marcus, 1952), and it was approximately 140 before for
298	Antonio Todaro and Carlos Rocha named the first new species from Brazil (Todaro & Rocha,
299	2004) 70% of the marine gastrotrich sampling sites around the world are located in the
300	Northern Hemisphere (mainly in Atlantic coast of United States, Mediterranean and Great
301	Britain coast Garraffoni & Balsamo, 2017 In recent years, the number of studies dealing
302	with the reconstruction of phylogenetic relationships within Gastrotricha based on molecular
303	data has increased (Todaro et al., 2011, 2012, 2014, 2015b). However, the majority of DNA used
304	in these studies was extracted from species collected in the Northern Hemisphere.
305	Despite the bias in sampling ef s, the geographic ranges of the Brazilian marine
306	gastrotrichs range fron. Latively restricted distributions, i.e., 1 or 2 ecoregions (6 species) to
307	widespread distributions, i.e., at least 4 ecoregions (22 species). These numbers have a totally



308	opposite tendency compared to marine gastrotrichs worldwide, as 80% of the species are
309	distributed in only 2 ecoregions (Garraffoni et al. unpublished data). A possible explanation for
310	this large number of widely distributed species may be related to the need for generalist
311	taxonomy studies, which are very important to begin the immense challenge of discovering a
312	very diverse and practically unknown (until less than 15 years ago) fauna (Todaro & Rocha,
313	2004, 2005; Garraffoni et al., 2017). As a consequence, the absence of wide-scale reviews in the
314	country can produce uncontextualized taxonomic revisions and spurious data on biodiversity.
315	Finally, in recent years, the ubiquitous distribution of marine gastrotrichs has been challenged
316	(Kieneke et al. 2012; Curini-Galletti et al., 2012; Garraffoni et al. 2016; Garraffoni & Balsamo,
317	2017), and it seems that the number of widespread species is not as high as previously thought.
318	
319	BRAZILIAN GASTROTRICHA RICHNESS
320	As reported above, due to the low number of taxonomic studies and sample bias along the
321	Brazilian coast, we can provide the estimated richness of gastrotrichs only for the coasts of the
322	states of São Paulo and Rio de Janeiro. Garraffoni et al. (2016) ugh a rarefaction function,
323	we estimated 155 Gastrotricha species from the southeast Brazilian coast. Despite the fact that
324	this last number is higher than the observed number species found in the present study, an
325	interesting clarification must be made. We counted at least 87 species registe in this area, but
326	65 of them were not formally described. Thus, we have good support to say that at least 130
327	species of marine gastrotrichs from only 5% of the Brazilian coast are waiting to be described.
328	Furthermore, many of these undescribed species belong to very rare taxa, e.g., Diplodasys sp.,
329	Dolichodasys sp., Mesodasys sp., Paradasys sp., (Todaro & Rocha, 2004), sometimes never
330	reported before from the Southern Hemisphere, e.g., Acanthodasys sp. 1 and sp. 2 (Garraffoni et
331	al. 2017) or Xenodasys sp. collected in 2018 at Fome Beach, Ilhabela Island, northern coast of
332	São Paulo state (Fig. 3). The last species belongs to a genus with only three species, each with
333	regional (limited) distributions (Schuster et al. 2018).
334	The large number of unknown species found on the southeastern Brazilian coast is not a
335	surprise. To date, 507 marine gastrotrichs (Garraffoni & Balsamo, 2017; Todaro, 2019a) have
336	been described from all the world's oceans, but at least 2,244 to 3,244 species are still unknown
337	and undiscovered (Appeltans et al. 2012). Using species richness as a metric for assessment of



338	the worldwide marine gastrotrich biodiversity, only less than 20% are known (Appeltans et al.
339	2012).
340	
341	Conclusions
342	Although the biogeographical knowledge about Brazilian gastrotrich fauna is greatly hampered
343	by regional discrepancies in taxonomic knowledge, there is no doubt about the high diversity of
344	the group and that many new species will be described. It is very important that to carry out
345	studies that aim to sample new areas in different regions along the Brazilian coastline, increase
346	the availability of Brazilian species deposited in museums and increase the amount of nuclear
347	research groups interested in contributing to the increase in the systematic, evolutionary and
348	ecological knowledge of the meiofauna organisms. The on-line map can be interpreted as a
349	starting point to increase the understanding of the diversity and biogeographic patterns of
350	gastrotrichs in Brazil and their affinities with other geographic regions.
351	
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353	
354	Additional Information and Declarations
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360	
361	COMPETING INTERESTS
362	The authors declare that they have no competing interests.
363	
364	DATA AVAILABILITY
365	The following information was supplied regarding data availability: Raw data are available in the
366	Supplemental Materials.
367	
368	FIGURE CAPTIONS





369	Figure 1. World map with the bioregionalization hierarchical system of ecoregions according to
370	Spalding et al. (2007). Ecoregions observed on the Brazilian coast are coloured light blue. Dots
371	are the sampling sites of the marine gastrotrich species found in Brazil (endemic or not).
372	
373	Figure 2. Screenshots of the interactive map of Marine Gastrotrichs of Brazil. (A) Row view.
374	(B) Card view. (C) Map view indicating the points where Gastrotricha species were collected.
375	The dataset can be used with the filter function and the card that appears in the point.
376	
377	Figure 3. Xenodasys sp., DIC images from Brazil. (A) Habitus. (B). Dorsal view of the head
378	region with tentacles. (C) Ventral view of the head region with tentacles. (D) Ventral view of the
379	middle with ventrolateral adhesive tubes. (E) Ventral view of the posterior end.
380	Abbreviations: co, chordoidorgan; cp, cephalic plates; lsp, lateral spines; TbA, anterior adhesive
381	tubes; TbP, posterior adhesive tubes; TbVL, ventrolateral adhesive tubes; ten, head tentacles.
382	Scales: A. 45 μm; B-E. 20 μm.



383

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Table 1(on next page)

Table 1

Table 1. List of marine species in different ecoregions reported by Spalding et al. (2007). Ecorregion: Eco; Number: N; Aspidiophorus: Asp; Chaetonotus: Cht; Halichaetonotus: Hal; Heteroxenotrichula: Het; Draculiciteria: Dra; Crasiella: Cra; Dactylopodola: Dact; Dendrodasys: Den; Macrodasys: Mac; Urodasys: Uro; Pseudostomella: Pse; Ptychostomella: Pty.

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Table 1. List of marine species in different ecoregions reported by Spalding et al. (2007). Ecorregion: Eco; Number: N; Aspidiophorus: Asp; Chaetonotus: Cht; Halichaetonotus: Hal; Heteroxenotrichula: Het; Draculiciteria: Dra; Crasiella: Cra; Dactylopodola: Dact; Dendrodasys: Den; Macrodasys: Mac; Urodasys: Uro; Pseudostomella: Pse; Ptychostomella: Pty.

Eco name	Eco	List of species	No of	No of
	Uo		taxa	gener
				а
Northern Norway and Finnmark	23	Het. intermedia	1	1
Baltic Sea	24	Het. intermedia, Dact. baltica	2	2
North Sea	25	Asp. mediterraneus, Asp. paramediterraneus, Cht. atrox, Cht. neptuni, Hal. decipiens, Hal. euromarinus, Het. pygmaea, Het. squamosa, Het. intermedia, Dra. tesselata, Dact. baltica	11	6
Celtic Seas	26	Asp. mediterraneus, Asp. paramediterraneus, Cht. atrox, Cht. dispar, Cht. neptuni, Hal. decipiens, Hal. euromarinus, Het. pygmaea, Het. squamosa, Het. intermedia, Dra. tesselata, Dact. baltica	12	6
South European Atlantic Shelf	27	Asp. mediterraneus, Asp. paramediterraneus, Hal. decipiens, Hal. euromarinus, Het. squamosa, Het. intermedia, Dra. tesselata	7	4
Azores Canaries Madeira	29	Cht. atrox, Het. pygmaea, Dra. tesselata	3	3
Adriatic Sea	30	Asp. mediterraneus, Asp. paramediterraneus, Cht. apechochaetus, Cht. atrox, Cht. dispar, Cht. neptuni, Hal. decipiens, Hal. euromarinus, Het. pygmaea, Het. squamosa, Het. intermedia, Dra. tesselata, Uro. viviparus	13	6
Aegean Sea	31	Asp. mediterraneus, Asp. paramediterraneus; Asp. tentaculatus, Cht. apechochaetus, Cht. atrox, Cht. neptuni, Hal. decipiens, Hal. euromarinus, Hal marivagus, Het. pygmaea, Het. squamosa, Het. intermedia, Dact. baltica, Uro. viviparus	14	6
Levantine Sea	32	Asp. paramediterraneus, Cht. apechochaetus,	11	6



		Cht. atrox, Cht. neptuni, Hal. decipiens, Hal. euromarinus, Het. pygmaea, Het. squamosa, Het. intermedia, Dact. baltica, Uro. viviparus		
Ionian Sea	34	Asp. mediterraneus, Asp. paramediterraneus, Cht. apechochaetus, Cht. atrox, Cht. dispar, Cht. neptuni, Het. squamosa, Het. intermedia, Dra. tesselata, Uro. viviparus	10	5
Western Mediterranean	35	Asp. mediterraneus, Asp. paramediterraneus, Asp. tentaculatus, Cht. apechochaetus, Cht. atrox, Cht. dispar, Cht. neptuni, Hal. decipiens, Hal. euromarinus, Hal marivagus, Het. pygmaea, Het. squamosa, Het. intermedia, Dra. tesselata, Uro. viviparus	15	6
Gulf of Maine/Bay of Fundy	40	Asp. mediterraneus, Asp. paramediterraneus, Hal. decipiens, Hal. euromarinus, Het. pygmaea, Het. squamosa, Het. intermedia, Dra. tesselata, Dact. baltica	9	5
Virginian	41	Asp. mediterraneus, Asp. paramediterraneus, Cht. atrox, Cht. dispar, Hal. euromarinus, Het. pygmaea, Het. squamosa, Het. intermedia, Dact. baltica	9	5
Carolinian	42	Asp. mediterraneus, Asp. paramediterraneus, Cht. neptuni, Hal. euromarinus, Het. pygmaea, Het. squamosa, Het. intermedia, Dra. tesselata, Dact. baltica	9	6
Northern Gulf of Mexico	43	Asp. mediterraneus, Asp. paramediterraneus, Cht. atrox, Cht. dispar, Hal. decipiens, Hal. euromarinus, Het. pygmaea, Het. squamosa, Het. intermedia, Dra. tesselata	10	5
Black Sea	44	Asp. mediterraneus, Hal. decipiens, Het. pygmaea, Het. intermedia	4	3
Oregon, Washington, Vancouver Coast and Shelf	57	Het. pygmaea	1	1
Southern California Bight	59	Het. intermedia	1	1
Bermuda	62	Uro. viviparus	1	1



Bahamian	63	Asp. mediterraneus, Asp. paramediterraneus, Het. pygmaea	3	2
Eastern Caribbean	64	Asp. paramediterraneus, Cht. dispar, Het. pygmaea, Dra. tesselata	4	4
Southwestern Caribbean	67	Uro. viviparus	1	1
Greater Antilles	65	Asp. tentaculatus	1	1
Western Caribbean	68	Asp. paramediterraneus	1	1
Floridian	70	Asp. mediterraneus, Asp. paramediterraneus, Asp. tentaculatus, Cht. atrox, Cht. dispar, Cht. neptuni, Hal. euromarinus, Het. pygmaea, Het. squamosa, Dra. tesselata, Dact. baltica, Uro. viviparus	12	7
Eastern Brazil	76	Pse. dolichopoda, Pse. squamalongispinosa	2	1
Northern and Central Red Sea	87	Asp. mediterraneus, Asp. paramediterraneus, Asp. tentaculatus, Cht. apechochaetus, Cht. atrox, Cht. neptuni, Hal. decipiens, Het. pygmaea, Het. squamosa, Uro. viviparus	10	5
Central Somali Coast	93	Asp. mediterraneus, Asp. paramediterraneus	2	1
Maldives	105	Cht. atrox, Uro. viviparus	2	2
Eastern India	107	Cht. atrox, Het. intermedia, Uro. viviparus	3	2
Andaman and Nicobar Islands	109	Cht. atrox, Uro. viviparus	2	2
South Kuroshio	121	Cht. atrox, Het. pygmaea	2	2
Hawaii	153	Asp. paramediterraneus, Het. pygmaea	2	2
Guayaquil	171	Asp. paramediterraneus, Het. intermedia	2	2
Eastern Galapagos Islands	173	Het. pygmaea	1	1
Southeastern Brazil	180	Asp. mediterraneus, Asp. paramediterraneus, Asp. tentaculatus, Cht. apechochaetus, Cht. atrox, Cht. dispar, Cht. neptuni, Hal. decipiens, Hal. euromarinus, Hal marivagus, Het. pygmaea, Het. squamosa, Het. intermedia, Dra. tesselata, Cra. fonseci, Dact. baltica, Dact todaroi, Den. aff. rubomarinus, Mac. fornerise, Uro. viviparus, Pse. dolichopoda, Pse. squamalongispinosa, Pty. lamelliphora	23	12





Figure 1

Figure 1

World map with the bioregionalization hierarchical system of ecoregions according to Spalding et al. (2007). Ecoregions observed on the Brazilian coast are coloured light blue. Dots are the sampling sites of the marine gastrotrich species found in Brazil (endemic or not).

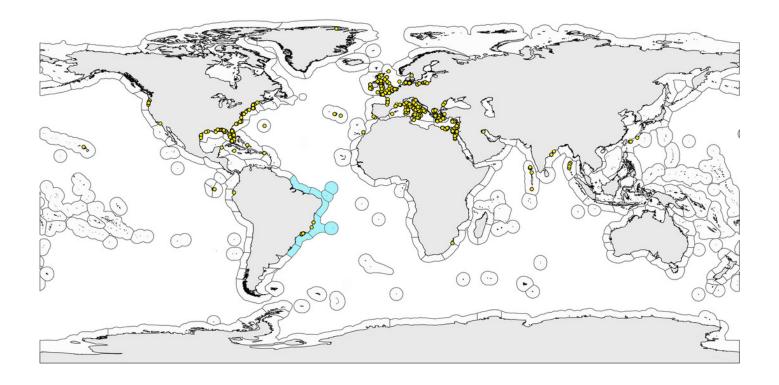




Figure 2

Figure 2

Screenshots of the interactive map of Marine Gastrotrichs of Brazil. (A-C) Map views indicating the points where Gastrotricha species were collected.





Figure 3

Figure 3

Xenodasys sp., DIC images from Brazil. (A) Habitus. (B). Dorsal view of the head region with tentacles. (C) Ventral view of the head region with tentacles. (D) Ventral view of the middle body with ventrolateral adhesive tubes. (E) Ventral view of the posterior end. Abbreviations: co, chordoidorgan; cp, cephalic plates; lsp, lateral spines; TbA, anterior adhesive tubes; TbP, posterior adhesive tubes; TbVL, ventrolateral adhesive tubes; ten, head tentacles. Scales: A. $45 \mu m$; B-E. $20 \mu m$.

