Revision of the Manefish Genus *Paracaristius* (Teleostei: Percomorpha: Caristiidae), with Descriptions of a New Genus and Three New Species

Duane E. Stevenson¹ and Christopher P. Kenaley²

The family Caristiidae, commonly known as manefishes or veilfins, includes seven species of mesopelagic, oceanic fishes found throughout the major ocean basins of the world. We present a partial revision of the family, including all of the “small mouth” species, which are distinguished from other species of the family by having an upper jaw that extends approximately to midorbit and is almost completely covered by the thin bones of the suborbital series, a broad suborbital space, and by the lack of palatine teeth. This group, previously thought to include only the genus *Paracaristius*, is described in full, including the establishment of a new genus and three new species. The new genus *Neocaristius* includes only *Neocaristius heemstraia*, a distinctive species that is distinguished from all other species in this group by dentition, lateral-line morphology, dorsal-fin origin, and orbit size, as well as other meristic and morphometric characters. *Neocaristius heemstraia* is a circumneutral species, known from the South Atlantic, South Pacific, and southern Indian Ocean. The genus *Paracaristius* includes four species, *P. maderensis* and three species newly described herein. Species of *Paracaristius* are distinguished from each other on the basis of meristics, dentition, presence or absence of papillae on the hyoid arch, and placement of the dorsal fin. Two species of *Paracaristius*, *P. nemorus*, new species, and *P. aquilus*, new species, are apparently restRICTED to the eastern tropical Atlantic, while the other two, *P. nudarcus*, new species, and *P. maderensis* are more widespread.

The family Caristiidae includes seven currently recognized species of mesopelagic fishes found throughout the tropical, temperate, and subarctic oceans of the world. Commonly known as manefishes or veilfins, these fishes are characterized by having large, delicate dorsal and anal fins, which can be retracted into a fleshy sheath on the dorsal or ventral surface of the body, respectively. Virtually every recent author dealing with caristiids (Scott et al., 1970; Heemstra, 1986; Post, 1990; Hartel and Triant, 1998; Paxton, 2001; Trunov et al., 2006; Tweddle and Anderson, 2008) has noted the need for a taxonomic revision of the family. In fact, there has clearly been a great deal of taxonomic confusion surrounding these fishes since the early 20th century.

Gill and Smith (1905) established the family Caristiidae for *Caristius japonicus*, a new genus and species briefly described on the basis of a specimen collected in Kagoshima Bay off southern Japan. Over the proceeding century, several additional caristiid species were described (*Platyberyx opalescens* Zugmayer, 1911; *Caristius groenlandicus* Jensen, 1941; *Caristius maderensis* Maul, 1949; all from the North Atlantic), and two species originally described in the bramid genus *Pteraclis* (*P. macropus* Bellotti, 1903, from the North Pacific; and *P. fasciatus* Borodin, 1930, from the North Atlantic) were recognized as caristiids. Most recent authors have included all these species in the genus *Caristius* (Post, 1990) or in the two genera *Caristius* and *Platyberyx* (Maul, 1949; Post, 1986).

Recently, Trunov et al. (2006) erected the genus *Paracaristius* to accommodate *P. heemstraia*, which they described from a single specimen collected in the South Atlantic. They included two species in *Paracaristius*, *P. heemstraia* and *P. maderensis*, established *Caristius maderensis* Maul, 1949, as the type species, and referred all other known caristiid species to *Caristius*. They also distinguished *Paracaristius* from *Caristius* on the basis of jaw morphology, dentition, and vertebral counts, among other characters. Externally, the most obvious characteristic that distinguishes *Paracaristius* from all other known species of Caristiidae is the expanded suborbital series, which creates a broad space between the orbit and mouth and overlaps the bones of the upper jaw (Trunov et al., 2006:figs. 1–3).

During the course of an ongoing worldwide revision of the Caristiidae, we have concluded that the genus *Paracaristius*, as defined by Trunov et al. (2006), includes several undescribed species, and that *P. heemstraia* is sufficiently different from all other caristiid species that it should be recognized in a separate monotypic genus. This work is the first of two published efforts, the components of which will constitute a full worldwide revision of the Caristiidae. The first part of this study covers the recently described genus *Paracaristius*, including the description of three new species, and establishes a new genus for *P. heemstraia*. A forthcoming contribution will address caristiid species with a narrow suborbital space, including the genera *Platyberyx* and *Caristius*.

MATERIALS AND METHODS

Methods of counting and measuring follow Hubbs and Lagler (1958). The last two rays of the dorsal and anal fins articulate with the same pterygiophore, and are here counted as a single element. Meristic data were obtained from standard and digital radiographs. Anomalous counts obtained from damaged fins are denoted by an asterisk (*) and are not included in ranges. Morphometric data are reported as a percent head or standard length (HL and SL) throughout. Body measurements were made with digital calipers, rounded to the nearest 0.1 mm. Counts and proportions for all species are summarized in Table 1 and are presented in the text as a range with the holotype value in parentheses. Only subadults and adults larger than 25 mm SL were included in the study. Sex was determined by gross microscopic examination of gonads. Institutional abbreviations are as listed by Sabaj Pérez (2010).

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KEY TO THE KNOWN SPECIES OF NEOCARISTIUS AND PARACARISTIUS

1a. Suborbital series expanded, overlapping bones of the upper jaw and creating a broad space between orbit and mouth; upper jaw short, extending approximately to midorbit; palatine teeth absent; vomerine teeth present or absent

1b. Suborbital series not expanded, space between orbit and mouth narrow; upper jaw relatively long, extending to posterior margin of orbit; palatine and vomerine teeth present

Caristius/Platyberyx group

2a. Vomerine teeth present (rarely absent); pharyngobranchial teeth shorter than rakers of first gill arch; lateral line present, pored scales terminating just beyond half SL; predorsal distance >87% HL; bony orbit >42% SL; anteriormost dorsal-fin pterygiophores oriented dorsoventrally, perpendicular to body axis (Fig. 1A); vertebral 32–35, usually 33 or 34; pectoral-fin rays 18–20; gill rakers 16 or more on lower portion of first gill arch

Neocaristius heemstrai

2b. Vomerine teeth absent; pharyngobranchial teeth long and needle-like, approximately the same length as rakers of first gill arch; lateral line absent; predorsal distance <87% HL; bony orbit <45% SL; anteriormost dorsal-fin pterygiophores radiating anteriorly, not perpendicular to body axis (Fig. 1B); vertebral 33–37, usually 35 or 36; pectoral-fin rays 16–18; gill rakers 16 or fewer on lower portion of first gill arch

Paracaristius madorensis

3a. Fingerlike papillae present along dorsal margin of hyoid arch and at articulation of interhyal and posterior ceratohyal; dorsal-fin rays 27–31; anal-fin rays 17–20

3b. Fingerlike papillae present along dorsal margin of hyoid arch and at articulation of interhyal and posterior ceratohyal (Fig. 2A); dorsal-fin rays 30–33; anal-fin rays 15–18

4a. Dorsal-fin origin posterior to orbit; jaw teeth arranged in multiple rows

Paracaristius madocaristius, new species

4b. Dorsal-fin origin above orbit; jaw teeth arranged in single row, except near symphyses

Paracaristius nemorosus, new species

5a. Body shape oval; maximum body depth ≥50% SL; caudal peduncle relatively short and deep, its depth greater than its length

Paracaristius aquilus, new species

5b. Body shape rectangular; maximum body depth ≤50% SL; caudal peduncle relatively long and shallow, its depth less than its length

Paracaristius maderensis

Neocaristius, new genus

Type species.—Paracaristius heemstrai Trunov et al., 2006, by monotypy.

Diagnosis.—Neocaristius is distinguished from all other caristiid genera by the presence of vomerine teeth and absence of palatine teeth (versus vomerine and palatine teeth absent in Paracaristius, and vomerine and palatine teeth present in all other caristids), posteriorly placed dorsal-fin origin (predorsal distance >87% HL versus <87% HL in all other caristids), and vertically oriented anteriormost dorsal-fin pterygiophores (versus radiating anteriorly in all other caristiids). Neocaristius can additionally be distinguished from Paracaristius by the short pharyngobranchial teeth (versus long and needle-like in Paracaristius), presence of a lateral line, orbit size (>42% SL versus <45% SL in Paracaristius), and meristics. Neocaristius can additionally be distinguished from all other caristiid genera by the broad suborbital space, with an expanded suborbital shield of bony elements, and by the small mouth, with upper jaw covered laterally by suborbitals and not extending to posterior margin of orbit.

Description.—See species account.

Remarks.—The genus Neocaristius includes a single species, N. heemstrai. This species was originally placed in Paracaristius (Trunov et al., 2006) but is here placed in a separate new genus in order to recognize the significant morphological differences between it and the other species included here in Paracaristius.

Etymology.—From the Greek neo, meaning “new,” and Caristius, a genus masculine in gender.

Neocaristius heemstrai (Trunov, Kukuev, and Parin, 2006)

Figures 1A, 3, 4A, 5A; Table 1


Paracaristius heemstrai Trunov et al., 2006:445. Type locality: South Atlantic, 42°26’S, 0°15’E.

Holotype.—ZIN 52281, 118 mm, S Atlantic, Discovery Seamounts, 42°26’S, 0°15’E, 1300–1360 m, 30 March 1981 (not examined).

Non-type material.—(32 specimens, 93–220 mm SL) CSIRO 1136-01, 140 mm (♂), off Tasmania, 19 February 1985; CSIRO 1137-01, 150 mm (♂), off Tasmania, 47°52’S, 148°23’E, 1400 m, 22 March 1986; CSIRO 764-01, 148 mm (♂), off Tasmania, 12 February 1985; IORAS 02781, 170 mm (♂), Indian Ocean, off South Africa, 33°41’S, 27°26’E, 0–1220 m, 1 September 1973; IORAS 02790, 154 mm (♂), Indian Ocean, off South Africa, 34°2’S, 44°58’E, 1230–1280 m, 26 July 1976; IORAS 02791, 180 mm (♂), Indian Ocean, off South Africa, 31°58’S, 34°45’E, 1250–1275 m, 29 June 1979; NMNZ P14765, 92 mm (sex unknown), CS, off New Zealand, Challenger Plateau, 42°58.35’S, 168°46.9’E, 1035 m, 14 October 1983; NMNZ P15000, 125 mm (♂), off New Zealand, Challenger Plateau, 43°3.75’S, 168°23.75’E, 1092 m, 14 October 1983; NMNZ P17578, 140 mm (♂), off New Zealand, Chatham Is., 42°48.9’S, 175°43.8’W, 1100–1101 m, 20 July 1985; NMNZ P19675, 175 mm (♂), off New Zealand, Doubtless Bay, 34°51.65’S, 174°41.5’E, 923–955 m, 6 April 1986; NMNZ P21034, 175 mm (♂), off New Zealand, east coast, 38°30’S, 178°20’E; NMNZ P23778, 145 mm (♂), off New Zealand, Chatham Rise, 44°37.1’S, 178°4’W, 1141 m, 22 October 1988; NMNZ P24813, 185 mm (♂), off New Zealand, Hikurangi Trench, 39°41.2’S, 178°14.6’E, 1000–1074 m; NMNZ P25880, 174 mm (♂), off New Zealand, Chatham Rise, 42°38.75’S, 176°5.95’E, 1014–1022 m, 15 June 1990; NMNZ P27213, 2 (150–193 mm (♂), off New Zealand, Wairarapa Coast, 40°30’S, 176°45’E, April 1991; NMNZ P27569, 116 mm (♂), off New Zealand, Chatham Rise, 44°42.5’S, 174°39.8’W, 1010–1062 m, 28 October 1991; NMNZ P28682, 170 mm (♂), off New Zealand, Chatham Is., 42°39.6’S, 176°43.25’W, 1396–1410 m, 14 July
Table 1. Meristic Characters and Proportional Morphometric Characters for All Species of *Neocaristius* and *Paracaristius*.

<table>
<thead>
<tr>
<th></th>
<th><em>Neocaristius heemstrai</em></th>
<th><em>Paracaristius maderensis</em></th>
<th><em>Paracaristius nudarcus</em></th>
<th><em>Paracaristius nemorosus</em></th>
<th><em>Paracaristius aquilus</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Range</td>
<td>Mean</td>
<td>n</td>
<td>Range</td>
<td>Mean</td>
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<tr>
<td>Standard length (mm)</td>
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<td>32</td>
<td>180–247</td>
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<td>22–223</td>
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<td>Vertebras</td>
<td>14–16</td>
<td>15.3 ± 32</td>
<td>16–17 ± 16</td>
<td>15.3 ± 18</td>
<td>16–19 ± 16</td>
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<tr>
<td>Dorsal-fin rays</td>
<td>28–31</td>
<td>29.9 ± 31</td>
<td>29–31</td>
<td>27–31</td>
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</tr>
<tr>
<td>Anal-fin rays</td>
<td>18–21</td>
<td>19.5 ± 31</td>
<td>18–19</td>
<td>17–20</td>
<td></td>
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<tr>
<td>Pectoral-fin rays</td>
<td>18–20</td>
<td>19.0 ± 31</td>
<td>16–18</td>
<td>16–18</td>
<td></td>
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<tr>
<td>Vomerine teeth</td>
<td>0–20</td>
<td>NA ± 30</td>
<td>Absent</td>
<td>Absent</td>
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<tr>
<td>Palatine teeth</td>
<td>NA ± 32</td>
<td>Absent</td>
<td>NA ± 8</td>
<td>Absent</td>
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<tr>
<td>Upper jaw teeth</td>
<td>17–58</td>
<td>NA ± 30</td>
<td>34–85</td>
<td>24–43</td>
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<tr>
<td>Lower jaw teeth</td>
<td>11–45</td>
<td>NA ± 31</td>
<td>20–72</td>
<td>16–36</td>
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<tr>
<td>Gill rakers</td>
<td>6–8 ± (24.0)</td>
<td>7 ± 15–16 ± (22.3)</td>
<td>5–8 ± (21.9)</td>
<td>6–8 ± (21.3)</td>
<td></td>
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<tr>
<td>As % SL</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Body depth</td>
<td>49.9–59.9</td>
<td>56.1 ± 28</td>
<td>49.6–57.6</td>
<td>62.5 ± 15</td>
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<tr>
<td>Head length</td>
<td>32.5–41.8</td>
<td>36.0 ± 30</td>
<td>29.0–34.3</td>
<td>37.8 ± 14</td>
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<td>Predorsal length</td>
<td>21.5–34.6</td>
<td>28.0 ± 30</td>
<td>15.9–24.5</td>
<td>19.6 ± 7</td>
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<td>Prepectoral length</td>
<td>33.2–41.2</td>
<td>37.4 ± 30</td>
<td>31.7–40.4</td>
<td>35.7 ± 12</td>
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<td>Prepelvic length</td>
<td>32.6–40.1</td>
<td>37.4 ± 30</td>
<td>27.8–46.2</td>
<td>34.5 ± 7</td>
<td></td>
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<tr>
<td>Pectoral-fin base</td>
<td>6.4–9.1</td>
<td>7.3 ± 30</td>
<td>6.7–7.6</td>
<td>7.1 ± 7</td>
<td></td>
</tr>
<tr>
<td>Preanal length</td>
<td>50.5–69.4</td>
<td>59.6 ± 29</td>
<td>59.0–69.6</td>
<td>64.3 ± 7</td>
<td></td>
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<tr>
<td>Dorsal-fin base</td>
<td>59.7–70.0</td>
<td>64.6 ± 29</td>
<td>66.0–75.3</td>
<td>72.4 ± 7</td>
<td></td>
</tr>
<tr>
<td>Anal-fin base</td>
<td>33.1–42.5</td>
<td>39.0 ± 29</td>
<td>33.7–38.0</td>
<td>35.6 ± 7</td>
<td></td>
</tr>
<tr>
<td>Peduncle length</td>
<td>11.4–16.0</td>
<td>14.3 ± 31</td>
<td>11.4–14.5</td>
<td>13.0 ± 8</td>
<td></td>
</tr>
<tr>
<td>Peduncle depth</td>
<td>10.5–13.3</td>
<td>12.3 ± 31</td>
<td>14.9–16.0</td>
<td>15.5 ± 8</td>
<td></td>
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<tr>
<td>As % HL</td>
<td></td>
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<tr>
<td>Upper jaw length</td>
<td>24.9–42.9</td>
<td>29.6 ± 30</td>
<td>44.4–52.2</td>
<td>48.0 ± 5</td>
<td></td>
</tr>
<tr>
<td>Lower jaw length</td>
<td>40.5–50.8</td>
<td>43.9 ± 30</td>
<td>39.5–49.2</td>
<td>43.9 ± 5</td>
<td></td>
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<tr>
<td>Bony orbit width</td>
<td>42.3–53.2</td>
<td>48.2 ± 31</td>
<td>37.0–43.8</td>
<td>41.6 ± 6</td>
<td></td>
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<tr>
<td>Preorbit length</td>
<td>10.7–22.1</td>
<td>15.4 ± 29</td>
<td>5.6–21.3</td>
<td>13.0 ± 6</td>
<td></td>
</tr>
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</table>

Stevenson and Kenaley—Partial revision of Caristiidae

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1992; NMNZ P30766, 155 mm (♂), off New Zealand, Hikurangi Trough, 41°4.35′S, 176°41.38′E, 930–1000 m, 8 April 1993; NMNZ P30767, 165 mm (♂), off New Zealand, Hikurangi Trough, 40°2.62′S, 177°41.82′E, 1339–1358 m, 31 March 1993; NMNZ P31056, 134 mm (♂), off New Zealand, Ritchie Bank, 39°29.17′S, 178°24.1′E, 818–956 m, 14 June 1993; NMNZ P31672, 194 mm (♀), off New Zealand, Mercury Knoll, 10 July 1994; NMNZ P33064, 118 mm (sex unknown), off New Zealand, East Cape Ridge, 37°42.42′S, 179°14.5′E, 974–1086 m, 16 May 1995; NMNZ P33436, 146 mm (♂), off New Zealand, Chatham Rise, 44°S, 178 W, 9 December 1993; NMNZ P35107, 203 mm (♀), off New Zealand, Mernoo Bank, 43°30′S, 176°E, 12 April 1998; NMNZ P37294, 219 mm (♀), off New Zealand, near White Island, 37°16′S, 177°12′E, 850–1200 m, 8 April 2000; NMNZ P37304, 204 mm (♀), off New Zealand, North Challenger Plateau, 37°29′S, 169°19′E, 1000 m, 7 March 2000; NMNZ P37336, 180 mm (♀), off New Zealand, eastern Bellona Trough, 39°49′S, 167°7′E, 10 June 1999; NMNZ P37690, 197 mm (♂), off New Zealand, Lord Howe Rise, 37°18′S, 167°16.3′E, 964 m, 7 June 2000; NMNZ P37885, 148 mm (♂), off New Zealand, east of Stewart I., 46°46.6′S, 170°29.8′E, 945 m, 13 September 2000; NMNZ P38215, 169 mm (♂), off New Zealand, northern Challenger Rise, 37°41′S, 169°19′E, 850 m, 19 March 2001; NMNZ P40994, 174 mm (♀), unplaced.

**Diagnosis.**—As given for genus.

**Counts and proportions.**—(32 specimens) Vertebrae 14–16 + 17–19 = 32–35 (33); dorsal-fin rays 28–31 (31); anal-fin rays 18–21 (22); pectoral-fin rays 18–20 (18); vomerine teeth 2–20 (absent in NMNZ P37294 and IORAS 02790); palatine teeth absent; gill rakers 6–8 + 16–19 = 22–26; pyloric caeca 5–8. Following proportions as percent SL: body depth 49.9–59.9%; head length 32.5–41.8%; predorsal length 21.5–34.6%; prepectoral length 33.2–41.2%; prepelvic length 32.6–40.1%; pectoral-fin base 6.4–9.1%; preanal length 50.5–69.4%; dorsal-fin base 59.7–70.0%; anal-fin base 33.1–42.5%; peduncle length 11.4–16.0%; peduncle depth 10.5–13.3%.

Following proportions as percent HL: upper jaw length 24.9–42.9%; lower jaw length 40.5–50.8%; bony orbit width 42.3–53.2%; preorbit length 10.7–22.1%.

**Description.**—Head laterally compressed, deep, relatively short; anterior profile rounded, steeply sloping. Preorbital space short, snout extremely compact. Nasal organ opening through two separate nares: anteroventral opening small, subcircular, surrounded by rudimentary tube, at or just dorsal to midorbit; posterodorsal opening slightly larger, subcircular, without tube, anterior to vertical midpoint of orbit; olfactory rosette conspicuous; external membrane and internal cavity of nasal organ sparsely pigmented. Eye size moderate, approximately one-half of HL, covered with thick sclera. Suborbital space broad, completely scaled, covered by thin, delicate bones; series of vertical lateralis canals radiating ventrally from suborbital canal coursing through bones just ventral to bony orbit. Opicular series thin and delicate, completely covered with cycloid scales; posterior edge of opercle, subopercle, and interopercle forming rounded margin, with shallow indentation between interopercle and subopercle. Exposed posterior margin of preopercle smooth. Scales also present on lower jaw, snout, predorsal area, and occipital region. Cephalic lateralis system opening through extensive series of supraorbital, occipital, suborbital, preopercular, and mandibular pores; series of 8 or more transverse canals radiating from anterior to posterior margins of preopercle.

*Fig. 1.* Radiographs showing orientation of anteriormost dorsal-fin pterygiophores in (A) *Neocaristius heemstrai* (NMNZ P27569, 116 mm SL), and (B) *Paracaristius nudarcus*, new species (FDNR 17906, 63 mm SL).

*Fig. 2.* Illustration of fingerlike papillae on dorsal margin of hyoid arch near articulation of interhyal and posterior ceratohyal in *Paracaristius nemorosus*, new species (BMNH 2010.11.24.2, 133 mm SL). Scale bar = 0.1 mm.
Mouth relatively small, oblique; anterior extent of upper and lower jaws equal; posterior margin of upper jaw not reaching midorbit; premaxilla and maxilla almost completely hidden by suborbital series; lower jaw deep, with broadly rounded anteroventral margin; anguloarticular–quadrate articulation at midorbit. Exposed skin of dentary, premaxilla and maxilla, and medial face of suborbital black. Dentary and premaxillary teeth small, depressible, curved posteriorly and

**Fig. 3.** *Neocaristius heemstrai* (NMNZ P27569, 116 mm SL).

**Fig. 4.** Medial view of first gill arch in (A) *Neocaristius heemstrai* (IORAS 02790, 152 mm SL), and (B) *Paracaristius aquilus*, new species (IORAS 02784, 120 mm SL). Scale bar = 1 mm.
slightly medially, in 2–3 distinct rows along most of dentary and premaxilla, diminishing to single row only near posterior terminus of dentition. Vomerine teeth rarely absent, depressible, slightly recurved, similar in size and shape to jaw teeth, in small triangular patch; palatine teeth absent. Flesh overlying dorsal surface of basihyal with simple, sparsely spaced, minute papillae, particularly near anterior margin. Dorsal and ventral oral valves broad, with lateral margins tapering to attachment with oral roof and floor; dorsal oral valve with minute papillae scattered on lingual surface, series of multifid, flailike papillae adjacent to premaxilla; ventral oral valve with small, simple, flailike papillae scattered on lingual surface.

Branchial chamber densely covered with black melanophores. Gill rakers on first arch in two series (Fig. 4A); lateral series long, knifelike, closely spaced, moderately pigmented, each with series of small bristles along dorso medial margin, more proximal bristles borne on 2–3 broadly expanded nodules, posterior half of rakers on lower portion of arch often curving slightly ventrally; medial series more stout, rounded, their lateral and medial surfaces and tips covered with small bristles; bristles borne on lateral and medial rakers interdigitating along axis of raker. Lateral and medial rakers separated by heavily pigmented fold of tissue. Pseudobranch present, bearing approximately 20 filaments equal in size and shape to gill filaments. Three distinct upper pharyngeal tooth patches, borne on pharyngobranchials 2–4, anterior and middle tooth patches each bearing approximately 40 short, depressible teeth; posterior tooth patch smaller, with approximately 20 teeth; ceratobranchials 5 with many short, depressible teeth curving slightly posteriorly, forming lower pharyngeal jaws; left and right lower pharyngeals divided by fleshy ridge. Flesh on ventromedial surface of pterygoids bearing single row of approximately 8–13 elongate, heavily pigmented, stalked multifid papillae (Fig. 5A), often surrounded by several smaller simple papillae, extending anteromedially directly anterior to most anterior pharyngobranchial tooth patch. Dorsal surface of hyoid series smooth, without papillae or projections; articulation of interhyal and posterior ceratohyal without fleshy folds.

Body somewhat ovate, maximum body depth at or near vertical through pectoral-fin base. Caudal peduncle short, deep. Scales imbricate, cycloid, distinctly annulated; small, not arranged in distinct rows, covering entire body, including isthmus and predorsal region, as well as base of pectoral and caudal fin; few scales of much larger size just posterior to pectoral-fin base. Exposed posterior margin of postcleithrum bearing one to several extremely large, fused scales forming flange in axillary space of pectoral fin. Lateral line originating at posterodorsal margin of opercle, arching posteriorly toward dorsal-fin base and extending to midbody, consisting of approximately 20 elongate, enlarged, poro-bearing scales. Dorsal fin large, delicate, rays unsegmented, anterior rays unbranched, posterior rays branched, its base extending nearly entire length of body, originating over dorsoposterior margin of preopercle, its anteriormost pterygiophores oriented vertically (Fig. 1A). Anal fin large, delicate, consisting entirely of unsegmented soft rays, its origin posterior to mid-body (beyond 50% SL) and its posterior insertion directly below insertion of dorsal fin. Dorsal-fin base and anal-fin base each flanked along their entire length by thin sheath, extending well onto posteriormost rays of both fins, scales present on sheath. Caudal fin truncate to slightly emarginate, lightly pigmented, scales covering proximal one-third or more of rays. Pectoral fin delicate, fan-like, longest rays extending beyond anal-fin origin; pectoral-fin base oblique, its dorsoanterior insertion well below lateral midline. Pelvic fins thoracic, delicate, elongate, originating under opercle, extending to anal-fin origin, retractable into deep furrow extending along ventral midline between pelvic-fin base and anal-fin origin. Scales present in furrow.

Peritoneum black. Viscera unpigmented, except for scattered melanophores present on ovary and mesenteries. Pyloric caeca long, fingerlike. Swim bladder absent.

Distribution.—Examined specimens were all collected from the southern hemisphere, from the southern Indian Ocean off the coast of Africa as well as from the South Pacific off the coasts of Tasmania and New Zealand (Fig. 6). The holotype was collected in the South Atlantic (Trunov et al., 2006).

**Paracaristius Trunov et al., 2006**

*Type species.*—*Caristius maderensis* Maul, 1949, by original designation.

*Diagnosis.*—*Paracaristius* is distinguished from all other caristiid genera by the absence of vomerine and palatine
teeth (versus vomerine teeth present and palatine teeth absent in Neocaristius, and vomerine and palatine teeth present in all other caristiids). Paracaristius can additionally be distinguished from Neocaristius by the long, needle-like pharyngobranchial teeth (versus short in Neocaristius), absence of a lateral line, orbit size (<45% SL versus >42% SL in Neocaristius), and meristics. Paracaristius can additionally be distinguished from all other caristiid genera by the broad suborbital space, with an expanded suborbital shield of bony elements, and by the small mouth, with upper jaw covered laterally by suborbitals and not extending to posterior margin of orbit.

Description.—Head laterally compressed, deep; anterior profile rounded, steeply sloping; snout extremely short. Nasal organ opening through two separate nares; anteroventral opening smaller, opening through rudimentary tube; olfactory rosette conspicuous. Eye moderate to large, covered with thick sclera. Suborbital space broad, covered by thin, delicate bones, perforated by series of vertical lateralis canals. Opercular series thin and delicate. Scales present on lower jaw, snout, predorsal area, and occipital region. Cephalic lateralis system extensive, consisting of supraorbital, occipital, suborbital, preopercular, and mandibular canals and pores.

Mouth small, oblique; premaxilla and maxilla almost completely hidden by suborbital shield; lower jaw deep, with broadly rounded anteroventral margin. Dentary and premaxillary teeth small, depressible, curved posteriorly and slightly medially. Vomerine and palatine teeth absent. Dorsal and ventral oral valves broad, with lateral margins tapering to attachment with oral roof and floor. Branchial chamber heavily pigmented. Gill rakers on first arch in two series; lateral rakers relatively long and pointed, medial rakers more stout and rounded; bristles borne on lateral and medial rakers interdigitating along axis of raker. Pseudobranch present. Three distinct upper pharyngeal tooth patches, borne on pharyngobranchials 2–4; ceratobranchials 5 with many short, depressible teeth curving slightly posteriorly, forming lower pharyngeal jaws; left and right lower pharyngeals divided by fleshy ridge.

Body laterally compressed, deep, ovate to rectangular; caudal peduncle short and deep. Scales imbricate, cycloid and distinctly annulated, covering entire body, including isthmus and predorsal region, as well as base of pectoral and caudal fin. Exposed posterior margin of postcleithrum bearing one to several extremely large, fused scales forming flange in the axillary space of pectoral fin. Lateral line not visible; modified lateral-line scales absent. Dorsal fin large, delicate, its base extending nearly entire length of body; dorsal-fin rays unsegmented, anterior rays unbranched, posterior rays branched. Anal fin large, delicate, its origin near mid-body and its posterior insertion directly below insertion of dorsal fin; anal-fin rays unsegmented. Dorsal-fin base and anal-fin base each flanked along their entire length by thin sheath, extending well onto posteriormost rays of both fins, scales present on sheath. Caudal fin truncate to slightly emarginate. Pectoral fin delicate, elongate, fan-like; longest rays extending beyond anal-fin origin; pectoral-fin base oblique, its dorsoanterior insertion well below lateral midline. Pelvic fins thoracic, delicate, elongate, extending well beyond anal-fin origin; retractable into deep furrow extending along ventral midline between pelvic-fin base and anal-fin origin.


Remarks.—The genus Paracaristius includes the type species, P. maderensis, and three new species described herein. This genus was erected by Trunov et al. (2006), who diagnosed it by the wide suborbital space, absence of teeth on the
palatine, and a vertebral count of 34. They also included in
the diagnosis the phrase “vomer with or without teeth” to
accommodate one species with vomerine teeth (which they
recognized as *P. heemstrai*; Trunov et al., 2006:442). We believe that this
difference in dentition, in addition to differences in the
pharyngeal dentition, lateral-line morphology, and orienta-
tion of the dorsal-fin pterygiophores, constitute generic-
level differences between *P. heemstrai* and the other small-
mouthed caristiid species. We therefore divide *Paracaristius*
sensu Trunov et al. (2006) into two genera: *Paracaristius*
and *Neocaristius*. Because Trunov et al. (2006) established
*P. maderensis* as the type species of *Paracaristius*, we place
*P. heemstrai* in *Neocaristius*.

**Etymology.**—From the Greek *para*, meaning “around” or
“near,” and *Caristius*, a genus masculine in gender.

**Paracaristius maderensis** (Maul, 1949)

Figure 7, Table 1

*Caristius macropus* (non Bellotti).—Norman, 1930:343–344.

**Material examined.**—(8 specimens, 180–247 mm SL) MMF 2343, holotype, 247 mm (♀), off Madeira; MMF 2344, paratype, 193 mm (sex unknown), off Madeira. Non-type material: MMF 9589 (♂), 215 mm, off Madeira; MMF 14971, 216 mm (♀), off Madeira; MMF 18669, 211 mm (♀), off Madeira; HUMZ 75114, 180 mm (♀), western central Pacific, Kyushu-Palau Ridge, 27°55’N, 134°45’E, 700 m; IORAS 02786, 185 mm (sex unknown), southern Indian Ocean, 27°58’S, 61°47’E, 0–85 m, 14 May 1981; USNM 235666, 204 mm (♂), western central Atlantic, off Bermuda, 32°4’N, 63°58’W, 0–1025 m, 22 August 1971.

**Diagnosis.**—A species of *Paracaristius* distinguished from *P. nemorosus* and *P. aquilus* by the absence of fingerlike papillae along the dorsal margin of the hyoid arch and at the interhyal–posterior ceratohyal articulation, as well as fewer dorsal-fin rays (29–31 versus 30–33 in *P. nemorosus* and *P. aquilus*) and more anal-fin rays (18–19 versus 15–18 in *P. nemorosus* and *P. aquilus*). *Paracaristius maderensis* is distinguished from *P. nudarcus* by the position of the dorsal-fin origin (posterior to orbit in *P. maderensis* versus above orbit in *P. nudarcus*) and by the arrangement of the jaw teeth (multiple rows in *P. maderensis* versus a single row, except near symphyses, in *P. nudarcus*).

**Counts and proportions.**—(8 specimens) Vertebrae 16–17 (16) + 19–20 (19) = 35–36 (35); dorsal-fin rays 29–31 (26*); anal-fin rays 18–19 (15*); pectoral-fin rays 16–18 (16); vomerine teeth absent; palatine teeth absent; gill rakers 7 + 15–16 = 22–23 (22); pyloric caeca 5–8. Following proportions as percent SL: body depth 49.6–57.6% (52.4); head length 29.0–34.3% (30.6); predorsal length 15.9–24.5% (18.5); prepectoral length 31.7–40.4% (32.5); prepelvic length...
27.8–46.2% (30.8); pectoral-fin base 6.7–7.6% (7.2); preanal length 59.0–69.6% (63.2); dorsal-fin base 66.0–75.3% (66.0); anal-fin base 33.7–38.0% (35.1); peduncle length 11.4–14.5% (13.8); peduncle depth 14.9–16.0% (15.8). Following proportions as percent HL: upper jaw length 44.4–52.2% (47.3); lower jaw length 39.5–49.2% (41.0); bony orbit width 37.0–43.8% (43.7); preorbit length 5.6–21.3% (11.9).

Description.—Head laterally compressed, deep, relatively short; anterior profile rounded, snout extremely compact. Anteroventral naris small, subcircular, surrounded by rudimentary tube, ventral to midorbit; posterodorsal naris larger, approximately twice size of anteroventral opening, more elongate, without tube, anterior to vertical midpoint of orbit; external membrane and internal cavity of nasal organ pigmented. Eye relatively large, approximately one-third to one-half of HL. Suborbital space broad, completely covered with scales; series of lateralis canals radiating ventrally from suborbital canal coursing through bones just ventral to bony orbit. Opercular series covered with cycloid scales; posterior edge of opercle, subopercle, and interopercle forming rounded margin; exposed posterior margin of preopercle smooth; series of 10–15 transverse canals radiating from anterior to posterior margins of preopercle.

Anterior extent of upper and lower jaws equal; upper jaw length approximately half of HL, posterior margin extending nearly to midorbit; anguloarticular–quadrate articulation well beyond midorbit. Dentary and premaxillary teeth in 2–3 indistinct rows along most of dentary and premaxilla, diminishing to single row only near posterior terminus of dentition. Flesh overlying dorsal surface of basihyal densely covered with multiform papillae, particularly near anterior margin. Vomer with several sparse multiform papillae. Dorsal oral valve with minute papillae scattered on lingual surface, single row of multiform papillae adjacent to premaxilla; ventral oral valve with minute multiform papillae scattered on lingual surface.

Gill rakers on first arch in two series; lateral series closely spaced, sparsely pigmented, each with approximately 20–25 needle-like bristles situated in two distinct rows along medial margin; posterior half of rakers on lower portion of arch often curving slightly ventrally; medial series with long needle-like bristles covering lateral surfaces and distal tips. Pseudobranch bearing approximately 15 filaments equal in size and shape to gill filaments. Upper pharyngeal tooth patches each bearing approximately 15–20 long, depressed needle-like teeth; lower pharyngeal toothplate with several long depressible, needle-like teeth curving slightly posteriorly. Flesh on medial surface of the pterygoids bearing 1–3 indistinct rows of stalked, multifid, shrub-like papillae, often surrounded by several smaller simple papillae, extending anteromedially directly anterior to most anterior pharyngobranchial tooth patch. Flesh overlying dorsal surface of hyoid series smooth, without papillae or projections; series of fleshy folds present at articulation of interhyal and posterior ceratohyal (few minute papillae present along junction of right interhyal and posterior ceratohyal in MMF 9589).

Body somewhat rectangular, maximum body depth at or near vertical through pectoral-fin base. Scales on body irregular in size, not arranged in distinct rows, covering entire body, including isthmus and predorsal region, as well as base of pectoral and caudal fin; several large scales just posterior to pectoral-fin base. Dorsal fin heavily pigmented, originating posterior to dorsal end of preopercle; anterior-most pterygiophores oriented diagonally, with proximal tips placed posteriorly. Caudal fin lightly pigmented, scales covering proximal one-third or more of rays. Anal fin, pectoral fins, and pelvic fins elongate, delicate, black.

Distribution.—Examined specimens were collected on both sides of the tropical North Atlantic, the Kyushu-Palau Ridge in the western tropical Pacific, and the southern Indian Ocean (Fig. 6).

Remarks.—The dorsal- and anal-fin ray counts for the holotype of this species (MMF 2343) were originally reported by Maul (1949) and later by Tolley et al. (1990) as 26 and 15, respectively. While these counts are accurate, radiographs reveal that the fins have been damaged. The presence of additional pterygiophores at the fin bases suggests that there were additional rays present at one time, and that this specimen originally had approximately 28 dorsal-fin rays and 18 anal-fin rays. The distribution of material examined indicates that P. maderensis is very broadly distributed but rarely collected.

Paracaristius nudarcus, new species

Figures 1B, 5B, 8; Table 1

Caristius sp.—Fujii, 1984:160, pl. 145C, D.
Caristius sp. cf. maderensis.—Tolley et al., 1990:159, fig. 1.

Holotype.—LACM 36068-36, 133 mm (♂), Banda Sea, 4° 17’S, 129° 34’E, 0–1800 m, 28 March 1975.

Paratypes.—(17 specimens, 22–223 mm SL) CAS 28242, 119 mm (♂), eastern North Pacific, off Baja California, 30° 12’N, 116° 34’W, 0–120 fm, 15 November 1969; FDNR 17905, 67 mm (sex unknown), CS, Gulf of Mexico, 28° 15’N, 86° 37’W, 0–900 m, 24 April 1987; FDNR 17906 (sex unknown), 63 mm, Gulf of Mexico, 27° N, 86° W, 0–600 m, 17 September 1984; GCRL 17426, 28 mm (sex unknown), western North Atlantic, off Florida, 29° 36’N, 80° 11’W, 226 m, 3 March 1977; IORAS 02774, 122 mm (♀), central North Pacific, 30° N, 176° 9’E, 0–800 m; IORAS 02779, 54 mm (sex unknown), eastern central Pacific, 1° 3’S, 97° W, 15 January 1974; IORAS 02780, 97 mm (sex unknown), western central Pacific, 2° 35’S, 147° 35’E, 14 May 1971; IORAS 02782, 63 mm (♂), CS, eastern central Pacific, 6° 25’N, 97° 20’W, 0–320 m, 11 November 1967; IORAS 02788, 223 mm (♂), southern Indian Ocean, 28° 39’S, 98° 36’E, 0–1180 m, 23 July 1977; IORAS 02789, 190 mm (♂), southern Indian Ocean, 30° 50’S, 93° 8’E, 1162 m, 2 April 1979; LACM 30189-36, 139 mm (♀), eastern central Pacific, 29° 52’N, 118° 25’W, LACM 33380-1, 65 mm (sex unknown), central Pacific, 22° N, 166° W; LACM 9507-10, 61 mm (sex unknown), eastern central Pacific, 33° 12’N, 118° 30’W, MCZ 66464, 22 mm (sex unknown), equatorial eastern Atlantic, 0° 1’N, 5° 21’E, 100–110 m; NSMT-P 59275, 125 mm (♂), western North Pacific, off Honshu, 39° N, 143° 30’E, 650–679 m; NSMT-P 59276, 199 mm (♂), western North Pacific, off Honshu, 38° 58’N, 143° 29’E, 600–627 m; UW 43326, 76 mm (♂), eastern North Pacific, off California, 35° 32’N, 121° 57’W.

Diagnosis.—A species of Paracaristius distinguished from P. nemorosus and P. aquilus by the absence of fingerlike papillae along the dorsal margin of the hyoid arch and at the interhyal–posterior ceratohyal articulation, as well as fewer dorsal-fin rays (27–31 versus 30–33 in P. nemorosus and P. aquilus) and more anal-fin rays (17–20 versus 15–18 in P. nemorosus and P. aquilus). Paracaristius nudarcus is distinguished from P. maderensis by the position of the dorsal-fin
origin (above orbit in *P. nudarcus* versus posterior to orbit in *P. maderensis*) and by the arrangement of the jaw teeth (single row, except near symphyses, in *P. nudarcus* versus multiple rows in *P. maderensis*).

Counts and proportions.—(17 specimens) Vertebrae 15–17 (17) +18–21 (19) = 33–37 (36); dorsal-fin rays 27–31 (29); anal-fin rays 17–20 (19); pectoral-fin rays 16–18 (17); vomerine teeth absent; palatine teeth absent; gill rakers 5–8 (5) + 14–16 (16) = 20–24 (21); pyloric caeca 6–9. Following proportions as percent SL: body depth 53.0–77.0% (59.1); head length 29.0–45.7% (29.0); predorsal length 6.5–17.9% (12.6); prepectoral length 30.4–43.2% (32.5); prepelvic length 30.5–42.1% (31.5); pectoral-fin base 6.4–11.9% (6.5); preanal length 55.5–70.9% (58.7); dorsal-fin base 72.2–86.3% (82.2); anal-fin base 34.1–49.6% (43.5); peduncle length 10.9–16.5% (13.2); peduncle depth 12.8–17.7% (15.2). Following proportions as percent HL: upper jaw length 34.7–52.8% (37.5); lower jaw length 39.3–50.4% (44.0); bony orbit width 33.1–45.5% (42.8); preorbit length 6.5–17.4% (12.1).

Description.—Head laterally compressed and deep; anterior profile rounded, snout extremely compact. Anteroventral naris small, subcircular, surrounded by rudimentary tube, near midorbit; posterodorsal naris larger, approximately twice size of anteroventral naris, more elongate, without tube, positioned dorsal to vertical midpoint of orbit; covered by pigmented membrane. Eye large, approximately one-third to one-half of HL. Suborbital canal coursing through bones just ventral to bony orbit. Opercular series with patches of cycloid scales; posterior edge of opercle, subopercle, and interopercle forming rounded margin; exposed posterior margin of preopercle smooth; series of 10–15 canals traversing exposed anteroposterior axis of preopercle with pores on both ends.

Anterior extent of upper and lower jaws equal; upper jaw length generally less than half HL; posterior margin of upper jaw extending to midorbit; anguloarticular–quadrate articulation anterior to posterior margin of orbit. Dentary and premaxillary teeth in 1–3 indistinct rows anteriorly at symphyses, diminishing to single row posteriorly. Flesh overlying dorsal surface of basihyal densely covered with multifid papillae, particularly near anterior margin. Vomer with several sparse multifid papillae. Dorsal oral valve with minute papillae scattered on lingual surface, single row of multifid papillae adjacent to premaxilla; ventral oral valve with minute multifid papillae scattered on lingual surface.

Gill rakers on first arch in two series; lateral series elongate, pointed, and well separated in smaller specimens, shorter and more closely spaced in larger specimens; rakers sparsely pigmented, each with approximately 10–15 needle-like bristles situated in two distinct rows along medial margin; medial series more stout, rounded, with long needle-like bristles covering lateral surfaces and distal tips. Pseudobranch bearing approximately 15–18 filaments equal in size and shape to gill filaments. Upper pharyngeal tooth patches each bearing approximately 15–20 long, depressible needle-like teeth; lower pharyngeal toothplate with several long depressible, needle-like teeth curving
slightly posteriorly. Flesh on medial surface of the pterygoids bearing 1–3 indistinct rows of stalked multifid and shrub-like papillae (Fig. 5B), often surrounded by several smaller simple papillae, extending anteromedially directly anterior to most anterior pharyngobranchial tooth patch. Flesh overlying dorsal surface of hyoid smooth, without papillae or projections (single papilla in FDNR 17906); series of fleshy folds at articulation of interhyal and posterior ceratohyal.

Body ovate, maximum body depth near vertical placed between pectoral-fin and pelvic-fin bases. Scales on body irregular in size, not arranged in distinct rows, covering entire body, including isthmus and predorsal region, and pectoral-fin and caudal-fin bases; few scales of much larger size just posterior to pectoral-fin base. Dorsal fin heavily pigmented, originating near midpoint of bony orbit; anteriormost pterygiophores oriented diagonally, with proximal tips displaced posteriorly. Caudal fin lightly pigmented, scales covering proximal one-third or more of rays. Anal fin, pectoral fins, and pelvic fins elongate, delicate, black.

Distribution.—Examined specimens were collected from the eastern and western Pacific Ocean, as well as the southern Indian and tropical Atlantic oceans (Fig. 6).

Remarks.—This species was first recognized by Tolley et al. (1990), who referred to it as Caristius sp. cf. maderensis. They distinguished it from C. maderensis on the basis of differences in gill raker morphology, dorsal-fin origin, and morphometric characters. We have confirmed that the placement of the dorsal-fin origin does distinguish these two species; in fact the dorsal-fin origin is more posterior in P. maderensis than in any other species of Paracaristius. However, the morphology of the gill rakers appears to change significantly with size in this and other species of Paracaristius; the lateral series of rakers become increasingly stout, rounded, and closely spaced in larger specimens. Therefore, gill raker morphology is not a reliably diagnostic character for any of the species of this genus. The specimen from the western North Atlantic (42°05′N, 63°35′W) reported by Trunov and Kukuev (2004) is clearly a species of Paracaristius, based on the broad suborbital space and anterior origin of the dorsal fin, and is most likely P. nudarcus, based on the reported meristic data.

Etymology.—The specific epithet is derived from the Latin adjective nudus, meaning “bare” or “naked,” and the Latin noun arcus, meaning arch, a reference to absence of fingerlike papillae on the dorsal surface of the hyoid arch.

Paracaristius nemorosus, new species
Figures 2, 9; Table 1

Holotype.—BMNH 2010.11.24.1, 82 mm (♂), eastern central Atlantic, 17°30′N, 25°01′W.

Paratypes.—(19 specimens, 36–200 mm SL) BMNH 1930.12.973, 58 mm (sex unknown), Gulf of Guinea, 2°43′S, 0°56′W; BMNH 2002.8.5.713, 138 mm (♂), Gulf of Guinea, 5°27′S, 0°31′E; BMNH 2006.8.18.1, 118 mm (♂), Cape Verde Plateau, 17°57′N, 25°8′W; BMNH 2008.3.20.4,
200 mm (♀), no collection data; BMNH 2010.11.24.2, 133 mm (♀), eastern central Atlantic, 10°46′N, 19°54′W; BMNH 2010.11.24.3, 138 mm (sex unknown), eastern central Atlantic, 17°33.5′N, 25°19′W; BMNH 2010.11.24.4, 49 mm (♀), eastern central Atlantic, 10°45′N, 20°4′W; BMNH 2010.11.24.5, 52 mm (♀), 10°38′N, 20°W; BMNH 2010.11.24.6, 36 mm, 11°58′N, 24°39′W; CAS 230837, 97 mm (♂), SE Atlantic, 742–758 m, 10 March 2007; IORAS 02784, 121 mm (♂), eastern central Atlantic, 9°55′N, 17°33′W, 750–780 m, 2 November 1969; IORAS 02793, 64 mm (sex unknown), eastern central Atlantic, 10°36′N, 17°38′W, 1450–1550 m; USNM 206895, 2 (115–170 mm ），10°52′N, 22°9′W, 608 m, 15 April 1971; ZMUC 4039, 116 mm (♂), 16°8′N, 22°22′W, 29 January 1968; ZMUC 4040, 135 mm (♂), 16°8′N, 22°22′W, 29 January 1968; ZMUC 4089, 126 mm (♀), 14°5′N, 23°12′W, 16 April 1971; ZMUC 4091, 91 mm (♂), 10°52′N, 22°9′W, 15 April 1971; ZMUC 4092, 144 mm (♂), 10°52′N, 22°9′W, 15 April 1971.

**Diagnosis.**—A species of *Paracaristius* distinguished from *P. maderensis* and *P. nudarcus* by the presence of fingerlike papillae along the dorsal margin of the hyoid arch and at the interhyal–posterior ceratohyal articulation, as well as more dorsal-fin rays (30–33 versus 27–31 in *P. maderensis* and *P. nudarcus*) and fewer anal-fin rays (15–18 versus 17–20 in *P. maderensis* and *P. nudarcus*). *Paracaristius nemorosus* is distinguished from *P. aquilus* by the greater body depth (>50% SL in *P. nemorosus* versus <50% SL in *P. aquilus*; Fig. 10A) and caudal-peduncle depth (short and deep in *P. nemorosus* versus relatively long and shallow in *P. aquilus*; Fig. 10B).

**Counts and proportions.**—(20 specimens) Vertebrae 16–19 (18) + 17–19 (18) = 34–37 (36); dorsal-fin rays 30–33 (32); anal-fin rays 15–18 (12); pectoral-fin rays 16–18 (17); vomerine teeth absent; palatine teeth absent; gill rakers 6–8 (7) + 13–16 (15) = 20–24 (22); pyloric caeca 8–12. Following proportions as percent SL: body depth 49.8–64.8% (60.3); head length 29.9–40.9% (39.5); predorsal length 5.6–18.6% (7.1); prepectoral length 23.6–41.8% (37.8); prepelvic length 30.3–38.6% (35.4); pectoral-fin base 6.1–10.0% (8.6); preanal length 57.3–69.3% (62.9); dorsal-fin base 74.5–85.8% (85.8); anal-fin base 29.8–38.3% (31.3); peduncle length 9.6–16.9% (15.1); peduncle depth 12.2–18.0% (15.6). Following proportions as percent HL: upper jaw length 31.7–59.5% (50.3); lower jaw length 40.7–52.7% (damaged); bony orbit width 33.7–43.7% (37.9); preorbit length 7.3–22.4% (10.9).

**Description.**—Head laterally compressed and deep; anterior profile rounded, snout compact. Anteroventral nasus small, subcircular, surrounded by rudimentary tube, ventral to midorbit; posterodorsal nasus larger, approximately twice the size of the anteroventral opening, more elongate, without tube, anterior to vertical midpoint of orbit; olfactory rosette conspicuous; external membrane and internal cavity of nasal organ pigmented. Eye size moderate, approximately one-third of HL. Suborbital space broad, completely covered with scales; series of lateralis canals radiating ventrally from suborbital canal coursing through bones just ventral to bony orbit. Opercular series completely covered with cycloid scales; posterior edge of opercle, subopercle, and interopercle forming rounded margin; exposed posterior margin of preopercle weakly serrated; series of 10–15 transverse canals radiating from anterior to posterior margins of preopercle.

Anterior extent of upper and lower jaws equal; upper jaw length approximately half of HL; posterior margin of upper jaw extending just beyond midorbit; anguloarticular–quadrate articulation positioned well beyond midorbit. Dentary and premaxillary teeth in one or two indistinct rows anteriorly at symphyses, diminishing to single row posteriorly. Flesh overlying dorsal surface of basihyal covered with dense, simple papillae (largest in larger specimens branched). Vomer with several sparse multifid papillae. Dorsal oral valve with minute papillae scattered on lingual surface, single row of multifid papillae adjacent to premaxilla; ventral oral valve with minute multifid papillae scattered on lingual surface.

Gill rakers on first arch in two series; lateral series relatively elongate, pointed, and well separated in smaller specimens, shorter, more closely spaced in larger specimens, sparsely pigmented, with approximately 10 needle-like bristles situated in two distinct rows along medial margin; medial series shorter, pointed, their lateral surfaces and tips covered with long needle-like bristles. Pseudobranch bearing approximately 9–15 filaments equal in size and shape to gill.
filaments. Upper pharyngeal tooth patches each bearing approximately 10 long, depressible needle-like teeth; lower pharyngeal tooth plate with several long depressible, needle-like teeth curving slightly posteriorly. Epithelium on medial surface of pterygoid series bearing irregular antero-posteriorly directed row of multifid papillae, directly anterior to most anterior pharyngobranchial tooth patch. Series of 10–15 fleshy fingerlike projections (Fig. 2) originating at articulation of interhyal and posterior ceratohyal and extending anteriorly along dorsal margin of hyoid series to proximity of first gill arch.

Body shape rhomboidal, maximum body depth near vertical placed between pectoral-fin and pelvic-fin bases. Scales on body somewhat regular in size, not arranged in distinct rows, covering entire body, including isthmus and predorsal region, as well as base of pectoral and caudal fin, a few scales of much larger size just posterior to pectoral-fin base. Dorsal fin heavily pigmented, originating near midpoint of bony orbit, its anteriormost pterygiophores oriented diagonally, with proximal tips displaced posteriorly. Caudal fin lightly pigmented, scales covering proximal one-third or more of rays. Anal fin, pectoral fins, and pelvic fins elongate, delicate, black.

**Distribution.**—Examined specimens were all collected in the eastern tropical Atlantic Ocean (Fig. 6).

**Remarks.**—*Paracaristius nemorosus* and *P. aquilus* are very similar species and can be difficult to distinguish. However, *P. nemorosus* has a consistently deeper body (Fig. 10A) and caudal peduncle (Fig. 10B) than *P. aquilus* across the examined size range and in both genders, and is generally not as darkly pigmented externally or on the peritoneum as *P. aquilus*.

**Etymology.**—The specific epithet comes from the Latin adjective *nemorosus*, meaning “forested” or “wooded,” and refers to the various series of multifid papillae in the mouth and branchial chamber.

**Paracaristius aquilus**, new species

Figures 4B, 11; Table 1

**Holotype.**—CAS 224589, 192 mm (♀), SE Atlantic, off Angola, 11°11’S, 13°24’E, 806–809 m, 4 April 2005.

**Paratypes.**—(8 specimens, 58–182 mm SL) BMNH 2008.3.20.1, 79 mm (♂), locality unknown, Discovery [?], STN 1647; CAS 222881, 129 mm (♂), SE Atlantic, off Angola, 6°57’S, 11°40’E, 705–708 m, 21 April 2005; CAS 222934, 58 mm (sex unknown), SE Atlantic, off Angola, 8°17’E, 12°42’E, 617–632 m, 15 April 2005; CAS 224587, 163 mm (♂), SE Atlantic, off Angola, 7°34’S, 12°13’E, 716–718 m, 19 April 2005; CAS 224914, 90 mm (♀), SE Atlantic, 637–646 m, 17 March 2007; CAS 230841, 182 mm (♂), off Ghana, 5°31’N, 0°18’E, 1 May 2010; IORAS 02775, 147 mm (♀), eastern central Atlantic, 22°50’N, 17°20’W, 1450–1480 m; IORAS 02784, 154 mm (♀), eastern central Atlantic, 9°55’N, 17°33’W, 750–780 m, 2 November 1969.

**Diagnosis.**—A species of *Paracaristius* distinguished from *P. maderensis* and *P. nudarcus* by the presence of fingerlike papillae along the dorsal margin of the hyoid arch and at the interhyal–posterior ceratohyal articulation, as well as more dorsal-fin rays (30–33 versus 27–31 in *P. maderensis* and *P. nudarcus*) and fewer anal-fin rays (15–18 versus 17–20 in *P. maderensis* and *P. nudarcus*). *Paracaristius aquilus* is distinguished from *P. nemorosus* by the lesser body depth (<50%
SL in *P. aquilus* versus >50% SL in *P. nemorosus*; Fig. 10A) and caudal-peduncle depth (relatively long and shallow in *P. aquilus* versus short and deep in *P. nemorosus*; Fig. 10B).

**Counts and proportions.**—(9 specimens) Vertebrae 16–18 (18) + 17–19 (18) = 35–37 (36); dorsal-fin rays 30–33 (32); anal-fin rays 16–17 (17); pectoral-fin rays 16–18 (17); vomerine teeth absent; palatine teeth absent; gill rakers 5–8 (7) + 13–15 (14) = 19–23 (21); pyloric caeca 7–11. Following proportions as percent SL: body depth 40.0–50.0% (43.4); head length 28.1–38.8% (28.1); predorsal length 5.9–16.2% (10.2); prepectoral length 30.0–39.9% (30.0); prepelvic length 26.5–36.3% (26.5); pectoral-fin base 5.5–8.3% (5.5); preanal length 53.3–65.6% (53.3); dorsal-fin base 71.9–83.9% (80.1); anal-fin base 29.8–37.3% (34.8); peduncle length 12.2–15.7% (15.3); peduncle depth 10.4–14.0% (13.7). Following proportions as percent HL: upper jaw length 33.5–55.4% (50.3); lower jaw length 42.9–51.6% (51.6); bony orbit width 30.8–40.6% (34.0); preorbit length 7.8–25.4% (16.9).

**Description.**—Head laterally compressed, deep, and relatively short; anterior profile rounded, snout compact. Anteroverentral naris small, subcircular, surrounded by rudimentary tube, ventral to midorbit; posterodorsal naris larger, approximately twice size of anteroverentral opening, more elongate, without tube, aligned with vertical midpoint of orbit; external membrane and internal cavity of nasal organ pigmented. Eye moderate, approximately one-third of HL. Suborbital space broad, completely covered with scales; series of lateralis canals radiating ventrally from suborbital canal coursing through bones just ventral to bony orbit. Opercular series completely covered with cycloid scales; posterior edge of opercle, subopercle, and interopercle forming rounded margin; exposed posterior margin of preopercle smooth; series of approximately 10–15 transverse canals radiating from anterior to posterior margins of preopercle.

Anterior extent of upper and lower jaws equal; upper jaw length usually greater than half HL, posterior margin extending beyond midorbit; anguloarticular–quadrate articulation well posterior to midorbit. Dentary and maxillary teeth in one or two indistinct rows anteriorly at symphyses, diminishing to single row posteriorly. Flesh overlying dorsal surface of basihyal densely covered with simple papillae. Vomer with several sparsely spaced multifid papillae. Dorsal oral valve with minute papillae scattered on lingual surface, single row of multifid papillae adjacent to premaxilla; ventral oral valve with minute papillae scattered on lingual surface.

Gill rakers on first arch in two series (Fig. 4B); lateral series relatively elongate, pointed, and well separated in smaller specimens, shorter and more closely spaced in larger specimens, sparsely pigmented with approximately 10 needle-like bristles situated in two distinct rows along median margin; medial series short and rounded, lateral surfaces and tips covered with long needle-like bristles. Pseudobranch bearing approximately 15 filaments equal in size and shape to gill filaments. Upper pharyngeal tooth patches each bearing approximately 10–20 long, depressible needle-like teeth; lower pharyngeal toothplate with several long depressible, needle-like teeth curving slightly posteriorly. Flesh on medial surface of pterygoid series bearing irregular anteroposteriorly directed row of 7–8 shrub-like papillae, directly anterior to most anterior pharyngobranchial tooth patch. Series of 8–13 fleshy fingerlike projections originating at articulation of interhyal and posterior ceratohyal and extending anteriorly along dorsal margin of hyoid series to proximity of first gill arch.

Body relatively elongate, maximum body depth near vertical placed between pectoral-fin and pelvic-fin bases. Scales on body somewhat regular and small in size, not arranged in distinct rows, covering entire body, including isthmus and predorsal region, as well as base of pectoral and caudal fin, few scales of much larger size just posterior to pectoral-fin base. Dorsal fin heavily pigmented, originating over midpoint of bony orbit, its anteriormost pterygiophores oriented diagonally, with proximal tips displaced posteriorly. Caudal fin lightly pigmented, scales covering proximal one-third or more of rays. Anal fin, pectoral fins, and pelvic fins elongate, delicate, black.

**Distribution.**—Examined specimens were all collected in the eastern tropical Atlantic Ocean (Fig. 6), although the locality of BMNH 2008.3.20.1 is uncertain (J. Maclaine, BMNH, pers. comm., 15 February 2011).

**Etymology.**—The specific epithet comes from the Latin *aquilus* meaning “dark in color,” and refers to the black peritoneum.

**DISCUSSION**

The “small mouth” manefishes share a number of morphological features that distinguish them from the other members of the family, notably the lack of palatine teeth and an expansion of suborbital bones that cover the upper jaw. These characters could perhaps justify the establishment of a subfamily for this group; however, our initial efforts to clear and stain specimens have not allowed us to characterize the bony elements of the suborbital space in any more detail, as they are delicate and weakly ossified. We have chosen to wait until the remainder of the family is examined to propose such a classification.

Much of the interspecific variation within this group appears in the mouth, and the morphology of the various series of teeth, gill rakers, and papillae are of vital importance in distinguishing the taxa. This is also true to some extent in the large-mouth species of the genus *Caristius* (pers. obs.), and may indicate that these fishes rely on different feeding strategies or are specialized for different prey types. The paucity of available material for *Neocaristius* and *Paracaristius* precludes a proper analysis of stomach contents, and the only previously published diet data for caristiids was based on a few specimens of *Caristius* sp. (Jansen et al., 1989). That study suggested that at least some caristiid species associate with siphonophores, either feeding directly on siphonophores or stealing their prey. Whether *Neocaristius* and *Paracaristius* associate with siphonophores is unknown, although a specimen in the Gulf of Mexico (probably *P. nudarcus*) was recently observed in close proximity to a siphonophore (Benfield et al., 2009).

For the most part, caristiids are widely distributed, occurring across several ocean basins at tropical and temperate latitudes. *Neocaristius heemstra*, *Paracaristius maderensis*, and *P. nudarcus* all fall into this category, having each been recorded from the Atlantic, Pacific, and Indian Ocean basins. *Neocaristius heemstra* appears to be restricted to the southern hemisphere, south of 30°S, while all other species treated here are found on both sides of the equator, ranging from about 40°N to 40°S. In contrast, the distributions of *P. nemorosus* and *P. aquilus* appear to be much more restricted, and specimens are known only off...
the west coast of Africa. Depth distributions are difficult to ascertain due to the broad depth ranges associated with many midwater samples, but all examined material of *N. heemstrai* was collected in hauls extending deeper than 800 m. In contrast, several examined specimens of *P. nudarcus* were collected in hauls that went no deeper than 300 m, and Benfield et al. (2009) recently reported an *in situ* observation of an unknown species of *Paracaristius*, probably *P. nudarcus*, at 496 m, indicating that this species is at least occasionally present in the upper mesopelagic zone.

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**LITERATURE CITED**


