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Taxonomic review of the deep water flathead genus *Parabembras* with description of the new species *Parabembras multisquamata* from the western Pacific Ocean (Teleostei, Parabembridae)

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Abstract
Three valid species of *Parabembras* are recognized: *P. curta*, *P. robinsoni*, and the new species *P. multisquamata*. *Parabembras robinsoni* from the southwestern Indian Ocean (South Africa to Mozambique) is easily distinguishable from the other species in having eleven spines in the first dorsal fin, a distinct symphyseal knob on the lower jaw, two preocular spines, and a single lachrymal spine. *Parabembras multisquamata* from the southwestern Pacific (Vanuatu, Papua New Guinea) and the Philippines, and *P. curta*, known from the northwestern Pacific (southern Japan to South China Sea), are similar in sharing the absence of a symphyseal knob on the lower jaw, the presence of two lachrymal spines, and a single preocular spine, but the former is clearly distinguished from the latter in usually having 10 spines in the first dorsal fin (vs. eight or nine spines in *P. curta*), 9–11 supraocular spines (vs. 6–8 in *P. curta*), 40–44 pored lateral line scales (vs. 34–39 in *P. curta*), and the pectoral fin extending beyond the level of the anus (vs. not reaching to the level of the anus in *P. curta*).

Keywords
New species, *Parabembras curta*, *Parabembras multisquamata*, *Parabembras robinsoni*, Papua New Guiana, Philippines, taxonomy, Vanuatu
Introduction

The family Parabembridae, or deep water flatheads, comprises only two species, Parabembras curta (Temminck & Schlegel, 1843) from the northwestern Pacific Ocean, and P. robinsoni Regan, 1921, from the western Indian Ocean (Eschmeyer et al. 2017). The former species was originally placed in the genus Bembras Cuvier, 1829, but assigned by Bleeker (1874) to the then monotypic genus Parabembras. Jordan and Hubbs (1925), established the family as Parabembradidae [currently Parabembradidae (van der Laan et al. 2014)], but several authors synonymized Parabembridae with Bembridae (e.g., Knapp 1986; Nelson et al. 2016).

Imamura (1996; 2004) recognized Parabembridae as a valid family on the basis of a phylogenetic analysis based on osteological and myological characters. According to Imamura (1996), the family is diagnosed by the presence of spines and absence of tubercles on the dorsal surface of the head; the lower jaw projecting beyond the tip of the upper jaw; the separation of the ascending process and the remaining part of the premaxilla; the absence of free fin rays from the pectoral fin; three spines in the anal fin; about 35–40 scales in the lateral line; and the absence of a swim bladder.

We examined four relatively recently collected (1980–2012) specimens of a species of Parabembras from the waters of Vanuatu, Papua New Guinea, and the Philippines. These specimens differ from the two currently known species of the family by the spines on the head, number of dorsal-fin spines and pored lateral line scales, and several proportional measurements, and are described herein as a new species of Parabembras. In addition, the two congeneric species P. curtus and P. robinsoni are redescribed, and a key to the species of Parabembras is presented.

Materials and methods

Counts and measurements follow Motomura (2004), except where otherwise noted. Body depths 1 and 2 are taken at the anterior insertions of the first and second dorsal fins, respectively; predorsal lengths 1 and 2 from tip the tip of the snout to the anterior insertion of the first and second dorsal fins, respectively; and the body width is measured between the uppermost part of the base of the right and left pectoral fins. Pored lateral line scales were counted from the first pored scale near the gill opening to the pored scale on the posterior margin of the hypural plate. The terminology of head spines follows Knapp et al. (2000). The standard length is abbreviated as SL. Characters given in the diagnosis of the genus were not repeated in the species descriptions. To provide an objectively defined score that summarizes the major components of variable measurements between specimens, a principal component analysis (PCA) was conducted on morphometric characters by using the function `prcomp` in the software package R 3.3.2. (R Core Team 2016). We removed the effect of changes in size by calculating the residuals from the linear regressions of changes in all variables on changes in SL (Revell et al. 2007). All variables were log-transformed prior to analysis.
The specimens examined in this study are deposited in the fish collections of the Natural History Museum, London (BMNH), Kyoto University, Kyoto and Maizuru (Faku), Muséum national d’Histoire naturelle, Paris (MNHN), National Museum of Marine Biology and Aquarium, Taiwan (NMBA), National Museum of Nature and Science, Tsukuba (NSMT), the National Taiwan University Museums, Taipei (NTUM), and the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (MCZ).

Taxonomy

Genus Parabembras Bleeker, 1874

Parabembras Bleeker, 1874: 370; Jordan and Richardson 1908: 644; Weber and de Beaufort 1911: 288; Jordan and Hubbs 1925: 281 (in family Parabembradidae); Barnard 1927: 936; Chu and Yin 1963: 478; Washington et al. 1984: 441; Knapp 1986: 481; Imamura 1996: 194 (in the monotypic family Parabembridae).

Type species. Bembras curtus Temminck & Schlegel, 1843 by monotypy.

Diagnosis. Body cylindrical, head somewhat depressed. Dorsal surface of head with spines only, tubercles absent. Ctenoid scales covering nape, postorbital, cheek, and opercular regions. Lower jaw projecting beyond upper jaw; dermal flap on posterior margin of maxillary. Two dorsal fins; first dorsal fin with 9 (rarely 8) to 11 spines; second dorsal fin with one spine and 8 or 9 soft rays. Anal fin with three robust spines and 5 soft rays. Pectoral fin without free rays. Pelvic fin with one spine and 5 soft rays, inserted below base of pectoral fin. Pored lateral line scales 34–44.

Remarks. Imamura (1996) diagnosed the then monotypic family Parabembridae on the basis of dissection of a single species, Parabembras curtus. Because of the rarity of the other species, we could not confirm the status of internal diagnostic characters given by Imamura (1996). Although Nelson et al. (2016) placed Parabembras under family Bembridae with Bembradium Gilbert, 1905: the former is clearly distinguishable from the latter in having three anal-fin spines (vs. anal-fin spines absent). In the phylogenetic analysis, Imamura (2004) recovered a sister relationship between Bembradium and Plectrogenium Gilbert, 1905, forming the family Plectrogeniidae.

Parabembras curta (Temminck & Schlegel, 1843)

Figs 1A, 2A

Bembras curtus Temminck & Schlegel, 1843: 42, pl. 16 (fig. 6–7), Nagasaki, Japan; Richardson 1846: 217, listed, Japan; Bleeker 1853: 11, listed, Japan; Bleeker 1855: 16, listed, Japan; Bleeker 1860: 49, listed, Japan; Günther 1860: 191, Sea of Japan; Boeseman 1947: 51, Nagasaki, Japan.
**Parabembras curtus**: Bleeker 1874: 370, new combination; Bleeker 1879: 12, listed, Japan; Jordan and Richardson 1908: 644, Kyushu, Japan (after Temminck and Schlegel, 1843); Weber and de Beaufort 1911: listed, 288; Jordan and Metz 1913: 54, listed, Busan, Korea; Jordan and Hubbs 1925: 281, Osaka, Japan; Reeves 1927: 12, listed, northeastern China and Korea; Liang 1951: 30, listed, Keelung, Taiwan; Kamohara 1952: 70, Tosa (= Kochi), Japan; Li 1955: 258, fig. 162, Yantai and Qingdao, Shandong, China; Nishibori 1959: 342, description of carotenoids; Chu and Jin 1963: 478, fig. 364, Zhejiang, East China Sea; Kamohara 1964: 77, listed, Tosa (=Kochi), Japan; Takegawa and Morino 1970: 386, listed, Wakasa Bay, Sea of Japan; Ochiai 1984: 321, pl. 288-A, in part, Pacific coast of Japan; Lindberg and Krasyukova 1987: 160, fig. 98 [after Temminck and Schlegel (1843)], Busan, Korea and East China Sea; Jean and Kuo 1988: 55, listed, northern Taiwan; Shen 1993: 260, pl. 66 (fig. 10), Taiwan; Suzuki and Kataoka 1997: 223, pl. 661, Owase, Mie, Japan; Randall and Lim 2000: 606, listed; Jin 2006: 490, fig. 233, Yellow Sea, Bohai Sea, northern Taiwan; Shao et al. 2008: 247, listed, Pintong, southern Taiwan; Shen and Wu 2011: 346, photo, Taiwan; Nakabo and Kai 2013: 718, 1950, key, Wakasa Bay and Kumano-nada, Japan southward to East China Sea; Shinohara et al. 2014: 247, listed, Sea of Japan; Yamamoto and Nagasawa 2015: 435, listed, East China and Yellow Seas.

**Parabembras curta**: Nakabo 2000: 614, Key, in part, Pacific coast of Japan; Shinohara et al., 2001: 318, listed, Tosa Bay; Nakabo 2002: 614 Key, in part, Pacific coast of Japan; Shinohara et al. 2005: 428, listed, Ryukyu Islands.

**Bembradium roseum** (not of Gilbert 1905): Shen and Wu 2011: 345, photo, Taiwan.

**Material examined.** FAKU 12176, 12280, 12371, 14289, 41439, 41441, 41443, 41445–41447, 106.0–193.1 mm SL (10 specimens), East China Sea, coll. Matsui and Takai, 20 Oct. 1949; FAKU 34911, 145.5 mm SL (1), Yawatamaha, Ehime, Japan, Kishida, Mar. 1962; FAKU 35093, 114.8 mm SL (1), Tosa Bay, Kochi, Japan, K. Amaoka, Mar. 1962; FAKU 37892, 37893, 37897, 143.9–154.1 mm SL (3), Shimonomoseki, Yamaguchi, Japan, N. Taniguchi, 10 Jun. 1965; FAKU 99918, 99919, 123.3–148.2 mm SL (2), Ki Oshima, Wakayama, Japan; FAKU 101901, 123.3 mm SL (1), Tsushima, Nagasaki, Japan, 31 Jul. 1973; FAKU 144461, 144462, 94.8–135.4 mm SL, Dong-gang, Pingtung, Taiwan, F. Tashiro and M. Y. Lee; NMMA 2820, 86.7 mm SL, Kaohsiung, Taiwan; NMMA 8359, 87.9 mm SL, Dong-gang, Pingtung, Taiwan, 17 Mar. 2005; NMMA 20313, 117.3 mm SL, Dong-gang, Pingtung, Taiwan, 25 May 2013.

**Diagnosis.** *Parabembras curta* is distinguished from *P. robinsoni* in the absence of a symphyseal knob on the lower jaw (vs. distinct symphyseal knob in *P. robinsoni*), presence of a single preocular spine (vs. two preocular spines), and presence of two robust lachrymal spines (vs. a single robust lachrymal spine). It is further distinguished from *P. multisquamata*, in having 6–8 supraocular spines (vs. 9–11 supraocular spines in *P. multisquamata*); nine (rarely eight) spines in the first dorsal fin (vs. 10 spines); 34–39 pored lateral-line scales (vs. 40–44 pored lateral line scales).
Figure 1. Lateral view of the three species of *Parabembras*. A. *P. curta*, FAKU 41447, 143.5 mm SL. B. *P. robinsoni*, NSMT-P 129791, 165.1 mm SL. C. *P. multisquamata*, holotype, MNHN-IC-2008-1516, 167.3 mm SL. White line indicates anus.

**Description.** Measurements are shown in Table 1. Body cylindrical, posteriorly weakly compressed, completely covered with ctenoid scales. Nasal spine simple, dorso-posteriorly directed. Anterior lachrymal with single robust spine, posterolaterally directed, in some specimens with small additional spine anteriorly; posterior lachrymal with sharp spine, posteroventrally directed. Single preocular spine present. Interorbital region narrow and weekly depressed, with 6–8 supraocular spines. Single postocular spine present, slightly larger than posteriormost supraocular spine. Suborbital ridge strongly or moderately developed, with three robust spines; tip of anteriormost spine below center of eye, second below posterior margin of eye, posteriormost below pterotic spine. Parietal spine robust and sharp, posteriolaterally directed. Three nuchal spines, one each on supratemporal, posttemporal, and supracleithrum, respectively; posttemporal in some specimens with additional spine. Pterotic with single sharp posteriorly directed spine. Preopercle with single robust posteriorly directed spine, in some specimens with supplementary spine; ventral margin of preopercle smooth. Opercle with upper and lower spines, directed slightly dorsoposteriorly and ventroposteriorly, respectively. Dermal flaps on head absent, except for flap on anterior nostril. Gill rakers blunt, usually four (in some specimens five) on upper limb; 11–13 (modally 12) on lower limb, including single (longest) raker at angle. Lateral line running parallel to dorsal contour of body, extending beyond caudal-fin base; 34–39 (modally 36) pored lateral line scales on body and 2–3 on caudal fin, each with single, robust tube.
### Table 1. Counts and measurements of three species of *Parabembras*.

|                     | *P. curtus* | *P. robinsoni* | *P. multisquamus* |
|---------------------|-------------|----------------|------------------|
|                     | *n*=23      | *n*=9          | Holotype         | Paratypes (n=3) |
| Standard length (SL in mm) |              |                |                  |                  |
| **in % SL**          |              |                |                  |                  |
| Head length          | 40.0–43.8   | 37.7–43.9      | 41.6             | 40.6             | 40.3–42.2        | 41.2             |
| Snout length         | 9.7–11.0    | 10.4           | 10.4–12.4        | 11.2             | 10.6             | 10.1–10.7        | 10.4             |
| Orbit diameter       | 11.3–14.2   | 12.5           | 11.7–14.1        | 12.6             | 12.0             | 12.3–13.9        | 13.0             |
| Body depth 1         | 16.0–20.6   | 18.2           | 14.7–18.6        | 17.1             | 16.9             | 17.9–19.8        | 18.7             |
| Body depth 2         | 15.2–18.1   | 16.6           | 13.6–16.2        | 14.8             | 16.1             | 16.5–17.4        | 17.0             |
| Body width           | 15.9–19.6   | 17.8           | 13.9–18.8        | 16.2             | 15.1             | 14.6–16.8        | 15.8             |
| Caudal peduncle depth| 8.3–10.1    | 9.1            | 7.6–8.9          | 8.1              | 9.6              | 9.6–10.4         | 10.0             |
| Upper jaw length     | 13.9–15.9   | 15.1           | 15.8–18.3        | 16.6             | 15.2             | 15.7–16.5        | 16.0             |
| Predorsal fin length 1| 37.8–41.2  | 39.3           | 37.4–41.3        | 39.2             | 40.3             | 38.1–40.9        | 39.6             |
| Predorsal fin length 2| 64.9–67.8  | 66.4           | 65.4–69.4        | 67.2             | 65.9             | 63.7–66.7        | 65.2             |
| Preanal fin length   | 66.9–71.7   | 69.0           | 64.7–66.3        | 65.4             | 65.3             | 66.0–68.5        | 66.9             |
| Preanal length       | 61.0–65.5   | 63.3           | 56.6–60.1        | 58.5             | 58.2             | 60.1–62.0        | 60.9             |
| Prepelvic length     | 34.5–39.8   | 37.5           | 36.5–39.1        | 37.5             | 37.2             | 37.5–40.3        | 39.2             |
| Pectoral fin length  | 22.5–28.4   | 26.3           | 22.6–27.3        | 25.4             | 26.4             | 24.2–28.5        | 26.6             |
| Prepectoral fin length| 36.9–40.9  | 38.4           | 38.8–42.2        | 40.0             | 38.9             | 38.9–39.6        | 39.3             |
| Pelvic fin length    | 16.7–19.8   | 18.5           | 16.3–18.8        | 17.5             | 16.3             | 16.0–19.4        | 17.2             |
| Pelvic fin spine length| 9.5–14.0  | 11.5           | 9.6–11.5         | 10.5             | 10.6             | 10.2–13.0        | 11.5             |
| **Lengths of first dorsal fin** |              |                |                  |                  |                  |                  |
| 1st dorsal-fin spine | 2.4–3.9     | 2.9            | 1.7–4.4          | 2.7              | 2.6              | 2.1–3.0          | 2.6              |
| 2nd dorsal-fin spine | 4.4–7.9     | 6.3            | 4.5–8.3          | 6.1              | 6.5              | 5.4–7.4          | 6.4              |
| 3rd dorsal-fin spine | 10.0–14.0   | 11.8           | 8.3–12.3         | 10.2             | 11.1             | 10.6–11.3        | 11.0             |
| 4th dorsal-fin spine | 14.4–20.6   | 16.5           | 11.6–15.3        | 14.0             | 14.6             | 14.7–14.7        | 14.7             |
| 5th dorsal-fin spine | 15.0–20.9   | 17.7           | 12.5–15.8        | 14.1             | 14.8             | 13.7–15.1        | 14.4             |
| **Lengths of second dorsal fin** |              |                |                  |                  |                  |                  |
| 1st dorsal-fin spine | 13.3–17.3   | 15.2           | 10.6–14.1        | 12.2             | 11.1             | 10.4–12.5        | 11.3             |
| 1st dorsal-fin ray   | 15.4–18.1   | 16.6           | 13.1–15.9        | 15.0             | 15.7             | 14.9–16.7        | 16.0             |
| 1st anal-fin spine   | 4.0–7.1     | 5.6            | 3.4–5.1          | 4.1              | 5.1              | 5.2–5.7          | 5.5              |
| 2nd anal-fin spine   | 7.8–14.8    | 11.3           | 8.9–11.2         | 10.1             | 11.9             | 10.6–13.1        | 12.0             |
| 3rd anal-fin spine   | 8.1–11.1    | 9.3            | 7.9–10.1         | 9.2              | 10.1             | 9.1–11.2         | 10.1             |
| 1st anal-fin ray     | 12.1–16.9   | 14.2           | 12.2–14.2        | 13.3             | 13.9             | 13.3–15.5        | 14.3             |
| **Counts**           |              |                |                  |                  |                  |                  |
| Dorsal fin           | VIII–IX–I, 8| IX–I, 8        | X–XI–I, 8–9      | XI–I, 9          | X–I, 8           | IX–X–I, 8        | X–I, 8           |
| Anal fin             | III, 5      | III, 5         | III, 5           | III, 5           | III, 5           | III, 5           | III, 5           |
| Pectoral fin         | 20–22       | 21             | 19–21            | 20               | 19               | 19–20            | 20               |
| Pored lateral line scales | 34–39      | 36, 37         | 38–41            | 40               | 44               | 40–44            | 43               |
| Gill rakers          | 4–5+11–13   | 4+12           | 4–5+14           | 5+15             | 5+14             | 4–5+12           | 5+12             |
Mouth large, slightly oblique; maxilla reaching anterior rim of pupil; posterior margin of maxilla with distinct notch. Upper half of maxilla fitting within groove below suborbital ridge. Symphyseal knob absent from lower jaw. Upper and lower jaws with villiform teeth arranged in a band; vomer V-shaped, with villiform teeth; tooth band on palatine narrow.

First dorsal fin originating above level of pectoral-fin base, with usually nine spines (rarely eight), gradually increasing in length to fifth spine. First and second dorsal fins well separated. Second dorsal fin with one spine and eight soft rays; first soft ray somewhat longer than spine. Second dorsal and anal fins opposite each other, nearly equal in length and height; origin of latter slightly posterior to that of former. Caudal fin rounded. Pectoral fin rounded, upper half somewhat longer than lower half; its tip not reaching to level of anus, usually with 20–22 rays (modally 21), the lower 3–8 rays unbranched.

**Coloration.** In fresh condition, head and body reddish orange, white ventrally; faint dark red saddle below first and second dorsal fins, respectively; fins red, interradial membranes pale red; posterior half of caudal fin dark red. In preserved specimens, head and body pale brown; fins pale gray without any markings.

**Geographical distribution.** Known from the western Pacific Ocean; Wakasa Bay of Sea of Japan and Kumano-nada, Pacific coast of Japan and Korea south to China and Taiwan (East China Sea, Yellow Sea, Bohai, and northern part of South China Sea) (Fig. 3). Benthic, on sandy mud substrate from depths of 60–141 m (Chu and Jin, 1963; Nakabo and Kai, 2013; present study).

**Remarks.** *Parabembras curta* was originally described as a member of *Bembras* by Temminck and Schlegel (1843) on the basis of the specimens collected in Japan 1823–1834 by Philipp von. Siebold and Heinrich Bürger. Boeseman (1947) reviewed the Siebold and Bürger’s collection, and designated RMNH-D 682 as the lectotype and RMNH-D 2057 as paralectotype of the species. According to Boeseman (1947), the lectotype has nine spines in the first dorsal fin and the paralectotype has eight spines. The figure of the species given in the original description is characterized as having
eight spines in first dorsal fin, one spine and eight rays in the second dorsal fin, a single preocular spine, seven supraorbital spines, and two robust lacrimal spines. The photo of RMNH-D 682 published by Yamaguchi and Machida (2003) indicates clearly the absence of a symphyseal knob on the lower jaw.

The short description of *P. curta* given by Günther (1860) agrees with the present specimens in the nine spines in the first dorsal fin. Jordan and Hubbs (1925), who established the family Parabembridae (originally as Parabembradidae), described *P. curta* as having nine spines in the first dorsal fin and two spines and seven rays in the second dorsal fin. Although the count of spines in the second dorsal fin is not usual for any three species recognized here, the counts of pored lateral line scales (37), gill rakers on lower limb (11) and supraocular spines (6) agreed well with the present specimens of *P. curta*. The descriptions of *P. curta* from the East China Sea given by Li (1955), Chu and Jin (1963) and Jin (2006) and that from Kochi, Japan by Kamohara (1952) are referable to the species identified here with reference to the counts of dorsal-fin spine (9) and lateral line scales (35–40). Lindberg and Krasyukova (1987) recorded *P. curta* on the basis of four specimens from Busan (Korea) and the East China Sea. They characterized the species as having nine spines in the first dorsal fin and 36–38 lateral line scales, which agrees with counts in the present specimens of *P. curta*. Suzuki and Kataoka (1997) characterized *P. curta* from Mie Prefecture, Japan as having 10 spines in the first dorsal fin. Although the count of dorsal–fin spines was rather similar to *Parabembras multisquamata* described below, the pectoral fin of their specimen does

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**Figure 3.** Distribution of the three species of *Parabembras* in the Indo-West Pacific. Circles, *P. curta*; squares, *P. robinsoni*; stars, *P. multisquamata*. Closed symbols - based on specimens examined in this study; open symbols - based on literature records. Map was made with layers from Natural Earth, free vector and raster map data at: http://naturalearthdata.com.
not reach to anus, matching the condition of the present specimens of *P. curta*. In addition, the established distributional range of *P. curta* is close to the locality of Suzuki and Kataoka’s (1997) specimen. The short description of *P. curta* given by Ochiai (1984) apparently includes several species recognized here, because he assumed that *P. curta* was widely distributed in the Indo-West Pacific, and also presented a wide range in the count of dorsal-fin rays (IX–X–I, 7–9) (which apparently also includes *P. multisquamata* and *P. robinsoni*). The photograph provided by Ochiai (1984) agrees with the present specimens of *P. curta* in the short pectoral fin (not reaching to the anus) and absence of a symphysial knob. The description of Shen (1993) apparently followed that of Ochiai (1984), but the photograph provided by him is referable to *P. curtus* recognized by the short pectoral fin (not reaching to the anus) and absence of a symphysial knob. The keys and short descriptions of *P. curtus* presented by Nakabo (2000; 2002) also apparently followed Ochiai (1984). The images of *P. curta* and *Bembradium roseum* Gilbert, 1905 published by Shen and Wu (2011) are here both identified as *P. curta* in having nine spines in the first dorsal fin and three spines in the anal fin. However, their description of *B. roseum* does not agree with the specimen shown in their photograph which has 11 anal-fin rays.

The record of *P. curta* from the eastern Indian Ocean by Lin (1974: 26, western Indonesia) cannot be verified; specimens from these regions are needed to establish their identity. Although Krakstad et al. (2014: 74, 75) listed *P. curtus* from Myanmar, this record is not based on a species of *Parabembras*, but of *Bembras* (Peter Psomadakis, pers. comm.).

**Parabembras robinsoni** Regan, 1921

Figs 1B, 2B

*Parabembras robinsoni* Regan, 1921: 418, KwaZulu-Natal, South Africa; Barnard 1927: 936; Smith 1949: 377, pl. 97, off Natal, South Africa; Smith 1961: 377, pl. 97, off Natal, South Africa; Smith 1965: 377, pl. 97, off Natal, South Africa; Knapp 1986: 482, pl. 29, fig. 154.1, Durban to southern Mozambique, South Africa; Schneider et al. 2005: 218, listed, Mozambique.

*Parabembras curtus* (not of Temminck and Schlegel 1843): Gilchrist 1922: 75, South Africa; Ochiai 1976: 105, pl. E. Afr-97, east coast of South Africa.

*Parabembras* sp.: Everett et al. 2015: 89, listed, Kenya, Tanzania, Mozambique.

**Material examined.** BMNH 1921.3.1.19 (holotype of *P. robinsoni*, photo only), 24–35 km off Umvoti River, KwaZulu-Natal, South Africa [ca. 29°32’S, 31°36’E], depth 120–130 fathoms [219–238 m], R. Robinson, 1921; MCZ 130275, 127.0 mm SL (1), off Mozambique, 25°26’S, 34°19’E, 356 m depth, RS Algoa-014, 21 June 1994 (3D CTs only); NSMT-P 129786–129792, 126.7–176.1 mm SL (9 specimens), east coast of South Africa, 25°21’S, 34°20.5’E 326 m depth, 6 Dec. 1970.

**Diagnosis.** *Parabembras robinsoni* is distinguished from its congeners in having usually 11 spines in the first dorsal fin (vs. 8–9 in *P. curta* and 9–10 in *P. multisqua-
mata), a distinct symphyseal knob in the lower jaw (vs. symphyseal knob absent in P. curta and P. multisquamata), two preocular spines (vs. single in P. curta and P. multisquamata), and single lachrymal spine (two in P. curta and P. multisquamata).

**Description.** Measurements are shown in Table 1. Body cylindrical, posteriorly moderately compressed, completely covered with ctenoid scales. Anterior lachrymal with single robust spine, posterolaterally directed, in some specimens with small additional spine anteriorly; posterior lachrymal without spine. Two preocular spines present. Interorbital region narrow and slightly depressed, with more than 12 small spines, forming a serrated ridge. Single small postocular spine present. Suborbital ridge strongly or moderately developed, with three robust spines, tip of anteriormost spine below center of eye, second below posterior margin of eye; posteriormost below pterotic spine. Parietal spine sharp, posterolaterally directed. Three nuchal spines, one each on supratemporal, posttemporal, and supracleithrum, respectively; posttemporal sometimes with additional spine. Pterotic with two sharp spines posteriorly directed. Posterior rim of orbit armed with small spines. Preopercle with single robust spine, posterolaterally directed; usually with supplementary spine; ventral margin of preopercle smooth. Opercle with upper and lower spines, slightly directed dorso-posterolaterally and posteriorly, respectively. Dermal flaps on head absent, except for flap on anterior nostril. Gill rakers blunt, usually 4–5 on upper limb; 14–16 (modally 15) on lower limb, including single (longest) raker at angle. Lateral line running parallel to dorsal contour of body, extending beyond caudal-fin base; 38–41 (modally 39) pored lateral-line scales on body and 2–3 on caudal fin, each with single, robust tube.

**Mouth large, slightly oblique; maxilla reaching level of anterior rim of pupil; posterior margin of maxilla weakly notched. Upper half of maxilla fitting within groove below suborbital ridge. Lower jaw with distinct symphyseal knob. Upper and lower jaws with villiform teeth in a band; vomer V-shaped with villiform teeth; tooth band on palatine narrow.**

**First dorsal fin originating above level of pectoral-fin base, usually with eleven spines (in some specimens ten), gradually increasing in length to fifth spine. Last spine of first dorsal fin separated from penultimate spine without membrane, positioned midway between penultimate spine of first dorsal fin and insertion of second dorsal fin. Second dorsal fin with one spine and 8–9 soft rays; first soft ray slightly longer than spine. Second dorsal and anal fins directly opposite each other, nearly equal in length and height. Caudal fin rounded. Pectoral fin usually with 19–21 rays (modally 20), lower 4–7 rays unbranched; its rounded upper half somewhat longer than lower half, slightly extending beyond level of anus.**

**Coloration.** In fresh condition, head and body reddish orange, white ventrally; fins red, interradial membranes pale red; distal margins of dorsal and anal fins dark red; posterior half of caudal fin dark red [based on pl. E. Afr-97 of Ochiai (1976)]. In preserved condition, head and body dark brown; fins pale gray; distal margin of second dorsal, anal and caudal fins dark brown.

**Geographical distribution.** Western Indian Ocean, from Durban to at least southern Mozambique, along the east coast of South Africa at depths of 200–600 m (Knapp 1986). According to Everett et al. (2015), the species may be distributed along the East African coast north to Kenya; however, these records need confirmation.
Remarks. *Parabembras robinsoni* was originally described by Regan (1921), characterized as having 10 spines in the first and one spine and nine soft-rays in the second dorsal fin. However, the last spine of the first dorsal fin, which is positioned between the penultimate ray of the first dorsal fin and the insertion of the second dorsal fin, is present in the holotype (BMNH 1921.3.1.19), which has eleven dorsal-fin spines, a distinct symphyseal knob in the lower jaw and a single lachrymal spine; hence, the present specimens are identified as *P. robinsoni*.

Barnard (1927) and Smith (1949, 1961, 1985) reported *P. robinsoni* from off the coast of KwaZulu-Natal, South Africa as having ten or eleven spines in the first dorsal fin. The short description by Knapp (1986) also characterized *P. robinsoni* as having ten or eleven spines in the first dorsal fin and a symphyseal knob in the lower jaw. These characters agree well with the present specimens of *P. robinsoni*. In contrast, Gilchrist (1922) described *P. curta* from South Africa and considered *P. robinsoni* as a junior synonym of *P. curta*. However, he described the species as having two preocular spines, agreeing with the present specimens of *P. robinsoni*, but not with *P. curta*. Similarly, Ochiai (1976) described *P. curta* from the east coast of South Africa. His photograph clearly shows *P. robinsoni*, judging by the presence of a distinct symphyseal knob in the lower jaw. Ochiai assumed that *P. curta* was widely distributed in the Indo-West Pacific, but apparently he confused *P. curta* and *P. robinsoni*. Probably due to this report, some subsequent authors mistakenly reported an occurrence of *P. curta* in the Indian Ocean (e.g., Nakabo 2000, 2002; Yamada et al. 2007).

*Parabembras multisquamata* sp. n.
http://zoobank.org/9342A016-DC81-4F49-A88E-FA17F64D42B3
Figs 1C, 2C

*Parabembras curtus* (not of Temminck and Schlegel 1843): Fricke 2015, 4, fig. 8, Morobe Province, Papua New Guinea.

**Holotype.** MNHN-IC-2008-1516, 167.3 mm SL, 15°4′12″S, 166°57′0″E, Big Bay, Espiritu Santo, Vanuatu, 408–444 m depth, R/V Alis, expedition name: SANTO 2006, Station: AT106, 15 Oct. 2006.

**Paratypes.** Four specimens. MNHN-IC-1984-0687, 170.1 mm SL, 13°49′1.2″N, 120°51′0″E, off southwestern Luzon, Philippines, 299–320 m depth, expedition name: MUSORSTOM 2; Station: 26cp4, 23 Nov. 1980; MNHN-IC-2008-2443, 2009-0115, 158.3–186.9 mm SL, 15°4′21″S, 166°51′46.8″E, Big Bay, Espiritu Santo, Vanuatu, 350–400 m depth, R/V Alis, expedition name: BOA1; Station: CP2416, 6 Sep. 2005; NTUM 10690, 146.4 mm SL, Papua New Guinea, Morobe Province, 28 km east of Lae, 06°45′03.90″S, 147°14′40.44″E – 06°45′18.24″S, 147°14′03.26″E, 360 m depth, R/V Alis, expedition name: PAPUA NIUGINI; Station: CP3999, 10 Dec. 2012.

**Diagnosis.** *Parabembras multisquamata* is distinguished from *P. robinsoni* in having two lachrymal spines and no symphyseal knob on the lower jaw. It is most similar to *P. curta*, but is clearly distinguished from the latter in having usually 10 first dorsal-
fin spines (vs. 8 or 9 spines in *P. curta*), 9–11 supraocular spines (vs. 6–8 in *P. curta*), and 40–44 pored lateral line scales (vs. 34–39 in *P. curta*).

**Description.** Measurements are shown in Table 1. Data of the holotype are given first, followed by data of the paratypes, in parentheses, if different from holotype. Body cylindrical, posteriorly weakly compressed, completely covered with ctenoid scales. Nasal spine simple, dorsoposteriorly directed. Anterior lachrymal with single robust spine, posterolaterally directed, with small additional spine anteriorly (without an additional spine in MNHN-IC-1984-0687); posterior lachrymal with sharp spine, directing posteroventrally. Single preocular spine present. Interorbital region narrow and weekly depressed, armed with 11 (9–11) supraocular spines. Single postocular spine present, somewhat larger than posteriormost supraocular spine. Suborbital ridge strongly developed (moderately developed), with three (three or four) robust spines; tip of anteriormost spine below center of eye, second below posterior margin of eye, third below pterotic spine (posteriormost on margin of preopercle). Three nuchal spines; one each on supratemporal, posttemporal, and supracleithrum, respectively. Pterotic with two sharp spines posteriorly directed. Posterior rim of orbit armed with small spines. Preopercle with single robust and several small supplementary spines, posteriorly directed; ventral margin of preopercle with three (0–5) tiny spines. Opercle with upper and lower spines, slightly dorsoposteriorly and ventoposteriorly directed, respectively. Dermal flaps on head absent, except for flap on anterior nostril. Gill rakers blunt, usually 5 (4–5) on upper limb; 14 (12–13) on lower limb, including single (longest) raker at angle. Lateral line running parallel to dorsal contour of body, extending beyond caudal-fin base; 44 (40–44) pored lateral-line scales on body and 2 (2–3) on caudal fin, each with single, robust tube.

Mouth large, slightly oblique; maxilla reaching anterior rim of pupil; posterior margin of maxilla with distinct notch. Upper half of maxilla fitting within groove below suborbital ridge. Symphyseal knob absent from lower jaw. Upper and lower jaws with villiform teeth arranged in a band; vomer V-shaped, with villiform teeth; tooth band on palatine narrow.

First dorsal fin originating above level of pectoral-fin base, usually with 10 spines (nine in MNHN-IC-2009-0115), gradually increasing in length to fifth (forth or fifth) spine. First and second dorsal fins well separated. Second dorsal fin with one spine and 8 soft rays; first soft ray somewhat longer than spine. Second dorsal and anal fins opposite each other, nearly equal in length and height; anterior insertion of latter slightly posterior to that of former. Caudal fin rounded. Pectoral fin rounded, upper half somewhat longer than lower half; its tip extending beyond level of anus, with 19 rays (19–21) of which lower 7 (6–7) rays unbranched.

**Coloration.** In fresh specimens [based on fig. 8 in Fricke (2015), NTUM 10690], head and body red, white ventrally; first dorsal fin dark red margined with black; second dorsal fin red with black marking; posterior half of caudal fin dark red; pectoral fin bright red; pelvic fin pale red. In preserved condition, head and body pale brown; first dorsal fin margined with black; second dorsal fin with dark brown marking.
Geographical distribution. Known from the western Pacific Ocean, off southwestern Luzon, Philippines, Morobe Province of Papua New Guinea, and Espiritu Santo, Vanuatu. The new species was collected at depths of 299–444 m (Fig. 3).

Etymology. The name *multisquamata* is derived from Latin *multus* meaning many and *squamatus* meaning scaled, in reference to the high number of pored lateral line scales. The name is an adjective, its ending following the feminine gender of the generic name *Parabembras*.

Remarks. Fricke (2015) reported *P. multisquamata* as *P. curtus* (non Temminck and Schlegel 1843) from Morobe Province of Papua New Guinea on the basis of a single specimen, NTUM 10690, which is now one of the paratypes of *P. multisquamata*. Judging from the collection data, the record of *P. curta* from off southwestern Luzon, Philippines by Fourmanoir (1985: 46, as *P. curtus*) was based on MNHN-IC-1984-0687, one of the paratypes of *P. multisquamata*.

Key to species of *Parabembras*

1 Lower jaw with a distinct symphyseal knob; lachrymal with single robust spine [western Indian Ocean] .................................*Parabembras robinsoni*  
  – Lower jaw without a symphyseal knob; lachrymal with 2 robust spines ......2

2 First dorsal fin usually with 10 (rarely 9) spines, head with 9–11 supraocular spines, pored lateral line scales 40–44, pectoral fin extending beyond the level of anus [southwestern Pacific Ocean and the Philippines] ............................
  .................................................................*Parabembras multisquamata*
  – First dorsal fin with 8 or 9 spines, head with 6–8 supraocular spines, pored lateral line scales 34–39, pectoral fin not reaching to the level of anus [northwestern Pacific Ocean] .................................*Parabembras curta*

Discussion

*Parabembras multisquamata* is most similar to *P. curta* in having two lachrymal spines and no symphyseal knob on the lower jaw, but is clearly distinguished as described above. These two species differ further in some morphometric characters, including the preanal length and the first spine of the second dorsal fin (Fig. 4). Furthermore, the pectoral fin of *P. multisquamata* extends beyond the level of the anus (vs. not reaching to the level of anus in *P. curta*). The PCA using 20 measurements (eight were eliminated due to the lack of data in some of the specimens) resulted in the rough separation of three species. The first and second principal components accounted for 34.4 % and 18.3 % of the variation. PC1 was heavily loaded on caudal peduncle depth, body depth 2, and length of second anal-fin spine, providing separation between *P. robinsoni* and the other two species (Fig. 5). PC2 was heavily loaded on length of second anal-fin
Figure 4. Comparison of selected morphometric characters of species of *Parabembras*; A proportion of preanal length B first spine of second dorsal fin. Circles, *P. curta*; squares, *P. robinsoni*; stars, *P. multisquamata*.

Figure 5. Plots of the first two principal components scores based on 20 body measurements of the three species of *Parabembras*. Circles, *P. curta*; squares, *P. robinsoni*; stars, *P. multisquamata*.

spine, body width, and body depth 1, providing separation between *P. multisquamata* and the other two species. These results also support the existence of three species in *Parabembras*. The distributional ranges of the three species are not overlapped, suggesting that they speciated allopatrically.
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References

Barnard KH (1927) A monograph of the marine fishes of South Africa. Part II. (Teleostei–Discocephali to end. Appendix). Annals of the South African Museum 21: 419–1065, pls. 18–37.

Bleeker P (1853) Nalezingen op de ichthyologie van Japan. Verhandelingen van het Bataviaasch Genootschap van Kunsten en Wetenschappen 25(7): 1–56. [pl. 1]

Bleeker P (1855) Nieuwe nalezingen op de ichthyologie van Japan. Verhandelingen van het Bataviaasch Genootschap van Kunsten en Wetenschappen 26(4): 1–132. [pls. 1–8]

Bleeker P (1860) Zesde bijdrage tot de kennis der vischfauna van Japan. Acta Societatis Regiae Scientiarum Indo-Neêrlandicae 8(1): 1–104.

Bleeker P (1874) Typi nonnulli generici piscium neglecti. Verslagen en Mededelingen der Koninklijke Akademie van Wetenschappen, Afdeeling Natuurkunde (Ser. 2) 8: 367–371.

Bleeker P (1879) Énumération des espèces de poissons actuellement connues du Japon et description de trois espèces inédites. Verhandelingen der Koninklijke Akademie van Wetenschappen, Afdeeling Natuurkunde (Amsterdam) 18: 1–33. [pls. 1–3]

Boeseman M (1947) Revision of the fishes collected by Burger and von Siebold in Japan. Zoologische Mededelingen 28: 1–242. [pls. 1–5]

Chu Y-T, Jin XB (1963) Cottoidei. In: Chu Y-T, Tchang T-L, Cheng Q-T (Eds) Fishes of the East China Sea. Science Press, Beijing, 451–504.

Cuvier G, Valenciennes A (1829) Histoire naturelle des poissons. Tome quatrième. Livre quatrième. Des acanthose à joue cuirassée. Levrault, Paris, 518 pp. [72–99 pls., 97 bis.]

Eschmeyer WN, Fricke R, van der Laan R (2017) Catalog of Fishes: Genera, Species, References. http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp [Electronic version accessed 31 August 2017]

Everett B, Groeneveld JC, Fennessey S, Porter S, Munga CN, Dias N, Filipe O, Zacarias L, Iglulu M, Kuguru B, Kumani E, Rabarison G, Razafindrakoto H (2015) Demersal trawl surveys show ecological gradients in Southwest Indian Ocean slope fauna. Western Indian Ocean Journal of Marine Science 14(1–2): 73–92.
Fourmanoir P (1985) Poissons. Liste et description de cinq espèces nouvelles (MUSORSTOM II). Mémoires du Muséum National d’Histoire Naturelle Serie A Zoologie 133: 31–54.

Fricke R (2015) Twenty-one new records of fish species (Teleostei) from Madang and Papua New Guinea (western Pacific Ocean). Marine Biodiversity Records 8(e70): 1–9. https://doi.org/10.1017/S1755267215000445

Gilbert CH (1905) The deep-sea fishes of the Hawaiian Islands. In: The aquatic resources of the Hawaiian Islands. Bulletin of the United States Fish Commission 23(2) (for 1903): 577–713. [pls. 66–101]

Gilchrist JDF (1922) Deep-sea fishes procured by the S.S. “Pickle” (Part I). Report Fisheries and Marine Biological Survey, Union of South Africa 2(3): 41–79. [pls. 7–12]

 Günther A (1860) Catalogue of the fishes in the British Museum. Volume second. Catalogue of the acanthopterygian fishes in the collection of the British Museum. Squamipinnes, Cirrhitidae, Triglidae, Trachinidae, Sciaenidae, Polynemidae, Sphyraenidae, Trichiuridae, Scombridae, Carangidae, Xiphiidae. British Museum, London, 548 pp.

Imamura H (1996) Phylogeny of the family Platycephalidae and related taxa (Pisces: Scorpaeniformes). Species Diversity 1: 123–233.

Imamura H (2004) Phylogenetic relationships and new classification of the superfamily Scorpaenoidae (Actinopterygii: Perciformes). Species Diversity 9: 1–36.

Jean C-T, Kuo C-L (1988) Study on trash fish resources in the northern waters of Taiwan - I. Percentage of catch, species composition, length frequency distribution, relationship between body length and weight. Bulletin of the Taiwan Fisheries Research Institute 44: 51–75.

Jin XB (2006) Fauna Sinica, Ostichthyes, Scorpaeniformes. Science Press, Beijing, 739 pp.

Jordan DS, Hubbs CL (1925) Record of fishes obtained by David Starr Jordan in Japan, 1922. Memoirs of the Carnegie Museum 10(2): 93–346. [pls. 5–12]

Jordan DS, Metz CW (1913) A catalog of the fishes known from the waters of Korea. Memoirs of the Carnegie Museum 6(1): 1–65. [pls. 1–10]

Jordan DS, Richardson RE (1908) A review of the flat-heads, gurnards, and other mail-cheeked fishes of the waters of Japan. Proceedings of the United States National Museum 33(1581): 629–670. https://doi.org/10.5479/si.00963801.33-1581.629

Kamohara T (1952) Revised descriptions of the offshore bottom-fishes of Prov. Tosa, Shikoku, Japan. Research Reports of the Kôchi University, Natural Science 3: 1–122.

Kamohara T (1964) Revised catalogue of fishes of Kochi Prefecture, Japan. Report of the Usa Marine Biological Station, Kochi University 11(1): 1–99.

Knapp LW (1986) Family No. 154: Bembridae. In: Smith MM, Heemstra PC (Eds) Smiths’ Sea Fishes. Macmillan South Africa, Johannesburg, 481–482.

Knapp LW, Imamura H, Sakashita M (2000) Onigocia bimaculata, a new species of flathead fish (Scorpaeniformes: Platycephalidae) from the Indo-Pacific. Special Publications of the JLB Smith Institute of Ichthyology 64:1–10.

Krakstad J-O, Michalsen K, Krafft B, Bagøien E, Alvheim O, Strømme T, Tun MT, Thein H, Tun ST (2014) Cruise report “Dr. Fridtjof Nansen”, Myanmar ecosystem survey, 13 November - 17 December 2013. Institute of Marine Research, Bergen, 99 pp.

Li S-C (1955) Cottoidei. In: Tchang T-L, Cheng C-T, Cheng P-S, Li S-C, Cheng W-L, Wang W-P (Eds) Fishes of the Yellow Sea and Pohai, China. Science Press, Beijing, 260–272.
Liang Y-S (1951) A check-list of the fish species in the Taiwan Fisheries Research Institute. Fisheries Research Institute, Taiwan, 35 pp.

Lin KB (1974) Fishing explorations for tuna and demersal fish in Indonesia waters. Bulletin of the Korea Fishing Technology Society 10: 19–29.

Lindberg GU, Krasyukova ZV (1987) Fishes of the Sea of Japan and adjacent parts of Okhotsk and Yellow Sea. Part 5. Nauka Publishers, Leningrad, 526 pp.

Motomura H (2004) New species of scorpionfish, Scorpaena cocosensis (Scorpaeniformes: Scorpaenidae) from the Cocos Islands, Costa Rica, Eastern Pacific Ocean. Copeia 2004: 818–824. https://doi.org/10.1643/CI-04-179R

Nakabo T (2000) Parabembridae. In: Nakabo (Ed.) Fishes of Japan with pictorial keys to the species. Second edition. Tokai University Press, Hadano, 614.

Nakabo T (2002) Parabembridae. In: Nakabo (Ed.) Fishes of Japan with pictorial keys to the species. English edition. Tokai University Press, Hadano, 614.

Nakabo T, Kai Y (2013) Parabembridae. In: Nakabo T (Ed.) Fishes of Japan with pictorial keys to the species. Third edition. Tokai University Press, Hadano, 718, 1950.

Nelson JS, Grande TC, Wilson MVH (2016) Fishes of the World, fifth edition. John Wiley & Sons, Hoboken, New Jersey, 707 pp. https://doi.org/10.1002/9781119174844

Nishibori K (1959) Studies on the pigments of marine animals. VII. Carotenoids in the skin and fins of some marine fishes. Publications of the Seto Marine Biological Laboratory 7: 339–348. https://doi.org/10.5134/174632

Ochiai A (1976) Parabembras curtus. In: Far Seas Fisheries Research Laboratory (Ed.) Colored illustrations of bottomfishes collected by Japanese trawlers, Vol. II. Japan Deep Sea Trawlers Association, Tokyo, 105.

Ochiai A (1984) Platycephalidae. In: Masuda H, Amaoka K, Araga C, Uyeno T, Yoshino T (Eds) The Fishes of the Japanese Archipelago. English Edition. Tokai University Press, Tokyo, 321–322.

Randall JE, Lim KKP (2000) A checklist of the fishes of the South China Sea. Raffles Bulletin of Zoology Supplement 8: 569–667.

R Core Team (2016) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reeves CD (1927) A catalogue of the fishes of northeastern China and Korea. Journal of the Pan-Pacific Research Institution 2(3): 3–16.

Regan CT (1921) New fishes from deep water off the coast of Natal. Annals and Magazine of Natural History (Series 9) 7(41): 412–420. https://doi.org/10.1080/00222932108632540

Revell LJ, Johnson MA, Schulte JA, Kolbe JJ, Losos JB (2007) A phylogenetic test for adaptive convergence in rock-dwelling lizards. Evolution 61: 2898–2912. https://doi.org/10.1111/j.1558-5646.2007.00225.x

Richardson J (1846) Report on the ichthyology of the seas of China and Japan. Report of the British Association for the Advancement of Science 15th meeting (1845): 187–320. https://doi.org/10.5962/bhl.title.59530

Schneider MF, Buramuge VA, Aliasse L, Serfontein F (2005) ‘Checklist’ de vertebrados de Moçambique. Universidade Eduardo Mondlane, Maputo, 227 pp.
Shao K-T, Ho H-C, Lin P-L, Lee P-F, Lee M-Y, Tsai C-Y, Liao Y-C, Lin Y-C (2008) A checklist of the fishes of southern Taiwan, Northern South China Sea. Raffles Bulletin of Zoology Supplement 19: 233–271.

Shen S-C (Ed.) (1993) Fishes of Taiwan. National Taiwan University, Taipei, 956 pp. [208 + 4 pls]

Shen S-C, Wu K-Y (2011) Fishes of Taiwan. National Museum of Marine Biology and Aquarium, Taiwan, 896 pp.

Shinohara G, Endo H, Matsuura K, Machida Y, Honda H (2001) Annotated checklist of the deepwater fishes from Tosa Bay, Japan. Monographs of the National Science Museum Tokyo 20: 283–343.

Shinohara G, Nakae M, Ueda Y, Kojima S, Matsuura K (2014) Annotated checklist of deep-sea fishes of the Sea of Japan. National Museum of Nature and Science Monographs 44: 225–291.

Shinohara G, Sato T, Aonuma Y, Horikawa H, Matsuura K, Nakabo T, Sato K (2005) Annotated checklist of deep-sea fishes from the waters around the Ryukyu Islands, Japan. Monographs of the National Science Museum Tokyo 29: 385–452.

Smith JLB (1949) The sea fishes of southern Africa. 1st edition. Central News Agency, Ltd., Cape Town, 550 pp. [103 pls]

Smith JLB (1961) The sea fishes of southern Africa. 4th edition. Central News Agency, Ltd., Cape Town, 580 pp. [111 pls]

Smith JLB (1965) The sea fishes of southern Africa. 5th edition. Central News Agency, Ltd., Cape Town, 580 pp. [111 pls]

Suzuki K, Kataoka T (1997) Marine fishes of Mie Prefecture, Japan. Toba Aquarium, Mie, 297 pp. [152 pls]

Takegawa Y, Morino H (1970) Fishes from Wakasa Bay, Japan Sea. Publications of the Seto Marine Biological Laboratory 17: 373–392. https://doi.org/10.5134/175616

Temminck CJ, Schlegel H (1843) Pisces. Parts 2–4. In: Siebold PF von (Ed.) P. F. de Siebold's Fauna Japonica. Müller, Amsterdam, 21–72. [pls. 10–36]

Van der Laan R, Eschmeyer WN, Fricke R (2014) Family-group names of recent fishes. Zootaxa 3882(2): 1–230. https://doi.org/10.11646/zootaxa.3882.1.1

Washington BB, Eschmeyer WN, Howe KM (1984) Scorpaeniformes: relationships. In: Moser HG, Richards WJ, Cohen DM, Fahaj MP, Kendall Jr. AW, Richardson SL (Eds) Ontogeny and systematics of fishes. American Society of Ichthyologists and Herpetologists, Special Publication 1, Allen Press, Kansas, 438–447.

Weber M, de Beaufort LF (1911) The fishes of the Indo-Australian Archipelago. Volume 1. Index of the Ichthyological papers of P. Bleeker. E. J. Brill, Leiden, 410 pp.

Yamada U, Tokimura M, Horikawa H, Nakabo T (2007) Fishes and fisheries of the East China and Yellow Seas. Tokai University Press, Hadano, 1262 pp.

Yamaguchi T, Machida Y (2003) Fish specimens collected in Japan by Ph. F. von Siebold and H. Bürger and now held by the National Natuurhistorisch Museum in Leiden and other two museums. Calanus, Bulletin of the Aitsu Marine Station, Kumamoto University, Japan, Special Number 4: 87–337.

Yamamoto K, Nagasawa K (2015) Temporal changes in demersal fish assemblage structure in the East China Sea and the Yellow Sea. Nippon Suisan Gakkaishi 81: 429–437. https://doi.org/10.2331/suisan.81.429