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## **Deep-sea manefishes (Perciformes: Caristiidae) from oceanic islands and seamounts off northeastern Brazil, with comments on the caristiids previously reported in Brazilian waters**

Mincarone Michael M. <sup>1,\*</sup>, Villarins Bárbara T. <sup>1</sup>, Eduardo Leandro N. <sup>2,3</sup>, Caires Rodrigo A. <sup>4</sup>,  
Lucena-Frédou Flavia <sup>2</sup>, Frédou Thierry <sup>2</sup>, Lira Alex Souza <sup>2</sup>, Bertrand Arnaud <sup>2,3</sup>

<sup>1</sup> Instituto de Biodiversidade e Sustentabilidade, Universidade Federal do Rio de Janeiro, Macaé, Brazil

<sup>2</sup> Departamento de Pesca e Aquicultura, Universidade Federal Rural de Pernambuco, Recife, Brazil

<sup>3</sup> Institut de Recherche pour le Développement, MARBEC, Sète, France

<sup>4</sup> Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil

\* Corresponding author : Michael M. Mincarone, email address : [mincarone@macae.ufrrj.br](mailto:mincarone@macae.ufrrj.br)

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### **Abstract :**

The manefishes of the family Caristiidae are rare, poorly known deep-sea species with broad geographical distribution. This study provides new information on the diversity and distribution of this family around the oceanic islands and seamounts off northeastern Brazil, reporting the first records of *Paracaristius nudarcus*, *Platyberyx andriashevi*, *Platyberyx paucus* and *Platyberyx pietschi* in Brazilian waters. Measurements and counts for all specimens examined are provided and compared with those available in the literature. In addition, the identity of caristiids previously reported from Brazil is discussed.

**Keywords :** *Paracaristius*, *Platyberyx*, mesopelagic fish, Brazil, western South Atlantic

26 **Introduction**

27 Fishes of the family Caristiidae are rare deep-sea species with broad geographical distribution,  
28 occurring in all oceans (Kukuev et al. 2013; Stevenson & Kenaley, 2013). The family comprises  
29 four genera and 18 species commonly known as manefishes (Stevenson & Kenaley, 2013).  
30 These species present epipelagic larvae and juveniles, occurring from the surface to the

31 mesopelagic zone, while adults have been reported at depths ranging from 100 to 2000 m  
32 (Benfield et al., 2009; Stevenson & Kenaley, 2011, 2013). The caristiids are characterized by  
33 having relatively short heads, steep snouts, large eyes, deep and strongly compressed bodies,  
34 very long and high dorsal fins and greatly elongated pelvic fins (Benfield et al., 2009; Kukuev et  
35 al., 2013; Stevenson & Kenaley, 2013).

36 Studies on the taxonomy and distribution of caristiids were historically scarce and  
37 fragmented. However, a series of taxonomic revisions has been recently conducted (Kukuev et  
38 al., 2012, 2013; Stevenson & Kenaley, 2011, 2013) and the knowledge on the taxonomy and the  
39 distribution patterns was significantly improved. The family Caristiidae is currently divided into  
40 two distinctly pronounced groups: Paracaristiinae and Caristiinae. The Paracaristiinae comprises  
41 two genera (*Neocaristius* and *Paracaristius*) and five species usually known as “small-mouth”  
42 caristiids (Stevenson & Kenaley, 2011), while the Caristiinae, in turn, includes two genera  
43 (*Caristius* and *Platyberyx*) and 13 species referred to as “large-mouth” caristiids (Stevenson &  
44 Kenaley, 2013).

45 In the current study, four species of Caristiidae are reported for the first time in Brazilian  
46 waters based on specimens collected around Rocas Atoll, Fernando de Noronha Archipelago,  
47 and sea mounts off Rio Grande do Norte. Meristic and morphometric data are provided for all  
48 specimens examined, and the identity of caristiids previously reported in Brazilian waters is  
49 further discussed.

50

## 51 **Materials and Methods**

52 The material examined in the current study is part of a large collection of mesopelagic  
53 invertebrates and fishes sampled during the ABRACOS expeditions (Acoustics along the  
54 BRAZilian COaSt), carried out in October 2015 and April 2017 and conducted by the French RV  
55 *Antea* off northeastern Brazil, including Rocas Atoll, Fernando de Noronha Archipelago, and  
56 seamounts off Rio Grande do Norte (Fig. 1). The extensive survey in 80 fishing stations from 0  
57 to 1113 m depth resulted in the collection of 11 specimens of Caristiidae, of which seven were  
58 identified at species level. Sampling was conducted using micronekton (body mesh: 40 mm, cod-  
59 end mesh: 10 mm) and mesopelagic (body mesh: 30 mm, cod-end mesh: 4 mm) nets. Trawl  
60 depth was continuously recorded using a Scanmar depth sensor fitted on the upper part of the  
61 trawl mouth.

62 Measurements and counts were mostly taken according to Hubbs & Lagler (1947). In  
63 addition, “preorbital length” and “predorsal length” were measured along the body axis  
64 (“horizontal distance”), from the tip of the snout to a vertical line passing through the anterior  
65 margin of orbit (preorbital) and through the dorsal-fin origin (predorsal). This was necessary for  
66 comparison with data provided by Stevenson & Kenaley (2011, 2013) (Duane Stevenson &  
67 Christopher Kenaley, pers. comm.). Radiographs of specimens were taken using a Faxitron LX-  
68 60 to aid fin-rays and vertebrae counts. Specimens were identified according to the keys  
69 provided by Stevenson & Kenaley (2011) and Stevenson & Kenaley (2013). All specimens  
70 examined were deposited at NPM - Fish Collection of the Núcleo em Ecologia e  
71 Desenvolvimento Socioambiental de Macaé, Universidade Federal do Rio de Janeiro (Macaé,  
72 RJ, Brazil).

73

## 74 **Results**

75

### 76 **Family Caristiidae**

77

#### 78 **Genus *Paracaristius* Trunov, Kukuev & Parin, 2006**

79

#### 80 ***Paracaristius nudarcus* Stevenson & Kenaley, 2011**

81 (Fig. 1)

82

83 **Material Examined.** NPM 4476 (1 specimen, 165 mm SL), RV *Antea*, ABRACOS #41A,  
84 Brazil, off northern Fernando de Noronha Archipelago, 03°19'59"S, 32°24'42"W to  
85 03°19'32"S, 32°25'05"W, 0–430 m depth, micronekton trawl net, 26 April 2017, 21:44–22:06h.

86

87 **Diagnoses.** According to Stevenson & Kenaley (2011), *Paracaristius nudarcus* can be  
88 distinguished from *P. aquilus* and *P. nemorosus* by the absence of fingerlike papillae along the  
89 dorsal margin of the hyoid arch and at the interhyal-posterior ceratohyal articulation, as well as  
90 dorsal-fin rays (27–31 vs. 30–33) and anal-fin rays (17–20 vs. 15–18) counts. *Paracaristius*  
91 *nudarcus* can be distinguished of *P. maderensis* by the position of the dorsal-fin origin (above

92 orbit vs. posterior to orbit) and by the arrangement of the jaw teeth (single row, except near  
93 symphyses vs. multiple rows).

94

95 **Distribution.** *Paracaristius nudarcus* has been previously reported in the western North  
96 Atlantic, eastern South Atlantic, eastern Indian Ocean, and eastern and western Pacific  
97 (Stevenson & Kenaley, 2011). The specimen reported off northern Fernando de Noronha  
98 Archipelago represents the first record of the genus and species in the western South Atlantic  
99 (Fig 2).

100

101 **Remarks.** Morphometric and meristic data for the specimen reported herein are within the range  
102 to those recorded by Stevenson & Kenaley (2011) (Table I).

103

104 **Genus *Platyberyx* Zugmayer, 1911**

105

106 ***Platyberyx andriashevi* (Kukuev, Parin & Trunov, 2012)**

107 (Fig. 3a)

108

109 **Material Examined.** NPM 4473 (1, 138 mm SL), RV *Antea*, ABRACOS #44A, Brazil, off  
110 eastern Fernando de Noronha Archipelago, 03°52'53"S, 32°17'33"W to 03°52'13"S,  
111 32°26'28"W, 0–850 m depth, micronekton trawl net, 28 April 2017, 12:44–13:17h. NPM 4475  
112 (2, 23–33 mm SL), RV *Antea*, ABRACOS #40B, Brazil, off northern Fernando de Noronha  
113 Archipelago, 03°31'12"S, 32°31'49"W to 03°31'03"S, 32°32'49"W, 0–230 m depth,  
114 micronekton trawl net, 26 April 2017, 12:14–12:37h.

115

116 **Diagnoses.** According to Stevenson & Kenaley (2013), *Platyberyx andriashevi* may be  
117 distinguished from all congeners by the following combination of characters: 36 or more  
118 vertebrae, 31 or more dorsal-fin rays, and 20 or more anal-fin rays. *Platyberyx andriashevi* may  
119 be further distinguished from its congeners, except *P. paucus* and *P. pietschi*, by the presence of  
120 laterally flattened, bladelike ventral procurrent caudal rays, and an anteriorly directed hook-like  
121 process on the third posterior-most ventral procurrent caudal ray.

122

123 **Distribution.** *Platyberyx andriashevi* has been previously reported in the north and southeast  
124 Atlantic, north and southwest Pacific, and Indian Ocean (Stevenson & Kenaley 2013; Okamoto  
125 & Stevenson 2015). The specimens reported around Fernando de Noronha Archipelago represent  
126 the first record of *Platyberyx andriashevi* in the western South Atlantic (Fig. 2).

127  
128 **Remarks.** Considering the high meristics and rigidly fixed jaw teeth of *P. andriashevi*, which  
129 argue for placement within the genus *Caristius*, the species was first described as *Caristius*  
130 *andriashevi* Kukuev, Parin & Trunov, 2012. However, due to the presence of a conspicuous  
131 lateral line, and its caudal skeleton similar to that of *P. paucus* and *P. pietschi*, Stevenson &  
132 Kenaley (2013) placed the species into the genus *Platyberyx*.

133 Morphometric and meristic data for the specimens reported herein were within the range  
134 of those recorded by Stevenson & Kenaley (2013), except for the number of pectoral-fin rays (19  
135 vs. 17-18), and the peduncle length (8.5-13.0 vs. 12.0-18.9 %SL), respectively (Table I).

136  
137 ***Platyberyx paucus* Stevenson & Kenaley, 2013**

138 (Fig. 3b)

139  
140 **Material Examined.** NPM 4474 (1, 85 mm SL), RV *Antea*, ABRACOS #44A, Brazil, off  
141 eastern Fernando de Noronha Archipelago, 03°52'53"S, 32°17'33"W to 03°52'13"S,  
142 32°26'28"W, 0–850 m depth, micronekton trawl net, 28 April 2017, 12:44–13:17h. NPM 4511  
143 (1, 97 mm SL), RV *Antea*, ABRACOS #35, Brazil, sea mounts off Rio Grande do Norte,  
144 04°19'37"S, 35°29'52"W to 04°18'32"S, 35°32'20"W, 0–630 m depth, micronekton trawl net,  
145 20 April 2017, 22:35–23:15h. NPM 4512 (1, 91 mm SL), RV *Antea*, ABRACOS #39, Brazil, off  
146 Rio Grande do Norte, 04°52'30"S, 34°35'23"W to 04°50'53"S, 34°51'05"W, 0–800 m depth,  
147 micronekton trawl net, 24 April 2017, 21:49–22:37h.

148  
149 **Diagnoses.** According to Stevenson & Kenaley (2013), *Platyberyx paucus* can be distinguished  
150 from all congeners by the following combination of characters: absence of palatine teeth and  
151 lower meristics (31 vertebrae, 24–26 dorsal-fin rays, and 15–16 anal-fin rays). It can be further  
152 distinguished from all congeners, except *P. andriashevi* and *P. pietschi*, by the presence of

153 laterally flattened, bladelike ventral procurrent caudal rays, and an anteriorly directed hook-like  
154 process on the third posterior-most ventral procurrent caudal ray (Stevenson & Kenaley, 2013).

155

156 **Distribution.** *Platyberyx paucus* is poorly known worldwide, reported from one specimen in the  
157 central North Pacific (Hawai'i, western O'ahu Island), and three specimens from the western  
158 Central Atlantic (off northern South America) (Stevenson & Kenaley, 2013). The current study  
159 reports the occurrence of three specimens off Rio Grande do Norte and around Fernando de  
160 Noronha Archipelago, which represent the first record of *P. paucus* in Brazilian waters (Fig. 2).

161 **Remarks.** Most of characters observed in our material (n=3) are within the ranges presented for  
162 the types of *Platyberyx paucus* (n=4). However, some measurements (head length, lower jaw  
163 length, prepectoral length, prepelvic length, and preanal length) of the specimens reported herein  
164 were smaller than those recorded by Stevenson & Kenaley (2013) (Table I).

165

#### 166 ***Platyberyx pietschi* Stevenson & Kenaley, 2013**

167 (Fig 3c)

168

169 **Material Examined.** NPM 4510 (1, 72 mm SL), RV *Antea*, ABRACOS #35, Brazil, sea mounts  
170 off Rio Grande do Norte, 04°19'37"S, 35°29'52"W to 04°18'32"S, 35°32'20"W, 0–630 m  
171 depth, micronekton trawl net, 20 April 2017, 22:35–23:15h.

172

173 **Diagnoses.** According to Stevenson & Kenaley (2013), *Platyberyx pietschi* can be distinguished  
174 from its congeners, except *P. andriashevi* and *P. paucus*, by the presence of an anteriorly  
175 directed hook-like process on the third posteriormost ventral procurrent caudal ray. *Platyberyx*  
176 *pietschi* can be distinguished from *P. andriashevi* by having fewer dorsal-fin rays (30–31 vs. 31–  
177 37), anal-fin rays (18–19 vs. 19–22), and vertebrae (33–35 vs. 36–39); and from *P. paucus* by  
178 having greater number of dorsal-fin rays (30–31 vs. 24–26), anal-fin rays (18–19 vs. 15–16),  
179 pectoral-fin rays (17–18 vs. 16–17), and vertebrae (33–35 vs. 31), respectively.

180

181 **Distribution.** *Platyberyx pietschi* is a poor known species, reported only from two specimens  
182 from the western Central Atlantic, one specimen from the central Pacific, and one from the

183 western South Pacific (Australia). The specimen currently reported off Rio Grande do Norte  
184 represents the first record of *P. pietschi* in the western South Atlantic (Fig. 2).

185  
186 **Remarks.** Morphometric and meristic data for the specimen reported herein were within the  
187 range of those recorded by Stevenson & Kenaley (2013), except by its number of anal-fin rays  
188 (17 vs. 18–19), dorsal-fin base length (73.6 vs. 62.9–68.7 % SL), and lower jaw length (42.9 vs.  
189 55.6–70.7 % HL), respectively (Table I).

## 190 191 **Discussion**

192 Among more than 7000 mesopelagic fish specimens caught during the two ABRACOS  
193 expeditions (October 2015 and April 2017), only 11 specimens of caristiids were collected, of  
194 which four could not be identified as they were in poor condition. Of the eighteen species of the  
195 family Caristiidae known to date, four have been reported for the first time in Brazilian waters:  
196 *Paracaristius nudarcus*, *Platyberyx andriashevi*, *Platyberyx paucus* and *Platyberyx pietschi*.

197 In addition to the caristiids reported herein, a few specimens have been previously  
198 recorded off Brazilian coast. Caires et al. (2008) recorded two specimens of *Caristius* collected  
199 off southern Brazil. The first one (MZUSP 93287) was identified as *Caristius macropus*  
200 (Bellotti, 1903), collected off State of Rio Grande do Sul, at 32°58'S, 50°35'W, 99 m depth; and  
201 the second (MZUSP 86699) was named as *Caristius* sp., collected off State of São Paulo, at  
202 26°19'49"S, 45°57'00"W, 600 m depth. The authors, however, recognized the identification of  
203 both specimens was tentative due to the lack of taxonomic revisions available at that time. Based  
204 on the recent reexamination of the specimens reported by Caires et al. (2008), *Caristius*  
205 *macropus* and *Caristius* sp. are herein reidentified as *Platyberyx andriashevi* and *Platyberyx*  
206 *pietschi*, respectively, extending the known distribution of both species to off southern Brazil.

207 Carvalho-Filho et al. (2009) also reported another caristiid, named *Caristius* sp., in the  
208 stomach content of a tropical pomfret *Eumegistus brevorti* (Poey 1860) (Bramidae), caught off  
209 State of Bahia, northeast Brazil. Unfortunately, we did not have access to this material and some  
210 important characters that allow identification are not visible on the picture (fig. 5) of the half-  
211 digested specimen.

212 Despite we consistently used two nets (micronekton and mesopelagic), specimens  
213 reported herein were caught only with the micronekton net, which has a greater mesh size and



214 seems to have a higher fishing efficiency for caristiids. This has also been found in many  
215 mesopelagic studies (e.g. Pakhomov & Yamamura 2010, Heino et al., 2011), where catch  
216 efficiency significantly differs among trawl types due to various influences from extrusion  
217 through meshes and net avoidance behavior (Kaartvedt et al., 2012). Thus, we believe the  
218 diversity of Caristiidae species observed here is not only a consequence of biogeographic  
219 patterns of this group, but also reflects the selectivity of sample methods employed. Further, as  
220 most of the Brazilian deep waters remain unexplored the current knowledge on the diversity of  
221 Caristiidae occurring in the region is probably underestimated. Additional deep-water sampling  
222 over banks, continental slopes, seamounts, and near oceanic islands would likely uncover new  
223 information on species composition and distribution of the family Caristiidae.

224

### 225 **Acknowledgment**

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236

### 237 **References**

- 238 Benfield, M.C., Caruso, J.H. & Sulak, K.J. (2009) *In Situ* video observations of two Manefishes  
239 (Perciformes: Caristiidae) in the mesopelagic zone of the northern Gulf of Mexico. *Copeia*  
240 2009, 637–641.
- 241 Caires, R.A., Figueiredo, J.L. & Bernardes, R.A. (2008) Registros novos e adicionais de  
242 teleósteos marinhos na costa brasileira. *Papéis Avulsos de Zoologia* 48, 213–225.
- 243 Carvalho-Filho, A., Marcovaldi, G., Sampaio, C. L. S., Paiva, M. I. G. & Duarte, L. A. G. 2009.  
244 First report of rare pomfrets (Teleostei: Bramidae) from Brazilian waters, with a key to

245 western Atlantic species. *Zootaxa*, 2290, 1–26.

246 Figueiredo, J.L., Santos, A., Yamaguti, N., Bernardes, R. & Rossi-Wongtschowski, C.L.D.  
247 (2002) *Peixes da Zona Econômica Exclusiva da região sudeste-sul do Brasil: levantamento*  
248 *com rede de meia-água*. Editora da Universidade de São Paulo, São Paulo.

249 Heino, M., Porteiro, F.M., Sutton, T.T., Falkenhaus, T., Godø, O.R. & Piatkowski, U. (2011)  
250 Catchability of pelagic trawls for sampling deep-living nekton in the mid-North Atlantic.  
251 *ICES Journal of Marine Science* 68, 377–389.

252 Kaartvedt, S., Staby, A. & Aksnes, D.L. (2012) Efficient trawl avoidance by mesopelagic fishes  
253 causes large underestimation of their biomass. *Marine Ecology Progress Series* 456, 1–6.

254 Kukuev, E.I., Parin, N.V. & Trunov, I.A. (2012) Materials for the revision of the family  
255 Caristiidae (Perciformes). 2. Manefishes from the East Atlantic (Redescription of  
256 *Platyberyx opalescens* Zugmayer and description of two new species *Platyberyx maui* sp.  
257 n. and *Caristius andriashevi*. *Journal of Ichthyology* 52, 185–199.

258 Kukuev, E.I., Parin, N.V. & Trunov, I.A. (2013) Materials for the revision of the family  
259 Caristiidae (Perciformes): 3. Manefishes (Genus *Caristius*) from moderate warm waters of  
260 the Pacific and Atlantic Oceans with a description of three new species from the Southeast  
261 Atlantic (*C. barsukovi* sp.n., *C. litvinovi* sp.n., *C. walvisensis* sp. n.). *Journal of Ichthyology*  
262 53, 541–561.

263 Okamoto, M., Duane E., S. & Motomura, H. (2014) First record of *Paracaristius maderensis*  
264 from the central North Pacific and a second specimen of *Platyberyx rhyton* (Perciformes:  
265 Caristiidae). *Biogeography* 16, 23–29.

266 Okamoto, M. & Stevenson, D.E. (2015) Records of two manefishes, *Platyberyx andriashevi* and  
267 *P. rhyton* (Teleostei: Perciformes: Caristiidae), from off the Ogasawara Islands, Japan.  
268 *Species Diversity* 20, 13–17.

269 Pakhomov, E.A., Yamamura, O., Brodeur, R.D., Domokos, R., Owen, K.R., Pakhomova, L.G.,  
270 Polovina, J., Seki, M. & Suntsov, A.V (2010) 38 PICES *Scientific Report of the Advisory*  
271 *Panel on Micronekton Sampling Inter-calibration Experiment*. North Pacific Marine Science  
272 Organization (PICES), Sidney, Canada.

273 Post, A. (1990) Caristiidae. In: J.-C. Quéro, J. C. Hureau, A. P. C. Karrer, and L. Saldanha (Eds),  
274 *Check-list of the Fishes of the Eastern Tropical Atlantic*. Unesco, Paris, pp. 765–766.

275 Stevenson, D.E. & Kenaley, C.P. (2011) Revision of the Manefish Genus *Paracaristius*

276 (Teleostei: Percomorpha: Caristiidae), with Descriptions of a New Genus and Three New  
277 Species. *Copeia* 3, 385–399.

278 Stevenson, D.E. & Kenaley, C.P. (2013) Revision of the Manefish Genera *Caristius* and  
279 *Platyberyx* (Teleostei: Percomorpha: Caristiidae), with Descriptions of Five New Species.  
280 *Copeia* 2013, 415–434.

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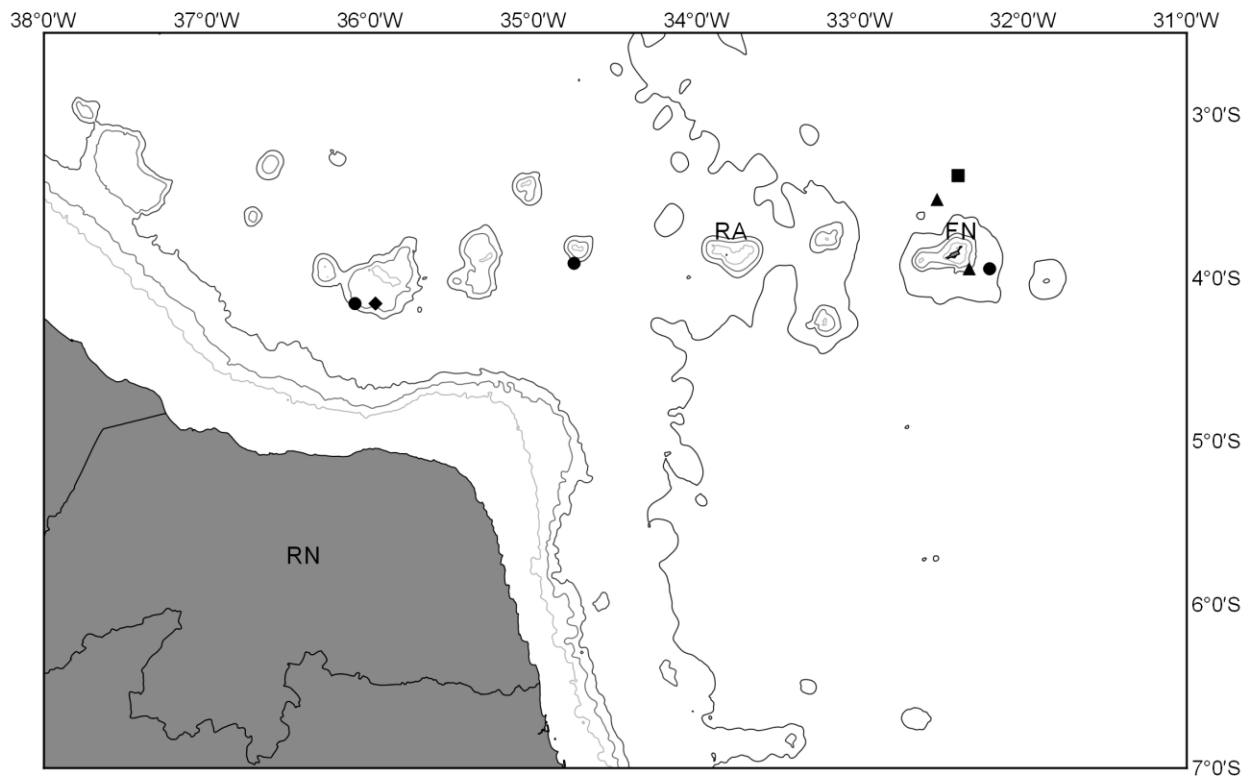
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Figures



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Figure 1. *Paracaristius nudarcus* (NPM 4476, 165 mm SL). Scale = 10 mm.



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326 Figure 2. Distribution of fishes of the family Caristiidae around oceanic islands and seamounts  
 327 off northeastern Brazil: *Paracaristius nudarcus* ( ), *Platyberyx andriashevi* ( ), *Platyberyx*  
 328 *paucus* ( ), and *Platyberyx pietschi* ( ). RN – State of Rio Grande do Norte; RA – Rocas Atoll;  
 329 FN – Fernando de Noronha Archipelago.

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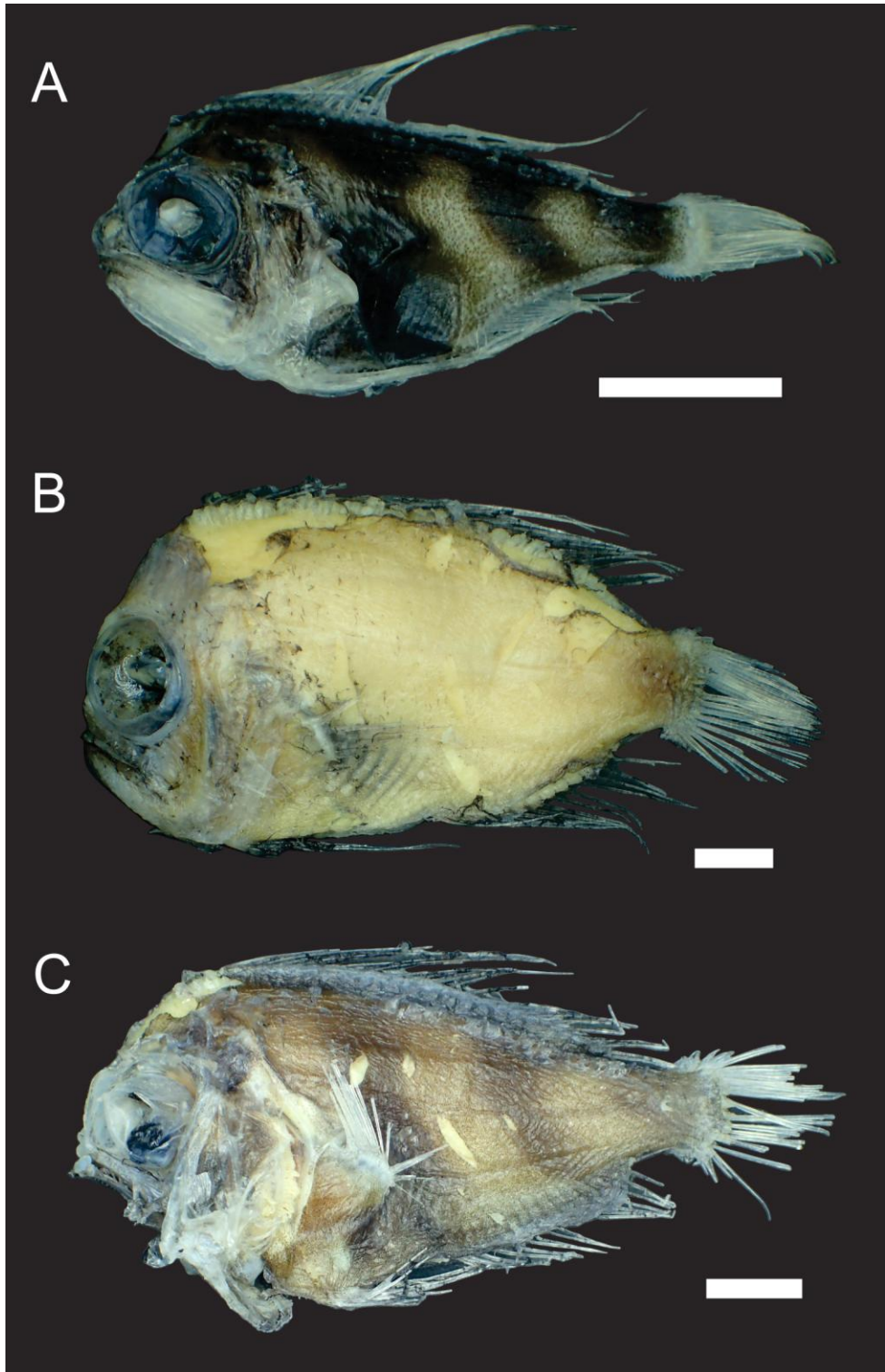
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Figure 3. A- *Platyberyx andriashevi* (NPM XXXX, XXX mm SL), B- *Platyberyx paucus* (NPM XXXX, XXX mm SL), and C- *Platyberyx pietschi* (NPM 4510, 72 mm SL). Scale = 10 mm.

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344

345 Table I. Proportions and counts for *Paracaristius nudarcus*, *Platyberyx andriashevi*, *Platyberyx*  
346 *paucus* and *Platyberyx pietschi* collected off northeastern Brazil (western South Atlantic) and  
347 compared with those reported in the literature.

Species	<i>Paracaristius nudarcus</i>		<i>Platyberyx andriashevi</i>		<i>Platyberyx paucus</i>		<i>Platyberyx pietschi</i>	
	Present study	Stevenson & Kenaley (2011)	Present study	Stevenson & Kenaley (2013)	Present study	Stevenson & Kenaley (2013)	Present study	Stevenson & Kenaley (2013)
Standard length (SL, mm)	165 (1)	22-223 (17)	23-138 (3)	32-196 (18)	85-97 (3)	21-100 (4)	72 (1)	34-93 (4)
Vertebrae	37 (1)	33-37 (16)	37-39 (3)	36-39 (16)	31-32 (3)	31 (4)	33 (1)	33-35 (3)
Dorsal-fin rays	28 (1)	27-31 (17)	31-35 (3)	31-35 (16)	25-26 (3)	24-26 (4)	30 (1)	30-31 (3)
Anal-fin rays	18 (1)	17-20 (17)	21-22 (3)	20-22 (16)	15-17 (3)	15-16 (4)	17 (1)	18-19 (4)
Pectoral-fin rays	16 (1)	16-18 (15)	19 (3)	17-18 (16)	16-17 (3)	16-17 (4)	18 (1)	17-18 (4)
Vomerine teeth	Absent	Absent	4-7 (3)	3-12 (15)	5 (1)	1-6 (4)	8 (1)	8-10 (4)
Palatine teeth	Absent	Absent	4-12 (3)	3-12 (15)	Absent	Absent	-	6-10 (4)
Upper jaw teeth	-	24-43 (10)	16-22 (3)	12-35 (12)	42-43 (2)	42 (1)	48 (1)	32-45 (3)
Lower jaw teeth	-	16-36 (7)	19-27 (2)	11-26 (7)	42-53 (2)	37 (1)	20 (1)	16-30 (2)
Upper gill rakers	8 (1)	5-8 (16)	7-8 (3)	5-8 (15)	7 (3)	6-7 (4)	7 (1)	6-7 (4)
Lower gill rakers	15 (1)	14-16 (16)	11-14 (3)	12-15 (15)	14-15 (3)	14-16 (4)	13 (1)	13-14 (4)
Total gill rakers	23 (1)	20-24 (16)	18-22 (3)	18-22 (15)	21-22 (3)	21-23 (4)	20 (1)	19-21 (4)
<i>Measurements in % of SL</i>								
Body depth	58.2 (1)	53.0-77.0 (15)	45.7-48.5 (2)	37.9-49.6 (18)	55.4-57.1 (3)	52.1-68.3 (4)	53.75 (1)	45.6-53.0 (4)
Head length	32.2 (1)	29.0-45.7 (14)	28.6-40.6 (2)	24.2-39.9 (18)	36.7-38.8 (3)	39.9-54.1 (3)	38.9 (1)	33.4-41.3 (4)
Predorsal length	31.5 (1)	-	25.7-30.3 (2)	-	34.5-37.2 (3)	-	34.7 (1)	-
Predorsal length (horizontal)	12.1 (1)	6.5-17.9 (15)	9.4-11.5 (2)	8.3-22.3 (18)	16.5-23.7 (3)	17.2-29.0 (3)	18.9 (1)	16.9-25.9 (4)
Prepectoral length	34.5 (1)	30.4-42.2 (12)	28.6-37.9 (2)	11.6-42.8 (18)	38.2-44.8 (3)	45.8-53.9 (3)	41.3 (1)	39.6-44.4 (4)
Prepelvic length	30.6 (1)	30.5-42.1 (15)	25.5-33.3 (2)	22.4-39.6 (18)	30.6-38.7 (3)	39.3-49.4 (3)	38.9 (1)	36.1-52.7 (4)
Pectoral-fin base	7.9 (1)	6.4-11.9 (15)	6.9-9.1 (2)	5.3-11.5 (17)	7.1-11.0 (3)	7.8-10.6 (4)	9.0 (1)	7.1-9.7 (4)
Preanal length	59.7 (1)	55.5-70.9 (15)	43.0-60.6 (2)	44.6-58.1 (18)	59.3-62.4 (3)	65.3-72.9 (3)	58.1 (1)	54.5-64.7 (4)
Dorsal-fin base	77.6 (1)	72.2-86.3 (15)	75.8-79.7 (2)	65.9-80.8 (18)	62.9-73.8 (3)	61.0-71.7 (4)	73.6 (1)	62.9-68.7 (4)
Anal-fin base	43.3 (1)	34.1-49.6 (15)	31.8-47.6 (2)	31.6-53.3 (18)	34.1-35.7 (3)	29.1-37.7 (4)	33.3 (1)	28.7-37.3 (4)
Peduncle length	16.5 (1)	10.9-16.5 (15)	8.5-13.0 (2)	12.0-18.9 (18)	13.9-17.0 (3)	12.1-14.8 (4)	13.9 (1)	13.5-17.4 (4)
Peduncle depth	15.8 (1)	12.8-17.7 (15)	10.3-10.9 (2)	8.5-12.8 (18)	14.4-15.9 (3)	14.5-16.6 (4)	12.5 (1)	10.7-14.6 (4)
Head length (HL, mm)	53.2 (1)	-	13.4-39.5 (2)	-	32.8-35.6 (3)	-	20.0 (1)	-
<i>Measurements in % of HL</i>								
Upper jaw length	37.6 (1)	34.7-52.8 (13)	64.3-68.7 (2)	58.8-74.7 (18)	45.3-51.8 (3)	49.8-71.0 (3)	67.9 (1)	58.6-69.4 (4)
Lower jaw length	36.7 (1)	39.3-50.4 (13)	51.4-54.5 (2)	52.2-84.6 (18)	39.7-46.1 (3)	48.8-57.3 (2)	42.9 (1)	55.6-70.7 (4)
Bony orbit length	38.3 (1)	33.1-45.5 (14)	45.6-52.2 (2)	40.0-52.6 (18)	44.8-50.6 (3)	49.1-51.4 (3)	46.4 (1)	43.7-51.9 (4)
Preorbital length	22.6 (1)	-	14.9-17.7 (2)	-	16.8-20.2 (3)	-	17.9 (1)	-
Preorbital length (horizontal)	13.2 (1)	6.5-17.4 (14)	14.4-14.9 (2)	-	7.6-11.2 (3)	-	10.7 (1)	-