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Descriptions of thirty-four new species of the fish genus *Pempheris* (Perciformes: Pempheridae), with a key to the species of the western Indian Ocean

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Abstract

The following thirty-four new species of the pempherid fish genus *Pempheris* are described from the western Indian Ocean, raising the total number for the region to 47 species: *P. andilana* from northwest Madagascar; *P. argyrea* from the Seychelles; *P. bineeshi* from southeast India; *P. bruggemanni* from Réunion and Mauritius; *P. connelli* from KwaZulu-Natal, South Africa; *P. ellipse* from the south coast of Oman; *P. hadra* from the Republic of the Maldives; *P. heemstraorum* from Rodrigues, Mascarene Islands; *P. hollemani* from southeast Madagascar; *P. ibo* from Mozambique and South Africa; *P. kruppi* from the Gulf of Aden and Socotra; *P. kuriamuria* from the south coast of Oman; *P. leioplepis* from Chumbe Island, Zanzibar; *P. megalops* from the Seychelles; *P. micromma* from the south coast of Oman; *P. muscat* from the Gulf of Oman; *P. orbis* from the Red Sea; *P. pathirana* from Sri Lanka; *P. peza* from southern Mozambique; *P. rochai* from the south coast of Oman; *P. rubricauda* from northwest Madagascar; *P. sergey* from the Red Sea; *P. shimoni* from Kenya; *P. shirleen* from the Red Sea; *P. smithorum* from Zanzibar; *P. tau* from the Red Sea; *P. ternay* from the Seychelles; *P. tilman* from the Gulf of Aqaba, Red Sea; *P. tiran* from the Strait of Tiran, Red Sea; *P. trinco* from Sri Lanka; *P. viridis* from the Red Sea; *P. wilsoni* from the Gulf of Oman; *P. xanthomma* from the Gulf of Aden (Yemen); and *P. zajonzi* from the Socotra Archipelago. Many of the new species are described from single specimens or one location, indicating a need for more collecting to resolve the taxonomy of this group: we emphasize that some decisions are tentative and apply to the state of collections at present. The barcode mtDNA COI sequences for 21 of the 47 WIO species are analyzed, showing some deep divergences between species, but also several sibling species or species complexes that apparently share COI sequences. The genetic analysis is also limited by small sample sizes; more extensive genetic surveys are required to confirm the results. An appendix includes the description of the hybrid *P. malabarica* × *P. russellii*, a discussion of a complex of *Pempheris* in St. Brandon's Shoals in need of further study, and underwater photographs of potential new species of *Pempheris* for which we have no specimens.

Key words: taxonomy, ichthyology, systematics, coral-reef fishes, sweepers, DNA barcoding.

Introduction

The fish family Pempheridae, with the common name sweepers, consists of two genera, *Pempheris* Cuvier 1829, with 35 previously described valid species, and *Parapriacanthus* Steindachner 1870, with five species (Eschmeyer & Fricke 2015). These fishes are found in all tropical to warm temperate seas, except the eastern Pacific Ocean. They are characterized by a compressed, rhomboid-shaped body; very large eyes; short snout; the dorsal fin near the middle of the body, with VI spines and 9 (rarely 10) rays; and a very long, low anal fin with III spines and 35–48 rays. They are unusual in having two layers of scales, those of the outer layer larger and very deciduous. These fishes typically form aggregations in caves or below ledges on reefs by day, and emerge from shelter at night to feed near the surface on zooplankton.

The South African Institute for Aquatic Biodiversity (SAIAB) will soon publish a series of volumes on all the coastal fishes of the western Indian Ocean (WIO), including the Red Sea and the Persian Gulf. Most of the family accounts have been written by author(s) recognized as authorities of the group. When it was determined that the family Pempheridae needed a more comprehensive review, the first author, as one of the editors of the SAIAB volumes, volunteered to prepare it. He enlisted the collaboration of the second author for the latter's expertise on the molecular taxonomy of coral-reef fishes. The family is now the last needed before the volumes can be published.

Pempheris is a particularly troublesome genus for taxonomists, since the species' morphology varies little, their few distinctive markings are frequently shared, their meristics broadly overlap, their outer scales are deciduous, and they are not frequently collected or targeted in surveys. As a result, most of the literature prior to 2013 on the genus for the western Indian Ocean is based on misidentifications. Of the checklists and guidebooks that have been published in the last 30 years that list species of *Pempheris* of the western Indian Ocean, none have any species of *Pempheris* correctly identified. The first author's book *Coastal Fishes of Oman*, published in 1995, will serve as an example. One species of *Pempheris* is illustrated on page 244 by two color figures identified as *P. vanicolensis*. The first photograph (Fig. 637) is *P. convexa*, described by the authors in 2014. The second (Fig. 638) is an underwater photograph of a species of *Pempheris* in the *schwenkii* complex, clearly not *P. vanicolensis* (a species known from the Andaman Sea and Pacific Ocean). An additional species is illustrated by Fig. 639, and identified only as *Pempheris* sp. It should have been labeled *P. malabarica* (however, we suspect that more than one species may be presently included in nominal *P. malabarica*).

Our research on the genus began in 2013 with the description of the new Indian Ocean species *Pempheris flavicycla*, which had long been misidentified as *P. vanicolensis* (Randall *et al.* 2013). For the first time, mtDNA sequencing was used in *Pempheris* to assist in differentiating similar-appearing specimens. Subsequently, Mooi & Randall (2014) described *P. bexillon* from the southwestern Indian Ocean, Randall & Bineesh (2014) clarified the species from India (with one new species), and Randall & Victor (2014) described four new species from Oman and the African coast. The *Pempheris* species of the Red Sea have also been recently revised: Koeda *et al.* (2014) described the new species *P. tominagai*, but then mistakenly listed three other species which do not occur in the Red Sea. Randall *et al.* (2014) corrected Koeda *et al.* (2014) and concluded that there were three Red Sea species. This was confirmed by Azzurro *et al.* (2015), who documented the invasion of the Mediterranean by *P. rhomboidea* and recorded *P. flavicycla* and *P. tominagai* as the two other Red Sea species. Only five of the now 47 species of *Pempheris* in the western Indian Ocean (including India and Sri Lanka) were described before 2013 (all before 1889), one was added in 2013, seven were added in 2014, and 34 more are described herein.

An appendix includes the description of the hybrid *Pempheris malabarica* × *P. russellii* from Pakistan; underwater photographs of unidentified species of *Pempheris* from the western Indian Ocean are also shown in the hope that specimens can be collected, including at least eight probable undescribed species of *Pempheris* represented by underwater photographs taken by Dawn Goebbels in the Watamu Marine National Park, Kenya; and a discussion of a complex of *Pempheris* in St. Brandon's Shoals in need of further study.

Little is known of the early life history of *Pempheris*, but their larvae are known to settle at a particularly small size for reef fishes, as small as 6 mm SL (Leis & Carson-Ewart 2000). This correlates with a relatively short larval life and reduced dispersal, which would promote local adaptation and the development of species complexes in areas with widely dispersed reef habitats such as the broad western Indian Ocean region. While checking the sex of specimens of *Pempheris*, we have noticed mature gonads in fish of surprisingly small size for the species, as well as a very high percentage of fish in spawning condition, indicating year-round spawning. Underwater

photographs and our observations of aggregations of *Pempheris* often reveal more than one species. *Pempheris* are broadcast spawners, which could facilitate hybridization and a degree of introgression that may slow the divergence of mitochondrial DNA lineages as species complexes evolve. These speculations require additional evidence, but may account for the high diversity in the genus in the western Indian Ocean and the frequent sharing of mitochondrial haplotypes within some species complexes.

Many of the species of *Pempheris* described below are without enough specimens for adequate description (nine from single specimens!), and most without knowledge of the life color. We hope that this publication, admittedly preliminary, will aid in acquiring more material of this troublesome genus.

Materials and Methods

Few species of fishes have proven more difficult to classify than those of the genus *Pempheris*. Most are morphologically very similar, the color is often a near-uniform copper, bronze or silver, and the dorsal fin is either broadly black-tipped, or the anterior margin black, or both. Of the fins, only the number of anal-fin soft rays is of diagnostic value, but the range is broad (Table 1); therefore, many specimens would be needed for this count to have value. The last segmented ray in the dorsal and anal fins is divided at its base: it is counted as a single ray. Counts of pectoral-fin rays include the rudimentary upper ray and vary from 16 to 19, usually 17 or 18; they can be of modal value only when many specimens are available. The pectoral-fin rays of both sides are counted but presented as separate counts (Table 1). The fins of museum specimens of *Pempheris* are often damaged, especially the dorsal and caudal fins.

Because the large scales of the outer layer are so easily shed, the only viable scale count is that of the more adherent small scales of the lateral line (Table 2); again, many specimens are needed to obtain the definitive range. The lateral-line of species of *Pempheris* continues to the end of the caudal fin; the lateral-line scales are counted to the base of the caudal fin. Occasional lateral-line scales on some specimens were found with two sensory pores. In such cases, the number of scales is counted, not the pores. Scales with two pores usually have two narrow columns of scales above. These double columns are more easily seen than the pores. The species of *Pempheris* have both ctenoid and cycloid scales. Whether the scales are ctenoid or cycloid, and on what parts of the body they are found, are also of importance for species identification. All species of the genus have a midventral row of small scales that bear a median ridge, and all have two rows of small, strongly ctenoid scales to each side of the median ventral row. The scales on the side of the chest (defined as above the ventral two rows of scales, below the base of the pectoral fin, posterior to the margin of the operculum, and anterior to a line from the rear base of the pectoral fins to the origin of the pelvic fins) may be ctenoid or cycloid, or divided into a ventroanterior ctenoid part and a dorsoposterior cycloid part. This is often of diagnostic importance when all of the scales of the outer layer are present on the side of the chest (too often they are not). All species of *Pempheris* have five longitudinal rows of ctenoid scales dorsally on the body posterior to the dorsal fin; the lower row on each side is only about half ctenoid. If any part of a scale is ctenoid, it is regarded here as ctenoid. Depending on the species, the scales may be either ctenoid or cycloid on the nape, below the dorsal fin, on the mid-side of the caudal peduncle, and on the chest. The caudal peduncle has the highest loss of scales of any part of the body, so one can rarely determine whether the scales on the side of the peduncle are cycloid or ctenoid.

Gill-raker counts are important meristic data, in general, but the range is also broad. The counts are divided into the dorsal and ventral parts, with the raker at the angle included in the ventral part. However, only the total count is recorded in the species accounts and Table 3. The low, rounded ventroposterior margin of the preopercle usually has one or two flat triangular spines and thin, flexible, translucent projections of variable shape, some with small holes. There is so much intraspecific variation with this ridge that we have not used it for species identification; also it is normally covered by scales.

The species of *Pempheris* have steeply oblique jaws, the edge of the maxilla varying from 59–75° to the horizontal axis of the body. The angle is a useful diagnostic character. It is measured by protractor at the ventral edge of the maxilla with the jaws slightly open. The horizontal axis of the body is taken from the tip of the snout through the center of the eye to a point at the middle of the ventral half of the caudal peduncle. The teeth in the jaws are small, but their features are often important for species identification. Very small teeth are consistently

present on the vomer and palatines, but they are of little diagnostic value. All specimens of *Pempheris* we have examined have a close-set pair of vertically oval nostrils directly anterior to the orbit.

Most of the specimens of *Pempheris* examined for this study are from the fish collections of the Bishop Museum, Honolulu (BPBM); South African Institute for Aquatic Biodiversity, Grahamstown, South Africa (SAIAB); and the United States National Museum of Natural History, Washington, D.C. (USNM). We have also obtained loans from the Natural History Museum, London (BMNH); California Academy of Sciences, San Francisco (CAS); Australian National Fish Collection at Hobart, Tasmania (CSIRO); Hebrew University of Jerusalem (HUJ); King Abdulaziz University Marine Museum, Jeddah (KAUMM); Muséum national d'Histoire naturelle, Paris (MNHN); National Bureau of Fish Genetic Resources, Kochi, India (NBFGR); Natural History Collection of Yemen (NHCY; now curated at SMF); Phuket Marine Biological Centre, Phuket, Thailand (PMBC); Senckenberg Museum, Frankfurt (SMF); Steinhardt Museum of Natural History, Tel Aviv University (SMNHTAU); the Université de La Réunion, St. Denis (URUN); and the Zoological Survey of India, Kozhikod (formerly Calicut), India (ZSI/CLT).

Data in parentheses in the descriptions refer to paratypes. Lengths of specimens are given as standard length (SL), measured from the median anterior end of the upper lip to the base of the caudal fin (posterior end of hypural plate); head length is measured from the same anterior point to the posterior end of the opercular flap, and upper-jaw length from the same anterior point to the posterior end of the maxilla; body depth is taken from the origin of the anal fin vertically to the internal base of the dorsal fin (not always the maximum depth); body width is measured just posterior to the opercular flap (used only for adults; juveniles are much thinner); predorsal and prepelvic lengths have proven to be of value as identification characters, often more important than the length of rays of the fins, because the latter are so often broken on museum specimens, the measurements are taken from the origin of the first spine to the tip of the upper lip; eye diameter is the horizontal length of the bony orbit; interorbital width the least bony width; lengths of spines and rays of median fins are measured from their extreme base to tip of longest ray; caudal-fin length is taken horizontally from the base to a perpendicular at the end of the longest ray, however, most museum specimens have lost enough of this fin to prevent taking this measurement, The same is true to a lesser extent for the dorsal fin. Pectoral- and pelvic-fin lengths are the lengths of the longest ray, taken to the extreme base. The head of fishes of the genus *Pempheris* is much broader (thickness) than the strongly tapering body. When photographing a specimen, it is necessary to elevate the tail end to have the fish in optimal focus. This results in a shorter snout in the photograph. Measurements of specimens were taken from specimens, not photographs. Proportional measurements are rounded to the nearest 0.05.

A small number of the more recently collected specimens have been preserved for DNA sequencing studies, a number clearly inadequate to assess the degree of genetic variation in the genus. DNA extractions were performed with the NucleoSpin96 (Machery-Nagel) kit according to manufacturer specifications under automation with a Biomek NX liquid-handling station (Beckman-Coulter) equipped with a filtration manifold. A 652-bp segment was amplified from the 5' region of the mitochondrial COI gene using a variety of primers (Ivanova *et al.* 2007). PCR amplifications were performed in 12.5 μ L volume including 6.25 μ L of 10% trehalose, 2 μ L of ultra pure water, 1.25 μ L of 10 \times PCR buffer (10 mmol/L KCl, 10 mmol/L $(\text{NH}_4)_2\text{SO}_4$, 20 mmol/L Tris-HCl (pH 8.8), 2 mmol/L MgSO_4 , 0.1% Triton X-100), 0.625 μ L of MgCl_2 (50 mmol/L), 0.125 μ L of each primer (0.01 mmol/L), 0.0625 μ L of each dNTP (10 mmol/L), 0.0625 μ L of *Taq* DNA polymerase (New England Biolabs), and 2 μ L of template DNA. The PCR conditions consisted of 94°C for 2 min, 35 cycles of 94°C for 30 s., 52°C for 40 s., and 72°C for 1 min, with a final extension at 72°C for 10 min. Specimen information and barcode sequence data from this study were compiled using the Barcode of Life Data Systems (Ratnasingham & Hebert 2007). The sequence data is publicly accessible on BOLD and GenBank. Additional sets of comparison COI sequences were obtained from prior studies compiled in GenBank. Sequence divergences were calculated using BOLD with the Kimura 2-parameter (K2P) model generating a mid-point rooted neighbor-joining (NJ) phenogram to provide a graphic representation of the species' sequence divergence.

Mitochondrial DNA lineages obtained in the BOLD database have been assigned code numbers, or BINs (Barcode Index Numbers), to permanently name lineages. BINs are clusters calculated by an algorithm taking into account similarities and connectivity and assessing cluster boundaries. The BINs occupied by the mtDNA lineages for the species that have been sequenced for this paper are presented under the species title after the Figures and Tables.

Key to the Species of the Genus *Pempheris* of the western Indian Ocean

- 1a. Band of small teeth anteriorly in lower jaw expanded medially to a semi-circular patch, partly exposed when mouth fully closed; the outer row of teeth in patch erect in females, enlarged and forward-projecting in males2
- 1b. No semicircular patch of teeth anteriorly in lower jaw partly exposed when mouth fully closed3
- 2a. Anal fin with a prominent jet-black margin; gill rakers 31 or 32; lateral-line scales 62–64 (two specimens, 121 & 122 mm SL, Strait of Tiran, Gulf of Aqaba, Red Sea)***P. tiran*, n. sp.**
- 2b. Anal fin without a black margin (tips of a few anterior rays blackish on some specimens); gill rakers 24–28; lateral-line scales 65–75 (Oman, India to Indonesia, Thailand, and Cambodia)***P. malabarica***
- 3a. Eyes extremely large, bony diameter of orbit 6.2 in SL; head length 2.95 in SL; gill rakers 31; teeth in upper jaw extremely small and slightly recurved, in five or six close-set rows to each side of symphyseal gap (one specimen, 121 mm SL, Seychelles)***P. megalops*, n. sp.**
- 3b. Eyes not extremely large, bony diameter of orbit of adults 6.7–9.35 in SL; head length 3.0–3.6 in SL; gill rakers 24–31; teeth in upper jaw not extremely small, mainly in two rows4
- 4a. A distinct dark-brown to black band at base of anal fin, narrowing posteriorly as fin narrows; dorsal fin with an anterior blackish margin which may darken distally, sometimes broadening to a large apical spot; no large, oval, dark brown to black spot at base of pectoral fin; no dark stripes along flanks (i.e. the 25 species of the *schwenkii* complex in the western Indian Ocean)23
- 4b. Usually no distinct dark-brown to black band at base of anal fin (exceptions either have a prominent dark edge to the anal fin [in *P. bexillon* below] or dark stripes along the flanks in *P. kuriamuria*, *P. russellii*, & *P. wilsoni*); no blackish band on anterior margin of dorsal fin; a large, oval, dark brown to black spot at base of pectoral fins present or absent5
- 5a. Anal fin with a complete black border (broad anteriorly, progressively narrower posteriorly; can be dark reddish in *P. mangula*)6
- 5b. Anal fin without a complete black border; usually dark stripes along flanks made up of darkened centers of lateral scale rows in life (i.e. the *rhomboidea* complex)8
- 6a. Dorsal fin all yellow with a full-depth black posterior margin, progressively broader dorsally to fin tip; lateral-line scales 57–64 (Chagos Archipelago, Mascarene Islands, Comoro Islands, and Mozambique Channel)***P. bexillon***
- 6b. Dorsal fin not all yellow, usually without a complete black posterior margin (if present, in some *P. flavicycla*, iris bright yellow); lateral-line scales 53–607

- 7a. A bright yellow ring around pupil of eye; an oval dark spot at base of pectoral fins; predorsal length 2.55–2.6 in SL; gill rakers 29–33 (Red Sea, Oman, and islands of Indian Ocean south to Kenya, Seychelles and Chagos Archipelago, east to Andaman Islands) ***P. flavicycla***
- 7b. No bright yellow ring around pupil of eye (can be dusky yellow); a narrow dark brown band across base of pectoral fins; predorsal length 2.65–2.75 in SL; gill rakers 27–30 (east and SW coasts of India, and eastward) ***P. mangula***
- 8a. Eyes very small, the orbit diameter in adults 8.0–9.45 in SL 9
- 8b. Eyes not very small, the orbit diameter in adults 7.0–8.2 in SL 10
- 9a. Body not elongate, the depth 2.0–2.1 in SL; silvery gray when fresh, scales below lateral line rimmed with yellowish brown (south coast Oman to Strait of Hormuz, Republic of Maldives) ***P. convexa***
- 9b. Body elongate, the depth 2.35 in SL; gray dorsally, often with iridescence, pale green or yellow below lateral line, scales rimmed in gray (one specimen, 116 mm SL, Oman, south coast) ***P. micromma*, n. sp.**
- 10a. Pectoral-fin rays 16 or 17; gill rakers 26–28 (3 specimens, 115–136 mm SL, northern Mozambique)
..... ***P. cuprea***
- 10b. Pectoral-fin rays 17–19 (modally 18, except *P. nesogallica* with mode of 17); gill rakers 28–34 11
- 11a. Pectoral fins very short, the longest ray 3.65 in SL; body depth 2.05 in SL; pectoral-fin rays 18 or 19 (mainly 19) (southeast coast of India) ***P. sarayu***
- 11b. Pectoral fins not very short, the longest ray 2.85–3.15 in SL; body depth 2.1–2.35 in SL; pectoral-fin rays 17–19 (rarely 19) 12
- 12a. Pectoral fins very long, the fin length 2.9–3.0 in SL 13
- 12b. Pectoral fins not very long, the fin length 3.0–3.55 in SL 14
- 13a. Scales on chest one-half cycloid and one-half ctenoid; longest dorsal-fin ray 4.05–4.25 in SL; lateral-line scales 52–58 (Red Sea, and as an immigrant to the Mediterranean Sea) ***P. rhomboidea***
- 13b. Scales on chest all ctenoid; longest dorsal-fin ray 3.65–3.75 in SL; lateral-line scales 59–61 (two specimens, 95 & 112.5 mm SL, Oman) ***P. kuriamuria*, n. sp.**
- 14a. Head length 3.0–3.05 in SL (Gulf of Oman) ***P. darvelli***
- 14b. Head length 3.1–3.45 in SL 15

- 15a. Prepelvic length 2.85 in SL; head length 3.45 in SL; anal-fin soft rays 45 (one specimen, 125 mm SL, Fahal Island, Gulf of Oman) ***P. wilsoni*, n. sp.**
- 15b. Prepelvic length 2.45–2.7 in SL; head length 3.1–3.4 in SL; anal-fin soft rays 35–44 16
- 16a. Scales on side of chest entirely ctenoid; pectoral-fin length 3.1–3.55 in SL 17
- 16b. Scales on chest divided into ventroanterior ctenoid and dorsoposterior cycloid parts; pectoral-fin length 3.0–3.15 in SL 21
- 17a. Tongue triangular basally, narrowing to a slender rectangle with rounded tip; head length 3.25–3.5 in SL (Sind coast of Pakistan) ***P. russellii***
- 17b. Tongue entirely triangular, without a slender rectangular tip; head length 3.1–3.4 in SL 18
- 18a. Pectoral-fin length 3.3–3.55 in SL; predorsal length 2.55–2.7 in SL; lateral-line scales 52–60 19
- 18b. Pectoral-fin length 3.0–3.4 in SL; predorsal length 2.7–2.8 in SL; lateral-line scales 55–64 20
- 19a. Predorsal length 2.55–2.6 in SL; prepelvic length 2.55–2.6 in SL; angle of maxilla to horizontal axis of body 65–70°; lower jaw not or only slightly protruding when mouth firmly closed (KwaZulu-Natal to Mozambique) ***P. eatoni***
- 19b. Predorsal length 2.7 in SL; prepelvic length 2.45–2.5 in SL; angle of maxilla to horizontal axis of body 61–66°; lower jaw strongly protruding when mouth firmly closed (two specimens, 126.5 & 139 mm SL, Zanzibar) ***P. smithorum*, n. sp.**
- 20a. Front of upper jaw with an outer row of sharply conical, recurved teeth, followed inwardly by a broad zone of progressively smaller teeth; upper lip with scattered, very small papillae; anal-fin soft rays 38–43; gill rakers 29 or 30 (14 specimens, 113–139 mm SL, Sri Lanka) ***P. pathirana*, n. sp.**
- 20b. Front of upper jaw with two irregular rows of sharply conical, recurved teeth, not followed inwardly by a broad zone of small teeth; upper lip densely covered with papillae of moderate size; anal-fin soft rays 37–41; gill rakers 29–32 (16 specimens, 106.5–124 mm SL, Gulf of Aden and Socotra) ***P. kruppi*, n. sp.**
- 21a. Pectoral-fin length 3.0–3.15 in SL; anal-fin soft rays 38–44; gill rakers 30–34 (Mascarene Islands, Madagascar, and KwaZulu-Natal) ***P. nesogallica***
- 21b. Pectoral-fin length 3.15 in SL; anal-fin soft rays 35–41; gill rakers 28–32 22
- 22a. Head length 3.3 in SL; tongue triangular, straight-sided, with a pointed tip; anal-fin soft rays 35–40; gill rakers 30–32 (5 specimens, 124–132 mm SL, east coast of Oman) ***P. muscat*, n. sp.**
- 22b. Head length 3.15 in SL; tongue triangular, concave-sided, ending in a thin, rounded, flexible flap; anal-fin soft rays 37–41; gill rakers 28–31 (12 specimens, 31–133 mm SL, Shimoni, Kenya) ***P. shimoni*, n. sp.**

P. schwenkii complex below: (note *P. bexillon* above is genetically also in the *schwenkii* complex)

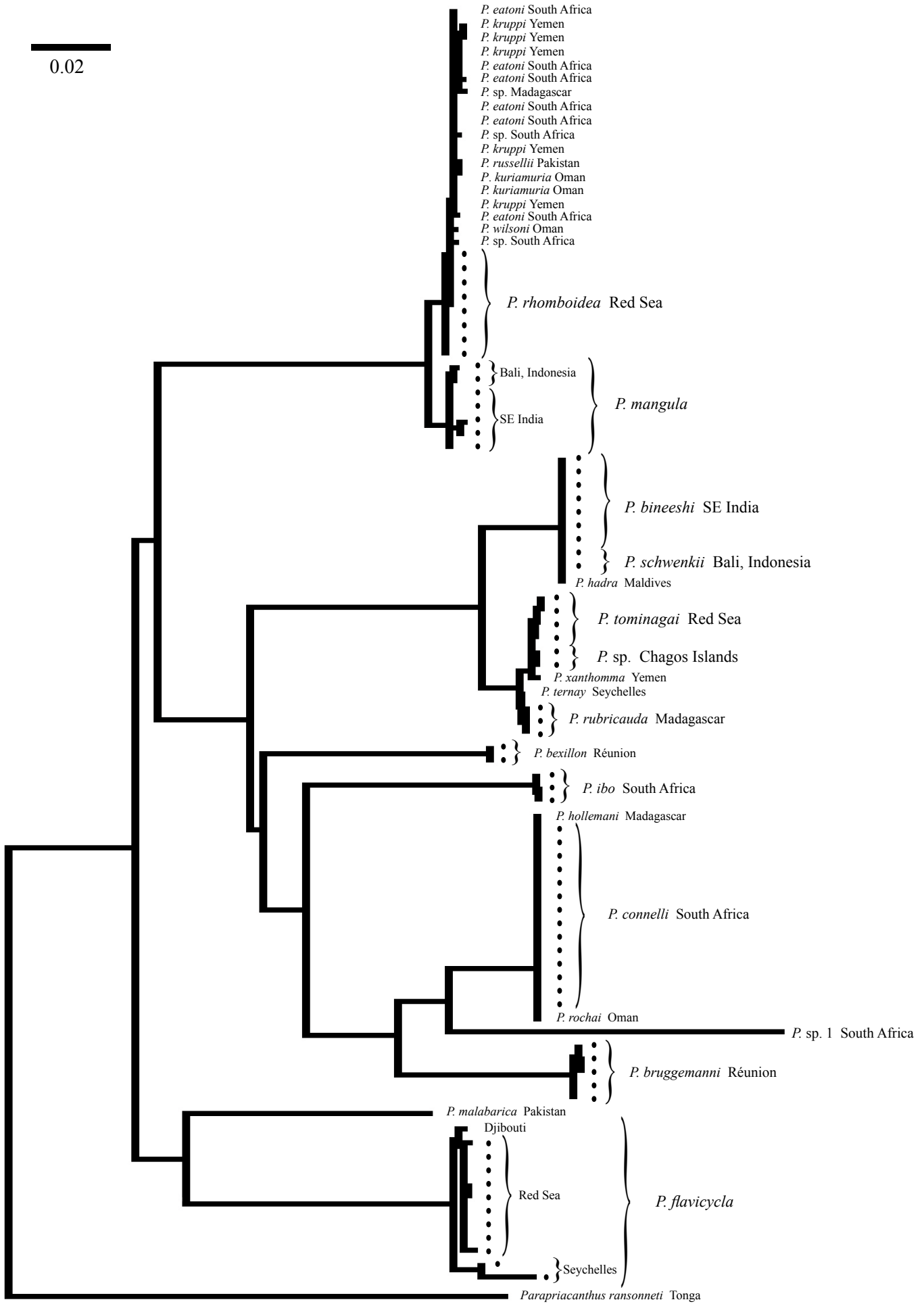
- 23a. Band at base of anal fin consisting of discrete black dots of variable size; head and body below lateral line light tan when fresh, near-white ventrally and posteriorly (two specimens, 117 & 118 mm SL, southeast Madagascar) ***P. hollemani*, n. sp.**
- 23b. Band at base of anal fin uniformly dark brown to black; color not as in 23a24
- 24a. Body strongly compressed, maximum body width 3.35 in body depth; pelvic fins long, 5.3 in SL (one specimen, 127 mm SL, Rodrigues, Mascarene Islands; largest specimen of the *schwenkii* complex examined) ***P. heemstraorum*, n. sp.**
- 24b. Body not strongly compressed, maximum width 2.2–3.1 in body depth; pelvic fins 5.3–7.45 in SL25
- 25a. Body thick, maximum width 2.2 in body depth; scales on caudal peduncle ctenoid (except those of lateral line); color when fresh bronze, except for broad central area of body enclosing pectoral fins with metallic green scale centers; caudal fin orange-red without black margins (one specimen, 118 mm SL, Republic of Maldives) ***P. hadra*, n. sp.**
- 25b. Body not thick, maximum width 2.35–3.1 in body depth; scales on caudal peduncle both ctenoid and cycloid; color not as in 25a26
- 26a. Lateral-line scales 43–49; straight ascending anterior part of lateral line abruptly angular below dorsal fin to remainder of lateral line that parallels dorsal body contour; color in life variable, often greenish yellow with copper iridescence dorsally, others iridescent silvery (largest of 14 type specimens examined, 93 mm SL, KwaZulu-Natal to Mozambique) ***P. ibo*, n. sp.**
- 26b. Lateral-line scales 46–59 (only *P. tominagai* with fewer than 49); ascending anterior part of lateral line bends in a gradual curve into posterior portion of lateral line; color not as in 26a27
- 27a. Dorsal-fin soft rays 10; a single row of projecting recurved conical teeth anteriorly in upper jaw (one specimen, 116.5 mm SL, south coast of Oman) ***P. rochai*, n. sp.**
- 27b. Dorsal-fin soft rays 9; two or more rows of recurved conical teeth anteriorly in upper jaw28
- 28a. Lateral line very strongly arched anteriorly, rising 3/4 orbit diameter above level of origin of lateral line; orbit of eye forming an ellipse, the vertical height 8.8% higher than width; body depth 2.1 in SL (one adult, 93.5 mm SL, and 15 juveniles, south coast of Oman) ***P. ellipse*, n. sp.**
- 28b. Lateral line not strongly arched anteriorly, rising at most 1/2 orbit diameter above level of origin of lateral line; orbit of eye circular or only slightly higher than wide; body depth 2.15–2.85 in SL (except *P. connelli* with body depth 2.0–2.25 in SL)29

29a.	Caudal fin bright red-orange with broad black dorsal, ventral, and posterior borders	30
29b.	Caudal fin not bright red-orange with broad black borders	31
30a.	Pectoral-fin length 3.0 in SL; lateral-line scales 51; maxilla forming an angle of 60° to horizontal axis of body; dark brown to black band at base of anal fin narrow, one-third pupil diameter in width at mid-length; anal fin with blackish margin; pectoral-fin rays 17 (one specimen, 92 mm SL, Mahé, Seychelles)	<i>P. ternay</i>, n. sp.
30b.	Pectoral-fin length 3.4–3.6 in SL; lateral-line scales 55–57; maxilla forming an angle of 69–73° to horizontal axis of body; dark brown to black band at base of anal fin broad; anal fin without a blackish margin; pectoral-fin rays 17 or 18 (modally 18)(5 specimens, 68.5–77 mm SL, northwestern Madagascar)	<i>P. rubricauda</i>, n. sp.
31a.	Body depth 2.0–2.25 in SL; gill rakers 29–32; color in life olivaceous dorsally, brassy yellow below lateral line, the scales with indistinct brown edges; largest specimen examined, 126.5 mm SL (39 specimens, 53–126.5 mm SL, KwaZulu-Natal, South Africa)	<i>P. conelli</i>, n. sp.
31b.	Body depth 2.2–2.7 in SL (except range down to 2.15 in <i>P. xanthomma</i>); gill rakers 25–30 (except <i>P. orbis</i> and <i>P. tau</i>); largest specimens usually less than 110 mm SL; color not as in 31a	32
32a.	Lateral-line scales 58–63; pectoral-fin length 3.0–3.1 in SL; color of body of adults when fresh dusky silver–gray, the scales below lateral line rimmed with brownish orange; caudal fin with dark brown band over lateral line, on upper and lower margins, but none on posterior margin (6 specimens, 83–118 mm SL, Réunion and Mauritius)	<i>P. bruggemanni</i>, n. sp.
32b.	Lateral-line scales 48–59; pectoral-fin length 3.0–3.9 in SL; color not as in 32a	33
33a.	Teeth at front of upper jaw in three or more irregular, close-set rows, more recurved inwardly	34
33b.	Teeth at front of upper jaw in two rows, the outer slightly recurved, the inner larger and more strongly recurved	42
34a.	Head length 3.0 in SL; dorsal profile of head straight (one specimen, 100 mm SL, Chumbe Island, Zanzibar)	<i>P. leiolepis</i>, n. sp.
34b.	Head length 3.05–3.35 in SL; dorsal profile of head convex (except for <i>P. viridis</i> where profile nearly straight)	35
35a.	Body thin, the width 2.75–2.9 in body depth	36
35b.	Body not thin, the width 2.4–2.7 in body depth	37

- 36a. Body very deep, the depth 2.2–2.25 in SL; predorsal length 2.4–2.55 in SL; pelvic fins not short, reaching anus, their length 5.7–6.8 in SL (10 specimens, 91–103 mm SL, northwestern Madagascar) ..
.....***P. andilana*, n. sp.**
- 36b. Body not very deep, the depth 2.4 in SL; predorsal length 2.6–2.7 in SL; pelvic fins short, not reaching anus, their length 7.45 in SL (two specimens, 103 & 105 mm SL, Hurghada, Egypt, Red Sea)***P. shirleen*, n. sp.**
- 37a. Body depth 2.65 in SL; dorsal profile of head nearly straight; gill rakers 28; color when fresh metallic green, scale edges yellowish brown (one specimen, 79.5 mm SL, Al Lith, Saudi Arabia, Red Sea)***P. viridis*, n. sp.**
- 37b. Body depth 2.3–2.7 in SL; dorsal profile of head convex; gill rakers 26–33; color not as in 37a38
- 38a. A copper-colored ring around pupil of eye in alcohol; lateral-line scales 58–64; dark brown band at base of anal fin equal in width to pale outer part of fin (fully pigmented width measured at mid-length of fin) (3 specimens, 74–85 mm SL, Gulf of Aqaba)***P. orbis*, n. sp.**
- 38b. No copper ring around pupil of eye in alcohol; lateral-line scales 46–59; dark brown band at base of anal fin not equal in width to pale outer part of fin39
- 39a. Dark brown band at base of anal fin broader than pale outer part of fin (measured at mid-length of fin); caudal fin without a broad black posterior border (dark border present only on dorsal and ventral margins of fin); scales on side of chest entirely cycloid; lateral-line scales 46–51 (Red Sea)***P. tominagai***
- 39b. Dark brown band at base of anal fin narrower than pale outer part of fin; caudal fin with a broad black posterior margin (also present on dorsal and ventral margins of fin, but half as broad); scales on side of chest cycloid, except for a few ctenoid scales ventrally at edge of opercle (chest scales missing on *P. tau*); lateral-line scales 49–5940
- 40a. Prepelvic length 2.4–2.45 in SL; eyes large, orbit diameter less than 7.1 in SL in large adults; color of body when fresh silvery below lateral line, the scale centers broadly pale blue-green in pectoral region (17 specimens, 61–102 mm SL, Seychelles)***P. argyrea*, n. sp.**
- 40b. Prepelvic length 2.55–2.7 in SL; eyes small, orbit diameter 7.9–8.65 in SL in adults; color not as in 40a41
- 41a. Prepelvic length 2.65–2.7 in SL; head length 3.25–3.3 in SL; gill rakers 30–33 (3 specimens, 95–116.5 mm SL, Gulf of Aqaba and southern tip of Sinai Peninsula)***P. tau*, n. sp.**
- 41b. Prepelvic length 2.55 in SL; head length 3.15 in SL; gill rakers 28–30 (one 89-mm SL specimen and four juveniles, Socotra Archipelago)***P. zajonzi*, n. sp.**

- 42a. Scales all ctenoid on nape and partly ctenoid below dorsal fin; lateral line scales 50–59 (16 specimens, 75–114 mm SL, southern Mozambique)***P. peza*, n. sp.**
- 42b. Scales cycloid on nape and below dorsal fin; lateral-line scales 46–5843
- 43a. Prepelvic length 2.8–2.85 in SL; body depth 2.5–2.7 in SL; gill rakers 25–27; caudal fin with a black border only on posterior margin (7 specimens, 95–108 mm SL, southern India)***P. bineeshi*, n. sp.**
- 43b. Prepelvic length 2.45–2.8 in SL; body depth 2.15–2.55 in SL; gill rakers 26–30; caudal fin with a black border on all outer margins (may be narrower and only blackish on upper and lower margins)44
- 44a. Prepelvic length 2.7–2.8 in SL; gill rakers 29 or 30; a dark brown to blackish line at base of rays and in axil of pectoral fin (3 specimens, 75–97 mm SL, Gulf of Aqaba)***P. tilman*, n. sp.**
- 44b. Prepelvic length 2.5–2.65 in SL; gill rakers 26–29; a black band across base of pectoral fin below base of rays (straight ventrally and rounded dorsally)45
- 45a. Dark brown band at base of anal fin broader than pale outer part of fin; predorsal length 2.7–2.8 in SL; margin of upper jaw forming an angle of 67–70° to horizontal axis of body (11 specimens, 57–100 mm SL, Yemen, Gulf of Aden)***P. xanthomma*, n. sp.**
- 45b. Dark brown band at base of anal fin narrower than pale outer part of fin; predorsal length 2.6–2.75 in SL; margin of upper jaw forming an angle of 60–68° to horizontal axis46
- 46a. Body depth 2.5–2.55 in SL; head length 3.3–3.4 in SL; pectoral-fin rays modally 17; ground color when fresh greenish yellow, the scales rimmed with brown (5 specimens, 88–105 mm SL, Sharm Obhur, Saudi Arabia, Red Sea)***P. sergey*, n. sp.**
- 46b. Body depth 2.3–2.5 in SL; head length 3.2–3.3 in SL; pectoral-fin rays modally 18; ground color when fresh silver-gray, the scales rimmed in copper (22 specimens, 75–108 mm SL, Sri Lanka) ..***P. trinco*, n. sp.**

0.02



DNA Barcoding Results. Mitochondrial DNA sequences can assist in decisions on the taxonomic status of populations, but cannot be used in isolation to decide species status (Victor 2015). Although most reef fish species show monophyletic mtDNA COI lineages more than 2% different from their nearest relatives (Steinke *et al.* 2009, Ward *et al.* 2009), there is no clear threshold degree of divergence between the mtDNA lineages of established species. Indeed, many cases of species that share COI sequences (the “barcode” mtDNA marker used in the Barcode of Life project) have been documented, i.e. “phenovariant” species *sensu* Victor (2015). Two species that are on their own evolutionary trajectories can share mtDNA sequences due to insufficient time since speciation events for mitochondrial mutations to accumulate (incomplete lineage sorting) or some degree of hybridization allowing mitochondrial haplotypes to be traded (via maternal descent, and then taking extensive time to be eliminated by chance). In cases of phenovariant populations, a close look at the morphological, meristic, and marking differences is required to make taxonomic decisions about species status.

Where we find non-overlapping monophyletic sets of haplotypes (i.e. divergent lineages), it confirms that there is some degree of reproductive isolation between populations. This alone does not define species, and when there are no corresponding morphological, meristic, and marking differences of a “sufficient” degree, the populations would be considered “genovariant” populations of the same species (Victor 2015). The final decision on species status is essentially a taxonomist’s subjective determination.

In the case of the western Indian Ocean *Pempheris*, there is limited information on the genetic structure of populations and species. At present, 21 of the 47 regional species have been barcoded (sequenced for the COI marker), however many are based on single specimens. An additional lineage occurs in South Africa based on a sequence from an egg (*P. sp.* 1); it may represent one of the many unsequenced species or an additional species.

The phenetic tree based on the COI sequences of Indian Ocean populations of *Pempheris* is presented in Fig. 1. Many species form deeply divergent monophyletic lineages well isolated from their nearest relatives, but some are only minimally divergent lineages, although clearly distinct (e.g. the 1% divergence between the *P. rhomboidea* complex vs. *P. mangula*). Several new species described here have sequences only slightly different from their nearest relatives, but, since they are based on single sequences, the consistency of the divergence is untested. Several more new species share identical haplotypes with their closest relatives, but those are also mostly based on single sequences. In general, most phenovariant species documented in this study are allopatric, suggesting that regional species complexes are in the process of diverging. In one case the phenovariants are both from Oman (*P. kuriamuria* from the south coast of Oman and *P. wilsoni* from the northern coast in the Gulf of Oman), but this is also based on single sequences and clearly needs to be confirmed.

The *P. rhomboidea* species complex appears to be the largest complex of phenovariant species documented to date, with six putative species in the region mostly sharing haplotypes (and many more unsequenced) and ranging from the Red Sea (and invasive in the Mediterranean), south to South Africa, and eastward to Pakistan. The six sequenced phenovariants are mostly allopatric, but several species in the complex occupy the coastline from Yemen to Oman; unfortunately these species are among the least well documented and this area is now one of the more difficult places to work on the globe. The true *P. schwenkii* complex (excluding the distantly related “schwenkioid” species, most of which are from the southwestern Indian Ocean) is another group that contains sets of phenovariant species, falling into two distinctly divergent sets of species that either share haplotypes (*P. bineeshi/hadra/schwenkii*) or are fractionally different (*P. tominagai/xanthommal/ternay/rubricauda*). The true *P. schwenkii* complex in the Indian Ocean is entirely allopatric, with the larger genetic split between the far western Indian Ocean species and the central/eastern species, i.e. from Maldives, India, to Indonesia.

It is unclear what exactly is the origin and significance of these shared lineages in *Pempheris*; it is an unusual finding among tropical marine reef fishes that needs to be further explored. One could speculate that it may be a result of an increased opportunity for accidental hybridization among crepuscular or nocturnal group-spawning fishes, or something to do with the presumably short larval duration of *Pempheris* facilitating regional differentiation, but not complete enough to develop corresponding genetic structure. Clearly, much more information on the genetics of this particularly difficult genus is needed.

Figure 1 (opposite). The neighbor-joining phenetic tree of COI sequences for Indian Ocean populations of *Pempheris* following the Kimura two-parameter model (K2P) generated by BOLD (Barcode of Life Database). The scale bar at left represents a 2% sequence difference. Collection locations for specimens are indicated, and the pempherid *Parapriacanthus ransonneti* is used as the outgroup. GenBank accession numbers and collection data for the sequences are listed in Appendix A.

TABLE 1
Anal-fin and pectoral-fin ray counts of specimens of *Pempheris* of the western Indian Ocean
(pectoral-fin rays counted separately on both sides)

	Anal-fin soft rays														16	Pectoral-fin rays					
	35	36	37	38	39	40	41	42	43	44	45	46	47	48		17	18	19			
<i>P. andilana</i>			2	3	1	3	1									7	13				
<i>P. argyrea</i>		1	5	5	4	2										1	21	12			
<i>P. bexillon</i>							6	7	3	1	1					2	16	16	2		
<i>P. bineeshi</i>				1	3	2	2										4	10			
<i>P. bruggemanni</i>						3	2	1									1	11			
<i>P. connelli</i>			1	5	16	4	5	2	1								16	49	3		
<i>P. convexa</i>					1	2			1								1	5	2		
<i>P. cuprea</i>					1	1	1									1	5				
<i>P. darvelli</i>							1		1									4			
<i>P. eatoni</i>				3	11	15	10	6	2	1							30	51	12		
<i>P. ellipse</i>		1	5	6	3	1											5	26	1		
<i>P. flavicycla</i>				1	3	6	6	5	3	2							2	26	22	2	
<i>P. hadra</i>				1														2			
<i>P. heemstraorum</i>			1																2		
<i>P. hollemani</i>				1		1												2	2		
<i>P. ibo</i>	1	5	4	2	2													6	22		
<i>P. kruppi</i>			3	4	4	3	2											3	29		
<i>P. kuriamuria</i>				1		1													3	1	
<i>P. leiolepis</i>			1																2		
<i>P. malabarica</i>								2	10	13	9	6		1				2	42	38	
<i>P. mangula</i>				4	4	7	1											2	25	5	
<i>P. megalops</i>								1										2			
<i>P. micromma</i>									1										2		
<i>P. muscat</i>	1		1	1	1	2												1	10	1	
<i>P. nesogallica</i>				1	4	4	4	3	3	2								2	21	18	1
<i>P. orbis</i>				2	1														2	4	
<i>P. pathirana</i>				1	3	1	3	2	1										1	18	3
<i>P. peza</i>		1	6	4	3	2													13	19	
<i>P. rhomboidea</i>		3	5	6	7	8	2	1											15	45	4
<i>P. rochai</i>					1														1	1	
<i>P. rubricauda</i>		1		1	1		2												4	6	
<i>P. russellii</i>					1	5	6	1											3	19	4
<i>P. sarayu</i>			1		1	1			1											2	6
<i>P. sergey</i>				1	2		1	1											8	2	
<i>P. shimoni</i>			1	2	2	4	2												7	13	2
<i>P. shirleen</i>			1	1															3	1	
<i>P. smithorum</i>						1	1												2	2	
<i>P. tau</i>				2	1														4	2	
<i>P. ternay</i>		1																	2		
<i>P. tilman</i>		1				1	1												6		
<i>P. tiran</i>								1		1									1	3	
<i>P. tominagai</i>		1	1	1	2														8	2	
<i>P. trinco</i>			1	5	7	6	2												17	23	
<i>P. viridis</i>		1																	1		
<i>P. wilsoni</i>											1								2		
<i>P. xanthomma</i>		5	8	6	3	2	2												4	39	9
<i>P. zajonzi</i>		2	1	2															10		

TABLE 2

Lateral-line scale counts of specimens of *Pempheris* of the western Indian Ocean

	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75							
<i>P. andilana</i>										1	1	2	1	1	2	2																								
<i>P. argyrea</i>								2	2	3	3	3	1	1	1																									
<i>P. bexillon</i>															2	3	4	3	2	1	2	1																		
<i>P. bineeshi</i>								1	1	2	2	2																												
<i>P. bruggemanni</i>																2	1	2				1																		
<i>P. connelli</i>								1	4	7	9	5	2	5		1																								
<i>P. convexa</i>										1	1			1																										
<i>P. cuprea</i>											1			1	1																									
<i>P. darvelli</i>														1	1																									
<i>P. eatoni</i>										1	5	4	7	9	10	7	7	3																						
<i>P. ellipse</i>								1	1	2	4	3	3	1	1																									
<i>P. flavicycla</i>											1	1	2	8	8	4	4	3																						
<i>P. hadra</i>							1																																	
<i>P. heemstraorum</i>																	1																							
<i>P. hollemani</i>													1			1																								
<i>P. ibo</i>	1	1	2	2	4	3	1																																	
<i>P. kruppi</i>														1	1	3	2	1	2	1	2	2	1																	
<i>P. kuriamuria</i>																	1		1																					
<i>P. leiolepis</i>											1																													
<i>P. malabarica</i>																								2	3	4	7	8	5	5	2	3	1	1						
<i>P. mangula</i>												3	4	5	2	1	1																							
<i>P. megalops</i>																1																								
<i>P. micromma</i>														1																										
<i>P. muscat</i>											1		1	2	1	1																								
<i>P. nesogallica</i>										1	2	1	3	6	4	2	1	1																						
<i>P. orbis</i>																1			1				1																	
<i>P. pathirana</i>														2	2	1	1	2	2	1																				
<i>P. peza</i>								1	2	1		2	1	3	3	2	1																							
<i>P. rhomboidea</i>										2	2	5	6	6	5	5																								
<i>P. rochai</i>																	1																							
<i>P. rubricauda</i>													3	1	1																									
<i>P. russellii</i>											1	5	4	1	2																									
<i>P. sarayu</i>													2		1		1																							
<i>P. sergey</i>									1		2	1	1																											
<i>P. shimoni</i>											2	1	2	3	2	1																								
<i>P. shirleen</i>								1				1																												
<i>P. smithorum</i>															1			1																						
<i>P. tau</i>								1		1			1																											
<i>P. ternay</i>										1																														
<i>P. tilman</i>								1	1		1																													
<i>P. tiran</i>																							1		1															
<i>P. tominagai</i>				1	2	1	1		1																															
<i>P. trinco</i>								1	1	2	2	4		4	4	1	1																							
<i>P. viridis</i>											1																													
<i>P. wilsoni</i>																																								
<i>P. xanthomma</i>								1	3	5	4	5	1	3	1	3																								
<i>P. zajonzi</i>								1	1			2	1																											

TABLE 3

Gill-raker counts of specimens of *Pempheris* of the western Indian Ocean

	24	25	26	27	28	29	30	31	32	33	34
<i>P. andilana</i>			1	4	4	1					
<i>P. argyrea</i>			1	1	9	5	1				
<i>P. bexillon</i>							1	3	6	6	2
<i>P. bineeshi</i>		2	3	3							
<i>P. bruggemanni</i>					1	5					
<i>P. conelli</i>						11	14	7	2		
<i>P. convexa</i>						1	1	1			
<i>P. cuprea</i>			1	1	1						
<i>P. darvelli</i>								1	1		
<i>P. eatoni</i>					1	6	15	14	11	1	
<i>P. ellipse</i>			2	3	6	4	1				
<i>P. flavicycla</i>						1	5	10	7	3	
<i>P. hadra</i>			1								
<i>P. heemstraorum</i>								1			
<i>P. hollemani</i>			1	1							
<i>P. ibo</i>				2	4	7	1				
<i>P. kruppi</i>						2	5	8	1		
<i>P. kuriamuria</i>							2				
<i>P. leiolepis</i>					1						
<i>P. malabarica</i>	1	11	18	10	1						
<i>P. mangula</i>				3	6	6	1				
<i>P. megalops</i>								1			
<i>P. micromma</i>							1				
<i>P. muscat</i>							2	2	2		
<i>P. nesogallica</i>							4	9	3	4	1
<i>P. orbis</i>							2	1			
<i>P. pathirana</i>						5	6				
<i>P. peza</i>					3	4	9				
<i>P. rhomboidea</i>						5	11	9	3	3	1
<i>P. rochai</i>					1						
<i>P. rubricauda</i>					3	2					
<i>P. russellii</i>							10	3			
<i>P. sarayu</i>					2		1	1			
<i>P. sergey</i>			2	3							
<i>P. shimoni</i>					2	4	4	1			
<i>P. shirleen</i>				1	1						
<i>P. smithorum</i>							1	1			
<i>P. tau</i>							1	1		1	
<i>P. ternay</i>					1						
<i>P. tilman</i>						1	2				
<i>P. tiran</i>								1	1		
<i>P. tominagai</i>					4	1					
<i>P. trinco</i>			12	5	3						
<i>P. viridis</i>		1									
<i>P. wilsoni</i>						1					
<i>P. xanthomma</i>			1	8	14	3					
<i>P. zajonzi</i>					3	1	1				

Pempheris andilana Randall & Victor, n. sp.

Figure 2, Tables 1–3.

Holotype. USNM 307628, male, 102.5 mm SL, Madagascar, Nosy Be, off Andilana Beach, near hotel at beach, Cruise 17 of R/V *Vityaz*, J.R. Paxton, D.M. Cohen, & B.B. Collette, rotenone, Nov. 9, 1988.

Paratypes. USNM 435863, 5: 93–103 mm SL, & BPBM 41193, 96 mm SL, same data as holotype; SAIAB 31327, 2: 91.5–102.5 mm SL, Madagascar, off Andilana Beach Hotel, rotenone, M. Anderson, Nov. 9, 1988; SAIAB 52862, 100.5 mm SL, Madagascar, Ambariotelo, 13.416° S, 48.366° E, rotenone, P.C. Heemstra & D.A. Hensley, Sep. 5, 1995.

Description. Dorsal-fin rays VI,9; anal-fin rays III,38 (37–41); pectoral-fin rays 17 or 18 (modally 18); lateral-line scales 56 (52–58); gill rakers 27 (26–29); body depth 2.2 (2.2–2.25) in SL; body width 2.75 (2.75–2.9) in body depth; head length 3.35 (3.15–3.35) in SL; eye moderate in size for the genus, orbit diameter 7.35 (7.3–8.0) in SL; interorbital width 10.9 (11.2–11.8) in SL; mouth oblique, forming an angle of 63° (62–65°) to horizontal axis of body; maxilla reaching posterior to a vertical at center of eye; tip of lower jaw projecting anterior to upper jaw when mouth fully closed; teeth in upper jaw in three irregular rows medially, soon narrowing laterally to a double row, and finally to a single row of very small but still pointed teeth in posterior fifth of jaw; teeth in lower jaw very small and densely spaced, in a band of about four to six rows medially, where broadest, progressively more retrorse and more pointed inwardly, the innermost largest and nearly horizontal (larger in males than females); tongue triangular, narrowing to a small, rounded, rectangular tip; lips smooth (densely and finely papillate by microscope); scales on nape and below dorsal fin cycloid; scales on ventroanterior fourth of side of chest ctenoid, the rest cycloid; scales dorsally on caudal peduncle ctenoid to one scale row above lateral line, cycloid below lateral line except midventrally; origin of dorsal fin at greatest body depth, the predorsal length 2.5 (2.4–2.55) in SL; longest dorsal-fin ray 3.4–3.8 in SL (broken in holotype); caudal fin forked, the caudal concavity about 4 in head length; pectoral-fin length 3.2 (3.0–3.2) in SL; prepelvic length 2.45 (2.45–2.5) in SL; pelvic fins reaching anus or extending slightly posterior, their length 6.8 (5.7–6.8) in SL. Color of body in alcohol light brown, many scales with very narrow pale yellowish edges, becoming darker above lateral line, and much darker on nape; chest notably lighter brown; fins yellowish, the dorsal fin with a black anterior band, not becoming broader at tip; caudal fin with wide blackish margins, broadest posteriorly; dark brown band at base of anal fin almost as broad anteriorly as outer yellowish part of fin, but narrower posteriorly; and pectoral fins with a blackish line centered on upper part of fin base. Color in life unknown.

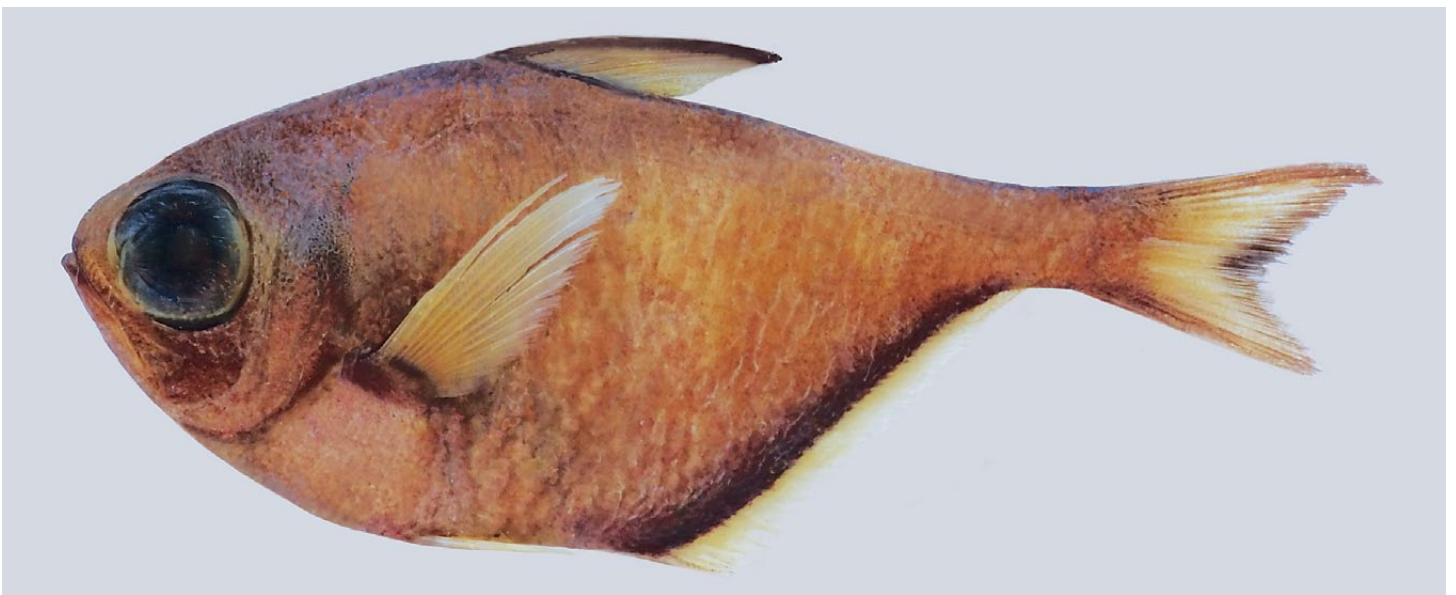


Figure 2. *Pempheris andilana*, holotype, USNM 307628, 102.5 mm SL, Andilana Beach, Nosy Be, Madagascar (H.A. Randall).

Etymology. This species is named *Pempheris andilana* for the beach on the island of Nosy Be, NW Madagascar, adjacent to the reef from which the type specimens were collected. The specific epithet is a noun in apposition.

Remarks. This new species is one of the large group of species of *Pempheris* that we term the *schwenkii* complex, named for the first species, *P. schwenkii* Bleeker, that was described from the Batu Islands off the SW coast of Sumatra in 1855. The last twenty-five species in the above key are from this group. They tend to be more slender, on average, than the remaining species of *Pempheris*, and all have a broad, dark brown to black band at the base of the anal fin, as well as a dark brown to black anterior margin on the dorsal fin that, on some species, expands to a dark distal spot. Also they lack the lateral dark stripes on the flanks made up of darkened scale centers characteristic of the *rhomboidea* complex of species. Two other members of the *schwenkii* complex are known from Madagascar: *P. rubricauda* from the same region as *P. andilana* and *P. hollemani* from the SE of the island: both differ in having a shorter predorsal length. No DNA sequences are available for *P. andilana*.

***Pempheris argyrea* Randall & Victor, n. sp.**

Figures 3 & 4, Tables 1–3.

Pempheris schwenkii [non Bleeker] Randall & Bineesh 2014: 37.

Holotype. BPBM 21599, female, 102 mm SL, Seychelles, La Digue, North Point, rocky shore, 0–1 m, rotenone, J.E. Randall, H.A. Randall, & D.J. Woodland, June 1, 1977.

Paratypes. SAIAB 51264, 90 mm SL, Seychelles, Mahé, 4.616° S, 55.450° E, J.L.B. Smith & M.M. Smith, Sept. 1954; SAIAB 51265, 90.5 mm SL, Praslin, 4.316° S, 55.733° E, J.L.B. Smith & M.M. Smith, Oct. 11, 1954; BPBM 22980, 5: 61–86 mm SL, CAS 237995, 2: 77–79 mm SL, & USNM 434841, 6: 65–91 mm SL, all with same data as holotype; BPBM 22937, 90 mm SL, Mahé, W coast, off Residence Danzilles, 2–3 m, speared from aggregation, J.E. Randall, April 6, 1980 (specimen in poor condition).



Figure 3. *Pempheris argyrea*, holotype, BPBM 21599, 102 mm, La Digue, Seychelles (J.E. Randall).

Description. Dorsal-fin rays VI,9; anal-fin rays III,38 (36–40); pectoral-fin rays 17 (16–18, modally 17); lateral-line scales 53 (50–57); gill rakers 28 (26–30); body depth 2.4 (2.3–2.5) in SL; body width 2.65 (2.55–2.7) in body depth; head length 3.15 (3.05–3.25) in SL; dorsal profile of head strongly convex; orbit diameter 7.35 (6.9–7.75) in SL; interorbital width 11.3 (10.9–11.5) in SL; mouth oblique, forming an angle of 62°(62–65°) to horizontal axis of body; tip of lower jaw projecting anterior to upper jaw when mouth fully closed; teeth in upper jaw in three irregular, close-set rows medially, soon narrowing to two well-separated rows, and finally to a single row of very small teeth on about posterior fifth of jaw; teeth in lower jaw very small and densely spaced, in a band of four to five irregular rows medially, where broadest, progressively more retrorse and more pointed posteriorly, the innermost teeth largest and nearly horizontal; tongue narrowly triangular and pointed; lips smooth (dense low papillae by microscope); scales on nape and below dorsal fin cycloid; scales on ventroanterior fourth of side of chest ctenoid, the rest cycloid; scales ctenoid on caudal peduncle only dorsally and ventrally; predorsal length 2.65 (2.55–2.7) in SL; dorsal fin broken (longest ray 4.3 in SL from photograph); caudal fin slightly forked, the caudal concavity about 4–5 in head length; pectoral-fin length 3.1 (3.1–3.3) in SL; prepelvic length 2.5 (2.4–2.45) in SL; pelvic fins varying from just reaching anus to reaching anterior end of anal-fin base, their length 6.0 (5.8–6.55) in SL. Color in alcohol light brown, the scales dorsally on head and nape a little darker; lateral line light brown with a slightly darker brown margin; fins pale yellowish, the dorsal with a broad brown anterior margin, expanding to a spot distally; anal fin with a broad dark brown band that narrows posteriorly; no dark spot at base or axil of pectoral fins; lips dusky. Color when fresh as in Fig. 3.

Etymology. This species is named *Pempheris argyrea*, from Greek for silvery, in reference to its overall silvery coloration, as noted when first collected and photographed as a specimen.

Remarks. This species has been observed and collected only from the three main islands of the Seychelles,



Figure 4. *Pempheris argyrea*, aggregation, La Digue, Seychelles (J.E. Randall).

with La Digue selected as the type locality. It is typically seen by day in aggregations in the shelter of coral reefs, at times in less than 1 m. One of 25 species of the broad *schwenkii* complex presently confirmed for the western Indian Ocean, distinguished by relatively large eyes, low count of 36–40 anal-fin soft rays, modally 17 pectoral-fin rays, 26–30 gill rakers, small size (largest specimen, the holotype, 102 mm SL), and silvery coloration. *P. ternay*, the other member of the *schwenkii* complex from the Seychelles, is distinguished by a black-bordered bright red-orange caudal fin. Two non-*schwenkii* complex species also occur in Seychelles: *P. flavicycla* and *P. megalops*. No DNA sequences are available for *P. argyrea*.

***Pempheris bineeshi* Randall & Victor, n. sp.**

Figures 5 & 6, Tables 1–3. BIN AAM9396 (in part).

Pempheris schwenkii [non Bleeker] Randall & Bineesh 2014: 36 (Tuticorin, India).

Holotype. NBFGR-CH-1143, female, 101 mm SL, India, Tamil Nadu, Tuticorin, trawler, 10–30 m, K.K. Bineesh, March 14, 2013.

Paratypes. BPBM 41096, 100 mm SL, India, Tamil Nadu, Tuticorin, from fisherman, K. Rama Rao & J.E. Randall, March 1, 1975; ZSI/CLT 2492, 5: 95–108 mm SL, same locality and date as holotype.

Description. Dorsal-fin rays VI,9; anal-fin rays 39 (38–41); pectoral-fin rays 17 or 18 (modally 18); lateral-line scales 49 (50–54); gill rakers 26 (25–27); body depth 2.5 (2.5–2.7) in SL; body width 2.6 (2.55–2.65) in body depth; head length 3.3 (3.2–3.35) in SL; dorsal profile of nape nearly straight, curving slightly to tip of snout; eye moderately large, 7.75 (7.5–7.85) in SL; interorbital width 11.9 (12.0–12.2) in SL; mouth oblique, forming an angle of 63°(60–64°) to horizontal axis of body; tip of lower jaw projecting slightly anterior to upper jaw when mouth firmly closed; small, strongly recurved, sharp teeth in two rows in upper jaw, those of upper row more forward-projecting, of lower row larger and more strongly recurved; teeth progressively smaller posteriorly in jaw, narrowing to a single row on about posterior fifth, and disappearing as maxilla expands; teeth in lower



Figure 5. *Pempheris bineeshi*, holotype, NBFGR-CH-1143, female, 101 mm SL, Tuticorin, India (K.K. Bineesh).



Figure 6. *Pempheris bineeshi*, paratype, ZSI/CLT 2492, 104 mm SL, Tuticorin, India (K.K. Bineesh).

jaw very small and densely spaced, in a band of four to five irregular rows medially, where band broadest, progressively larger, more retrorse and more pointed inwardly, the innermost teeth much the largest and nearly horizontal; lips smooth; tongue nearly forming an equilateral triangle; outer layer of scales, nearly all of inner layer, and even some of the strongly adhering lateral-line scales missing; predorsal length 2.8 (2.8–2.85) in SL; longest dorsal-fin ray 3.9 (3.95–4.05) in SL; caudal-fin length 3.55 in SL (broken on paratypes); caudal concavity 2.35 in head length of holotype; pectoral-fin length 3.15 (3.1–3.3) in SL; prepelvic length 2.8 (2.8–2.85) in SL; pelvic fins just reaching anus, their length 5.6 (5.75–5.9) in SL. Color in alcohol (Fig. 5) with the dorsal fin broadly bordered anteriorly and distally with black, the caudal fin with a blackish posterior border and no dark pigment on upper and lower margins, and two large dark areas forming an indistinct bar across nearly the basal half of fin; dark band at base of anal fin broad; only a faint narrow dark band across upper base of pectoral fins. Color when fresh as in Fig. 6.

Etymology. This species is named for K.K. Bineesh of the ICAR-National Bureau of Fish Genetic Resources (NBFGR) in Kochi, Kerala, in recognition of the extensive efforts he has made to collect, photograph, and DNA-barcode species of *Pempheris* in India.

Remarks. Presently known only from the type location, but to be expected elsewhere in SE India, and maybe well beyond. All of our specimens have been obtained from fishermen in Tuticorin, one of the oldest cities of India. The sweepers are typically collected as bycatch on small trawlers that fish in the evening and at night off the coast; the objective is shrimp and fishes of far more value than the small, thin-bodied species of *Pempheris*. Specimens collected by trawling have always lost nearly all of their scales. *P. bineeshi* is the only representative of the *schwenkii* complex from Indian waters, although *P. trinco* is described from nearby Sri Lanka. Other congeners from south India include *P. malabarica*, *P. mangula*, and *P. sarayu*. The barcode mtDNA COI sequences of *P. bineeshi* are the same as the sequence from *P. hadra* from the Maldives well to the south and specimens of presumed true *P. schwenkii* from Bali, Indonesia (the type location of *P. schwenkii* is Sumatra, midway between the Indian subcontinent and Bali). The three species form a lineage 3.4% divergent from a set of *schwenkii*-complex species from the western Indian Ocean, i.e. *P. tominagai* from the Red Sea, *P. xanthomma* from Yemen, *P. ternay* from Seychelles, and *P. rubricauda* from Madagascar (Fig. 1).

Pempheris bruggemanni Randall & Victor, n. sp.

Figures 7–9, Tables 1–3. BIN AAT9853.

Holotype. MNHN 2015-0002, male, 108 mm SL, Réunion, W side, S of Saint-Leu, 21°11.600 S; 55°16.946 E, 18 m, rotenone, H. Bruggemann, N. Hubert, & S. Planes, 13 Aug. 2007.

Paratypes. SMF 1537, 118 mm SL, Mauritius, 1885 (no further data); URUN 2007-1208, 83 mm SL & URUN 2007-1209, 86.5 mm SL, fore reef slope in front of Saint-Gilles, Réunion, 21°3.460 S, 55°13.280 E, 18 m, rotenone, H. Bruggemann, N. Hubert, & S. Planes, Aug. 12, 2007; URUN 2007-1419, female, 97 mm SL, & BPBM 41198, female, 103 mm SL (eyes missing), same data as holotype.

Description. Dorsal-fin rays VI,9; anal-fin rays III,41 (40–42); pectoral-fin rays 18 (17–18); lateral-line scales 60 (58–63); gill rakers 28 (28–29); body depth 2.3 (2.3–2.35) in SL; body width 3.1 (2.85–2.95) in body depth; head length 3.1 (3.1–3.2) in SL; nape slightly convex; orbit diameter 7.2 (7.2–7.3) in SL; interorbital width 10.8 (10.8–11.4) in SL; maxilla forming an angle of 68° (65–70°) to horizontal axis of body, reaching to or slightly posterior to a vertical at center of eye; tip of lower jaw projecting slightly anterior to upper jaw when mouth fully closed; teeth in upper jaw typical of genus, in two rows medially, soon narrowing to a single row; teeth in lower jaw very small, in 3 or 4 irregular rows medially, progressively more retrorse and more pointed medially, the innermost largest and nearly horizontal; lips smooth; scales on nape and below dorsal fin ctenoid; scales on ventroanterior two-thirds of side of chest ctenoid, the rest cycloid; scales ctenoid on caudal peduncle only dorsally and ventrally; predorsal length 2.5 (2.5–2.6) in SL; caudal and dorsal fins broken; pectoral-fin length 3.1 (3.0–3.1) in SL; prepelvic length 2.4 (2.35–2.4) in SL; pelvic fins reaching or extending slightly beyond anus, their length 5.7 (5.3–6.25) in SL. Color in alcohol gray, each scale of body with a vertically elongate brown bar; fins yellowish, the dorsal with a blackish anterior margin that expands distally; anal fin with a broad dark brown band at base that narrows posteriorly, and a broad blackish distal margin, also narrower posteriorly; caudal fin with dark upper and lower margins and a dark band enclosing the lateral line, but no black posterior margin; paired fins pale yellowish, the pectoral fins with a narrow, curved, dark brown band at extreme base of rays; no dark axillary spot. Color when fresh as in Figs. 7 & 8; color in life as in Fig. 9.

Etymology. This species is named for Professor Henrich Bruggemann of the Laboratoire d'Ecologie Marine, Université de la Réunion, who collected the type specimens with N. Hubert and S. Planes and provided the photographs. He was supported by the BIOTAS program of the French Agence Nationale de Recherche (ANR-06-BDIV), with the collaboration of Gustav Paulay (Florida Museum of Natural History).



Figure 7. *Pempheris bruggemanni*, holotype, MNHN 2015-002, male, 108 mm SL, Réunion (H. Bruggemann).



Figure 8. *Pempheris bruggemanni*, paratype, URUN 2007-1419, female, 97 mm SL, Réunion (H. Bruggemann).

Remarks. Presently known only from Réunion and Mauritius. The head of the holotype of *P. bruggemanni* must have been bent inwardly when photographed, resulting in an unnaturally short snout (a distortion also noted in some photographs of other species of the genus). The 83-mm male and 86.5-mm female paratypes are sexually mature. The paratype from Mauritius is in poor condition and was not used for measurements. Prof. Bruggemann confirms our identification of Alain Diringer's underwater photograph of Fig. 9 as the subadult of the present species. One other member of the *schwenkii* complex, *P. heemstraorum*, has also been collected in the Mascarene Islands, a single specimen from Rodrigues: it is a larger fish with a deeper body than the present species. The barcode mtDNA COI sequences of *P. bruggemanni* form a lineage 6.5% divergent (K2P; 6.3% uncorrected pairwise) from their nearest relatives, the clade including the common *P. connelli* of South Africa as well as *P. hollemani* from Madagascar and *P. rochai* from Oman (Fig. 1).



Figure 9. *Pempheris bruggemanni*, underwater photograph, Réunion (A. Diringer).

***Pempheris connelli* Randall & Victor, n. sp.**

Figures 10 & 11, Tables 1–3. BIN AAC6084 (in part).

Pempheris tominagai [non Koeda, Yoshino, Imai & Tachihara] Koeda *et al.* 2014: 317, in part.

Holotype. SAIAB 58560, female, 117 mm SL, South Africa, KwaZulu-Natal, Aliwal Shoal, 30.293° S, 30.817° E, ichthyocide, A. Bentley, P. Heemstra, E. Heemstra, & W. Holleman, June 14, 1998.

Paratypes. SAIAB 40347, 9: 60–111 mm SL, South Africa, KwaZulu-Natal, Park Rynie, Cowrie Reef, 30.3166° S, 30.733° E, C. Buxton, Aug. 4, 1992; SAIAB 43263, 2: 85–93 mm SL, KwaZulu-Natal, Horn's Reef, down beach from Mile 13, C. Buxton, June 24, 1993; SAIAB 46185, 2: 100–100.5 mm SL, South Africa, KwaZulu-Natal, Anchor Reef, 30° 25.00' S, 30.816° E, ichthyocide, C. Buxton, P. Heemstra, R. Tilney, & L. Berger, June 17, 1994; BPBM 41202, 106 mm SL; same data as SAIAB 46185; USNM 435889, 2: 116–119 mm SL, same data as holotype; SAIAB 61199, 3: 105–126.5 mm SL, Aliwal Shoal, 30° 25' S, 30.817° E, ichthyocide, P. Buchal, E. Heemstra, P. Heemstra, H. Larson, M. Smale, & A. Bentley, Nov. 25, 1999; SAIAB 62965, 2: 98–102 mm SL, Aliwal Shoal, ichthyocide, P. Buchal, P. Heemstra, E. Heemstra, H. Larson, M. Smale, & A. Bentley, Aug. 3, 2000; SAIAB 64662, 3: 91–99.5 mm SL, KwaZulu-Natal, 8-Mile Reef, 27.441° S, 32.717° E, ichthyocide, P. Heemstra, H. Larson, M. Smale, & A. Bentley, May 14, 2001; SAIAB 75776, 120 mm SL, female, KwaZulu-Natal, Aliwal Shoal, Cathedral Reef, 30.250° S, 30.81° E, spear, A. Connell, July 29, 2003; SAIAB 75850, 2: 78–103 mm SL, Aliwal Shoal, 30.300° S, 30.816° E, ichthyocide, P. Heemstra, E. Heemstra, J. Stapley, S. Warren, K. Hutchings, J. Dives, & R. Reaugh, Sept. 25, 2003; SAIAB 194781, 2: 96.5–98 mm SL, KwaZulu-Natal, Brighton Beach, 29.937° S, 31° 0.533' E, S. Chater *et al.*, Mar. 1, 2012; SAIAB 194782, 6: 53–63 mm SL, KwaZulu-Natal, Blood Reef (30 km S of Durban), 29° 53.041' S, 31° 3.606' E, 12 m, ichthyocide, A. Connell, Jan. 27, 2014; SAIAB 194783, 2: 102–113.5 mm SL, & BPBM 41204, 106 mm SL, Aliwal Shoal, 30° 16.682' S, 30° 48.555' E, ichthyocide and spear, A. Connell, July 5, 2014.

Description. Dorsal-fin rays VI,9; anal-fin rays III,39 (37–43); pectoral-fin rays 18 (17–19); lateral-line scales

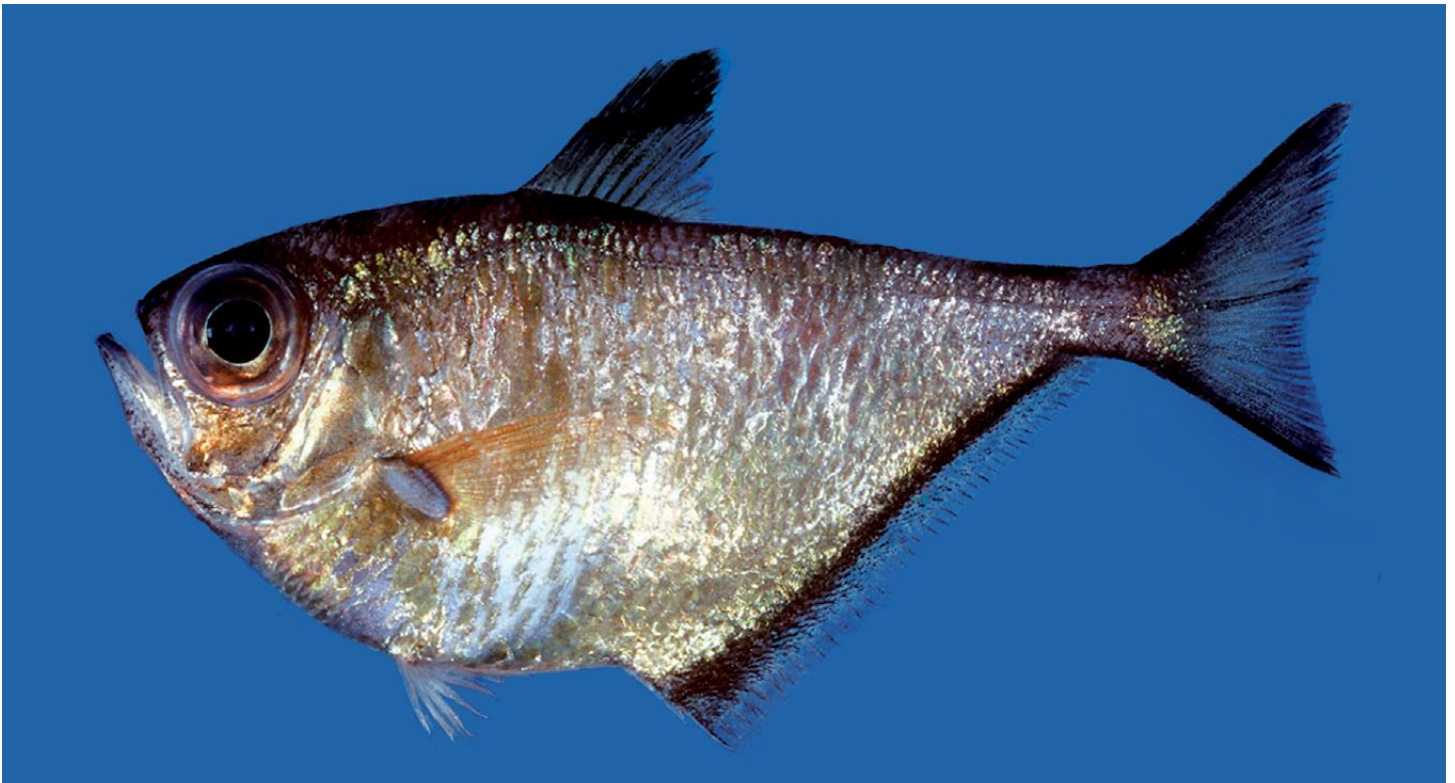


Figure 10. *Pempheris connelli*, holotype, SAIAB 58560, female, 117 mm, Aliwal Shoal, KwaZulu-Natal; pale blue areas on the body are where both layers of scales are missing (P.C. Heemstra).

53 (50–58); gill rakers 30 (29–32); body depth 2.2 (2.0–2.25) in SL; body width 2.95 (2.8–2.95) in body depth; head length 3.25 (3.2–3.3) in SL; eye moderately large, the orbit diameter 7.2 (7.05–7.55) in SL (in specimens 95–117 mm SL); interorbital width 10.6 (10.6–11.2) in SL; mouth oblique, forming an angle of 72° (67–72°) to horizontal axis of body; tip of lower jaw expanded to a small knob that projects slightly anterior to upper jaw when mouth fully closed; small, recurved, inwardly depressible teeth in two irregular rows anteriorly in upper jaw, soon narrowing to a single row posteriorly; small, recurved, depressible teeth in lower jaw in two to three rows medially, interspersed with tiny blackish nodules; lips with numerous, close-set papillae; tongue triangular, the sides indented near tip to form a small rectangle with rounded tip; scales on nape and below dorsal fin ctenoid; scales of side of chest about 3/4 cycloid, the ctenoid scales ventroanteriorly and adjacent to operculum; scales on side of caudal peduncle cycloid; predorsal length 2.6 (2.55–2.65) in SL; longest dorsal-fin ray 4.5 (4.1–4.9) in SL; pectoral-fin length 3.2 (3.0–3.2) in SL; prepelvic length 2.45 (2.4–2.45) in SL; pelvic fins not reaching anus, 6.5 (6.1–6.45) in SL. Color when fresh as in Fig. 10; no black spot at base of pectoral fins, but a narrow, curved dark brown line at base of pectoral-fin rays (not crossing entire base); axil of pectoral fins dark brown to black; no black posterior border on caudal fin; color in life as in Fig. 11. Largest specimen examined, 126.5 mm SL.

Etymology. This species is named for Dr. Allan D. Connell, whose untiring efforts to document the fishes of KwaZulu-Natal have resulted in the discovery of many new species. He collected several of the recent lots of the types of this species, as well as numerous specimens, photographs, and tissue samples of other species of fishes from southern Africa.

Remarks. Presently known only from KwaZulu-Natal, South Africa. A second member of the *schwenkii* complex, *P. ibo*, occurs in South Africa and Mozambique and can be found on the same reef and in the same collections as *P. connelli*. Dr. Connell speared one of each species in 24 m at Aliwal Shoal. The two species are easily confused as preserved specimens, but can be fully separated by the lateral-line scale count: 50–58 for *P. connelli* vs. 43–49 for *P. ibo*. Also *P. connelli* appears to attain larger size; the largest of 14 specimens of *P. ibo* examined by us measures 93 mm SL. Fortunately, despite their outward similarity, the barcode mtDNA COI sequences of the two species are very different: *P. connelli* sequences are 13.3% divergent (K2P; 12% uncorrected pairwise) from *P. ibo*. In fact, *P. bruggemanni* from the Mascarene Islands are actually closer genetically to *P. connelli* (6.3% divergent) and are the nearest-neighbor lineage (Fig. 1). The barcode sequence from the type specimens of *P. hollemani* from Madagascar and *P. rochai* from Oman have the same COI sequence as *P. connelli*, indicating either a recent split of closely related species or occasional hybridization may occur between the three species across the western Indian Ocean.



Figure 11. *Pempheris connelli*, underwater aggregation, Aliwal Shoal, KwaZulu-Natal (D. King).

Pempheris ellipse Randall & Victor, n. sp.

Figures 12 & 13, Tables 1–3.

Holotype. BPBM 35867, female, 93 mm SL, Oman, south coast, Rahah Bay, 16°57'4" N, 54°49'4" E, 6–9 m, spear, J.L. Earle, Oct. 10, 1993.

Paratypes. BPBM 41082, 15: 31–41 mm SL, Oman, south coast, Rahah Bay, tide pools at low tide, 0–2 m, rotenone, J.E. Randall, J.P. Hoover, & I. McLeish, Feb. 8, 1993.

Description. Dorsal-fin rays VI,9; anal-fin rays III,39 (36–40); pectoral-fin rays 18 (17–19, strongly modal 18; only one count of 19); lateral-line scales 53 (50–57); lateral line very strongly arched anteriorly, rising 3/4 orbit diameter above level of origin of lateral line; scales on nape and below dorsal fin ctenoid; scales on ventroanterior third of side of chest ctenoid, remaining chest scales cycloid; most scales missing from caudal peduncle, but the few intact scales are cycloid; gill rakers 27 (26–30); body deep, the depth 2.1 in SL, and moderately thick, the width 2.95 in depth; head length 3.35 in SL; eye forming a vertical ellipse (bony orbit width 12.2 mm; bony orbit height 13.9 mm); orbit diameter 7.45 in SL; interorbital width 10.9 in SL; jaws steeply oblique, the edge of maxilla forming an angle of 70° (69–75° in juveniles) to horizontal axis of body; upper jaw with a close-set, double row of small, recurved, sharply conical teeth that are progressively smaller laterally, ending in a single row of very small nodular teeth; band of teeth medially in lower jaw crossed by four to six irregular rows of very small recurved teeth, not clearly larger inwardly; tongue narrowly triangular with pointed tip; predorsal length 2.8 in SL; longest dorsal-fin ray 3.75 in SL; caudal fin broken; pectoral-fin length 3.3 in SL; prepelvic length 2.65 in SL; pelvic fins reaching origin of anal fin, their length 5.65 in SL. Color of holotype in alcohol as shown in Fig. 12; the body is uniform brown, only the scale edges a little lighter, except for a reddish hue on the chest and a faint greenish zone beneath the pectoral fin and continuing ventrally to the pelvic fins. Color of a juvenile in alcohol as in Fig. 13. Life color not reported.

Etymology. This species is named *Pempheris ellipse* in reference to the longer vertical axis of the orbit, giving the eye an elliptical shape. The specific epithet is a noun in apposition.



Figure 12. *Pempheris ellipse*, holotype, BPBM 35867, female, 93 mm SL, Rahah Bay, south coast of Oman, with two spear wounds on side below dorsal fin (H.A. Randall).



Figure 13. *Pempheris ellipse*, paratype, juvenile, 41 mm, Rahah Bay, southern Oman (H.A. Randall).

Remarks. Fifteen juveniles collected from a tidepool at Rahah Bay were identified as this species by the shape of the eye, the highly arched anterior end of the lateral line, the very steep angle of the upper jaw, and meristic characters. Three other species of *Pempheris* were collected in the bay: *P. convexa* Randall & Victor 2014, *P. micromma*, described in the present paper, and a subadult of an unidentified schwenkioid species collected from a cave in 14 m (BPBM 36325, 72 mm SL), for which no photograph or color note was taken. It has a very steep jaw angle, straight dorsal profile of the head and nape, ctenoid scales on the nape and below the dorsal fin (all scales missing from chest), but differs from *P. ellipse* in that the eye is round, the body more slender, and the anal fin has a blackish margin. *Pempheris rochai*, described herein from the nearby coast of Oman, might also be expected in the bay. A photograph of the tidal channels of Rahah Bay was published by Randall & Victor (2014: Fig. 2). No DNA sequences are available for *P. ellipse*.

***Pempheris hadra* Randall & Victor, n. sp.**

Figure 14, Tables 1–3. BIN AAM9396 (in part).

Holotype. SAIAB 187537, female, 118 mm SL, Republic of Maldives, Kaafu Atoll, 4°10.180' N; 73°30.800' E, rocky wall of swimming pool opposite power station, rotenone, O. Gon & G. Gouws, Dec. 6, 2010.

Description. Dorsal-fin rays VI,9; anal-fin rays III,38; pectoral-fin rays 17; lateral-line scales 49; gill rakers 26; body depth 2.45 in SL; body very stout, the width (taken just behind gill opening) 2.2 in body depth; head length 3.5 in SL; eye relatively small, orbit diameter 8.4 in SL; interorbital width 12.5 in SL; mouth oblique, forming an angle of 64° to horizontal axis of body; tip of lower jaw slightly anterior to upper jaw when mouth fully closed; teeth in upper jaw in two well-separated rows medially, narrowing to a single row posteriorly; conical teeth medially in lower jaw in four or five densely packed rows, those of outer row nearly erect, the remaining teeth progressively more recurved inwardly; scales on nape and below dorsal fin cycloid; scales on ventroanterior two-fifths of chest and along edge of operculum ctenoid, cycloid on the remaining three-fifths; scales on caudal peduncle ctenoid; predorsal length 2.7 in SL; longest dorsal-fin ray 3.95 in SL; caudal fin emarginate, the caudal



Figure 14. *Pempheris hadra*, holotype, SAIAB 187537, female, 118 mm SL, Kaafu Atoll, Republic of Maldives (O. Gon).

concavity 3.8 in head length; pectoral-fin length 3.25 in SL; prepelvic length 2.55 in SL; pelvic fins nearly reaching origin of anal fin, 6.2 in SL. Color in alcohol dark orangish brown, the scale edges narrowly pale yellow; fins yellowish, the leading edge of dorsal fin blackish, expanding into a large black apical spot; dark reddish streaks following longitudinal scale rows below lateral line: anal fin with a very dark brown band at base, 3 times broader anteriorly (comparable to the width of the fin); a middorsal V-shaped blackish mark on nape before dorsal fin; caudal fin with a broad blackish posterior margin, the upper and lower margins only slightly darker; no black spot on base or axil of pectoral fins, but a curving dark brown line following base of rays. Color when fresh as shown by Fig. 14.

Etymology. This species is named *Pempheris hadra*, from Greek for thick or stout, in reference to the unusual stocky body.

Remarks. We are aware of only a single specimen of *Pempheris hadra*. It is distinct in being more stout-bodied than any *schwenkii*-complex species we have examined, and unusual in having cycloid scales on the nape, but ctenoid scales on the side of the caudal peduncle. The unusual habitat is a pool constructed in the lagoon of Kaafu Atoll from which water is taken for cooling the electric power plant. The pool is also used for recreational swimming by the locals. We suspect that this fish found shelter in the incurrent cooling pipe (as have two other species of *Pempheris* we have documented in Guam). This species is the only *schwenkii*-complex species collected in Maldives; two unrelated species, *P. convexa* and *P. flavicycla*, are the other species known from the archipelago. The barcode mtDNA COI sequence of *P. hadra* is the same as a lineage of *Pempheris* that includes *P. bineeshi* from India and the probable true *P. schwenkii* (type location Sumatra) from Bali, Indonesia (Fig. 1). The lineage is 3.4% divergent from the nearest lineage in the neighbor-joining tree, which contains the western Indian Ocean complex of *P. tominagai* from the Red Sea, *P. xanthomma* from Yemen, *P. rubricauda* from Madagascar, and *P. ternay* from Seychelles.

Pempheris heemstraorum Randall & Victor, n. sp.

Figure 15, Tables 1–3.

Holotype. SAIAB 69487, female, 127 mm SL, Mascarene Islands, Rodrigues, 19.6502° S, 63.4297° E, reef in 4–7 m, ichthyocide, E. Heemstra, P. Heemstra, M. Smale, & J. Stapely, Oct. 8, 2001.

Description. Dorsal-fin rays VI,9; anal-fin rays III,37; pectoral-fin rays 18; lateral-line scales 59; gill rakers 31; body depth 2.2 in SL; body width 3.35 in body depth; head length 3.05 in SL; eye relatively small, the orbit diameter 8.45 in SL; interorbital width 10.7 in SL; mouth oblique, forming an angle of 63° to horizontal axis of body; tip of lower jaw slightly projecting when mouth fully closed; teeth anteriorly in upper jaw recurved, in two rows medially, reduced to an irregular single row of progressively smaller teeth about one-third back in jaw; teeth of lower jaw very small, conical and recurved, in a dense band of five to six rows medially, progressively more retrorse inwardly; upper lip with dense papillae; lower lip with small well-separated papillae; tongue narrowly triangular; outer layer of scales missing from nape, side of chest, and caudal peduncle; predorsal length 2.45 in SL; longest dorsal-fin ray 3.85 in SL; caudal fin slightly forked, caudal concavity about 5 in head length; pectoral fins long, 3.0 in SL; prepelvic length 2.5 in SL; pelvic fins long, reaching origin of anal fin, 5.3 in SL. Color in alcohol of body below lateral line nearly uniform light brown, the scale edges a little paler; head and body above lateral line darker brown; dorsal fin translucent with dusky rays, the spinous portion and first ray dark brown, with a little dark pigment extending onto distal end of next few rays; anal fin with a dark brown band at base, half depth of fin anteriorly, but narrowing posteriorly to only one-fifth height of fin; caudal fin with translucent yellowish membranes and light brown rays, the upper and lower margins dark brown, a narrow brown band following lateral line to end of fin, no posterior dark margin; paired fins pale yellowish, the pectoral fins without a dark brown spot on base or axil. Color when fresh as shown in Fig. 15.

Etymology. This species is named for Dr. Phillip C. Heemstra and Elaine Heemstra of the South African Institute for Aquatic Biodiversity, in recognition of their extensive body of work in ichthyology. They collected and photographed the holotype of this species, along with providing many other specimens and photographs of western Indian Ocean fishes.

Remarks. This species is unusually large for the *schwenkii* complex, although the markings are typical for the complex. Three other species are found in the Mascarenes: another *schwenkii*-complex species, *P. bruggemanni*, which has more anal-fin rays and fewer gill-rakers, and the *rhomboidea*-complex species *P. nesogallica*, which was described from Mauritius, and the unrelated *P. bexillon*. No DNA sequences are available for *P. heemstraorum*.



Figure 15. *Pempheris heemstraorum*, holotype, SAIAB 69487, 127 mm SL, Rodrigues, Mascarene Islands (P.C. Heemstra).

***Pempheris hollemani* Randall & Victor, n. sp.**

Figure 16, Tables 1–3. BIN AAC6084 (in part).

Pempheris tominagai [non Koeda, Yoshino, Imai & Tachihara] Koeda *et al.* 2014: 317, in part.

Holotype. SAIAB 200564, 118 mm SL, Madagascar, Anosy Region, Fort Dauphin, Libanona Beach, 25.5166° S, 32.6833° E, gill net, P.C. Heemstra, E. Heemstra, *et al.*, April 30, 2010.

Paratype. SAIAB 97406, 117 mm SL, same data as holotype.

Description. Dorsal-fin rays VI,9; anal-fin rays III,38 and 40; pectoral-fin rays 17 or 18; lateral-line scales 58 (55); gill rakers 27 (26); body depth 2.3 (2.2) in SL; body width 2.65 (2.6) in body depth, head length 3.6 (3.5) in SL; eye relatively small, the orbit 7.7 (7.85) in SL; interorbital width 12.1 in SL; mouth oblique, forming an angle of 70° to horizontal axis of body; tip of lower jaw projecting when mouth fully closed; small slender teeth in two rows anteriorly in upper jaw, soon narrowing to a single row; very small teeth in a dense band in lower jaw, also forming a single row posteriorly; tiny black nodules scattered within band of teeth of lower jaw; tongue triangular, the dorsal surface with scattered small black spots; scales cycloid, except ctenoid on nape, below and posterior to dorsal fin, and below a line from midway along edge of opercle to base of pelvic fins; predorsal length 2.7 in SL; longest dorsal-fin ray 4.1 in SL; caudal fin forked, length 4.0 (4.3) in SL, the caudal concavity 4.3 (4.0) in head length; pectoral-fin length 3.2 in SL; prepelvic length 2.5 in SL; pelvic fins not reaching anus, 6.9 (6.75) in SL. Color in alcohol pale brown, the head and body above lateral line a little darker; dorsal fin with dense melanophores anteriorly and distally; caudal fin with fine melanophores on rays, fewer on membranes, the margins of fin a little darker; a broad dark band at base of anal fin, as if stippled with large melanophores; a curved blackish line at base of pectoral-fin rays, and a large black spot in axil of fins. Color when fresh as in Fig. 16.

Etymology. This species is named for Dr. Wouter Holleman of the South African Institute for Aquatic Biodiversity, in recognition of his extensive research on western Indian Ocean ichthyology. He provided the data on this species from the two type specimens when they could not be sent on loan.

Remarks. The two specimens of *P. hollemani* were collected during the *Atimo Vatae* Expedition to southern Madagascar (Philippe Bouchet of the Museum national d'Histoire naturelle, Principal Investigator). Koeda *et al.* (2014: 317) erred by including this species as a paratype of their new species *P. tominagai*, type locality Sharm



Figure 16. *Pempheris hollemani*, holotype, SAIAB 200564, 118 mm, SE Madagascar (E. Heemstra).

el-Sheikh, northern Red Sea. The specimens are clearly not *P. tominagai*, a Red Sea species with a different color pattern and more than 15% different mtDNA sequences (Randall *et al.* 2014). All species of *Pempheris* of the *schwenkii* complex share a broad dark brown to black band at the base of the anal fin. *Pempheris hollemani* has this dark anal-fin band, but instead of being uniformly dark brown or black, it is unique in consisting of discrete black dots of variable size. The barcode mtDNA COI sequence of *P. hollemani* is the same as *P. connelli* from South Africa and *P. rochai* from Oman, indicating either a recent split of closely related species or some degree of gene flow across the western Indian Ocean between the three species (Fig. 1).

***Pempheris ibo* Randall & Victor, n. sp.**

Figures 17 & 18, Tables 1–3. BIN AAF8820.

Holotype. SAIAB 191483 (out of SAIAB 3874), female, 93 mm SL, Mozambique, Ibo Island, lighthouse, 12.3333° S, 40.6166° E, M.M. Smith & R. Stobbs, Oct. 1, 1973.

Paratypes. SAIAB 3759, 8: 35–45 mm SL, Mozambique, Quilalea Island, 12.4891° S, 40.5994° E, M.M. Smith & R. Stobbs, Oct. 12, 1973; BPBM 41201, 80 mm SL, male, Mozambique, 15°32.91' S, 40°38.57' E, R/V *Fridtjoff Nansen*, M. Lisher, Aug. 13, 2009; SAIAB 189307, 2: 54.5–65 mm SL, South Africa, KwaZulu-Natal, sunken barge DAR 1, 28°09.682' S, 32°33.649' E, 25 m, A.D. Connell, spear, Apr. 13, 2010; SAIAB 189165, 2: 41.5–60 mm SL, South Africa, KwaZulu-Natal, sunken barge DAR 1, 25 m, A.D. Connell, Aug. 1, 2011.

Description. Dorsal-fin rays VI,9; anal-fin rays III,39 (35–39); pectoral-fin rays 18 (17 or 18, modally 18); lateral-line scales 48 (43–49); lateral line rising steeply and straight from origin to a level about 2/3 orbit diameter above origin, then forming a distinct sharp angle with remaining lateral line; scales on nape and below dorsal fin ctenoid; scales on ventroanterior three-quarters of side of chest ctenoid, remaining scales cycloid; scales on caudal peduncle ctenoid, except for scale row above and below lateral line; gill rakers 30 (27–30); body depth 2.35 (2.2–2.45) in SL, moderately compressed, width 2.8 (2.75–3.0) in body depth; head length 3.3 (3.25–3.3) in SL; orbit diameter 7.8 (7.25–7.95) in SL; interorbital width 11.6 (11.3–12.4) in SL; mouth oblique, forming an angle of 68° (66–69°) to horizontal axis of body; dentition typical of most species of the genus; tongue slender,



Figure 17. *Pempheris ibo*, holotype, SAIAB 191483, female, 93 mm, Mozambique, Ibo Island (H.A. Randall).

triangular, and sharply pointed; predorsal length 2.7 (2.7–2.75) in SL; longest dorsal-fin ray 3.9 (3.9–4.15) in SL; caudal fin forked, the caudal concavity about 2.6 in SL; pectoral-fin length 3.0 (2.95–3.1) in SL; prepelvic length 2.6 (2.55–2.6) in SL; pelvic fins just reaching anus, fin length 6.45 (5.75–6.65) in SL. Color in alcohol of holotype shown in Fig. 17. The faint blackish border on the anal fin is not shared by all specimens. The life color is variable, as shown in Fig. 18.

Etymology. This species is named for the type locality, Ibo Island, Mozambique. The specific epithet is a noun in apposition.

Remarks. The 34-m lighthouse at Ibo Island, Pinda, Mozambique was erected in 1923 to warn mariners of nearby shoal waters. Fifty years later, Margaret M. Smith and Robin Stobbs made a small collection of fishes off the lighthouse that included 11 specimens of *Pempheris*. Ten were identified as *P. adusta* Bleeker, later corrected by us to *P. eatoni* Randall & Victor. The remaining 93-mm specimen is the holotype of the present species. Ten days later, Smith & Stobbs made an inshore fish collection at Quilalea Island, Mozambique that included eight juveniles of *P. ibo*. Recent collections have extended the range to KwaZulu-Natal, the most southern at Aliwal Shoal, where *P. ibo* can be found in the same collections as their similar-appearing and more abundant relative, *P. connelli*.

The small size, slender body, meristic data, broad blackish band at base of anal fin, and dark leading edge of the dorsal fin identify this species as one of the *schwenkii* complex. It is readily identified as a distinct species by having 43–49 lateral-line scales (lowest for any species of the genus in the western Indian Ocean– see Table 2), steeply angular anterior lateral line, relatively low count of anal-fin soft rays, long pectoral fins, and short predorsal length. The fish of Fig. 18 are readily identified as *P. ibo* by the slender body, relatively small eye, angular anterior lateral-line, long pectoral fins, and especially by being able to count the low number of anal-fin soft rays and lateral-line scales. One other species of the *schwenkii* complex, *P. peza*, has been collected in Mozambique and one other in South Africa, the common *P. connelli*; both have many more lateral-line scales. Despite the similarity in appearance, the barcode mtDNA COI sequences of *P. ibo* are very different from the *P. connelli* lineage, 13.3% divergent (K2P; 12% uncorrected pairwise). The nearest-neighbor lineage to *P. ibo* is *P. bruggemanni* from the Mascarenes, but still far distant with 11.8% divergence (K2P; 11% uncorrected pairwise)(Fig. 1).



Figure 18. *Pempheris ibo*, underwater aggregation, note color variation, Mozambique (D. Polack).

***Pempheris kruppi* Randall, Victor & Aided, n. sp.**

Figures 19 & 20, Tables 1–3. BIN AAD1777 (in part).

Pempheris sp. Zajonz *et al.* 2000: 156 (Socotra Archipelago).

Holotype. SMF 35711, female, 123.5 mm SL, Gulf of Aden, Yemen, Ras Belhaf, 13°58.361' N, 48°11.743' E, 8 m, moderately steep reef that shelves southward, high live coral cover of massive *Porites*, abundant foliose *Montipora*, and encrusting *Echinopora*, rotenone, E. Lavergne, M. Schneider, & U. Zajonz, June 3, 2006.

Paratypes. SMF 35528, 6: 106.5–123 mm SL, & NHCY-P-12, 6: 108–118.5 mm SL, Gulf of Aden, Yemen, Ras Majdaha, 14°00.868' N, 48°25.572' E, steep rocky slope to 6 m, collected with rotenone from 8–11 m, live coral cover less than 20%, isolated corals, mainly *Porites*, some *Pocillopora*, rotenone, F. Krupp, M. Schneider, & E. Lavergne, May 20, 2005; BPBM 41214, 121 mm SL, USNM 435864, 124 mm SL, & NHCY-P-13, 123 mm SL, all with same data as holotype.

Description. Dorsal-fin rays VI,9 (rarely VI,10); anal-fin rays III,39 (37–41); pectoral-fin rays 18 (17 or 18, rarely 17); lateral-line scales 60 (55–64); scales on nape and chest ctenoid, mixed cycloid and ctenoid below dorsal fin, and cycloid on side of caudal peduncle; gill rakers 30 (29–32); body depth 2.15 (2.15–2.25) in SL; body width 2.7 (2.6–2.7) in body depth; head length 3.2 (3.1–3.35) in SL; eye relatively small, the orbit diameter 7.4 (7.15–7.45) in SL; interorbital width 10.9 (10.7–11.0) in SL; mouth strongly oblique, forming an angle of 69° (67–70°) to horizontal axis of body; very small, slender, recurved, conical teeth in a double row in medial third of upper jaw, continuing as a single row to end of jaw; slender, conical, recurved teeth in lower jaw in a narrow band of four to five rows medially, narrowing to a single row at nearly the same point as upper jaw; tongue triangular, straight-sided and pointed; predorsal length 2.7 (2.6–2.7) in SL; longest dorsal-fin ray 4.0 (3.8–4.0) in SL; caudal fin moderately forked, the caudal concavity about 4–5 in head length; pectoral-fin length 3.35 (3.15–3.4) in SL; prepelvic length 2.6 (2.5–2.6) in SL; pelvic fins reaching or extending slightly posterior to anus, 5.85 (5.1–6.05) in SL. Color in alcohol as in Fig. 19; dark brown, the scale edges silvery gray; dorsal fin yellowish gray with a distal black spot on first six soft rays, its length two-thirds eye diameter; caudal fin gray-brown, progressively lighter

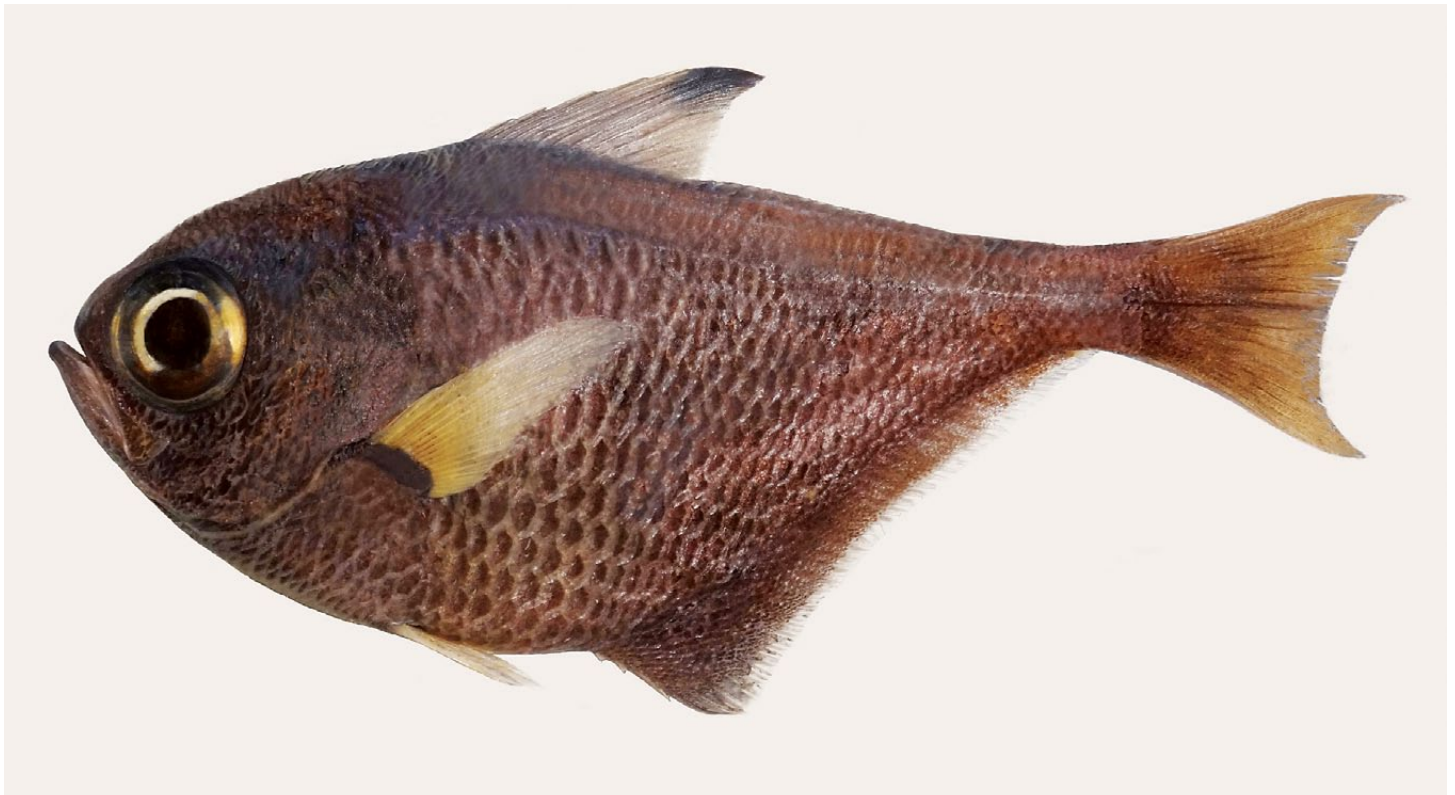


Figure 19. *Pempheris kruppi*, holotype, SMF 35711, female, 123.5 mm, Gulf of Aden, Yemen, off Ras Belhaf (H.A. Randall).



Figure 20. *Pempheris kruppi*, Gulf of Aden off Majdahah, south coast of Yemen; note the variation in the color of the posterior margin of the caudal fin (M. Shaikh Aideed).

posteriorly, except for a blackish posterior border (when fin intact); anal fin reddish brown on basal half, followed by a middle zone of brownish yellow, finely flecked with black dots, and a narrow translucent outer zone about one-third pupil diameter in average width; paired fins yellowish, the pectoral-fin base with a purplish black band across base, one-half pupil diameter in depth; axil of pectoral fins black; iris brassy yellow with a black circle that expands dorsally. Color in life dark brown with prominent lateral dark stripes; yellowish to orange fins and a distinct oval apical spot on the dorsal fin; anal fin with dark-tipped membranes on first few rays (Fig. 20). Largest specimen examined, the holotype.

Etymology. This species is named for Dr. Fareed Krupp of the Forschungsinstitut Senckenberg, authority on the fishes of the Gulf of Aden and Red Sea, and principal collector of the first series of type specimens of the species.

Remarks. Presently known only from the Gulf of Aden off Yemen and from the islands of the Socotra Archipelago. It is one of several species in the *rhomboidea* complex in the region, and is closely related to *P. pathirana* from Sri Lanka, from which it primarily differs by tooth arrangement. *Pempheris rhomboidea* from the adjacent Red Sea and *P. kuriamuria* from Oman have longer pectoral fins; *P. darvelli* from Oman has a longer head length; *P. wilsoni* from Oman has a shorter head and prepelvic length; *P. muscat*, also from Oman, has divided scale types on the chest (vs. entirely ctenoid); and *P. russellii* from Pakistan has a different shape of the tongue. Moteah Shaikh Aideed earned a coauthor role for the description of this species by providing specimens, collection data, tissue samples, and photographs. The barcode mtDNA COI sequences of *P. kruppi* from Yemen are the same as others of the *rhomboidea* complex, including two species described from specimens from nearby Oman: *P. kuriamuria* and *P. wilsoni* (Fig. 1).

Pempheris kuriamuria Randall & Victor, n. sp.

Figures 21 & 22, Tables 1–3. BIN AAD1777 (in part).

Holotype. CAS 236521, female, 112.5 mm SL, Oman, south coast, Ras Hamar, 16°54'44.3" N, 53°47'25.9" E, reef, ichthyocide, L.A. Rocha, J.D. DiBattista, M. Priest, T. Sinclair, & J.H. Choat, March 17, 2013.

Paratype. BPBM 41239, gender unknown, 95 mm SL, Oman, Gulf of Oman, Jissah Island, 23°33.513' N, 58°39.144' E, spear, B.W. Darvell & K.D.P. Wilson, Nov. 27, 2013.

Description. Dorsal-fin rays VI,9; anal-fin rays III,40 (38); pectoral-fin rays 18 (one side 19); lateral-line scales 61 (59); scales on nape and side of chest ctenoid, mixed cycloid and ctenoid below dorsal fin, and cycloid on side of caudal peduncle; gill rakers 30; body depth 2.15 in SL; body width 2.95 (2.85) in body depth; head length 3.3 (3.35) in SL; eye relatively small, equal to postorbital length, the orbit diameter 7.45 (7.3) in SL; interorbital width 12.4 (10.4) in SL; mouth forming an angle of 66° (69°) to horizontal axis of body; upper jaw with small, slender, recurved, conical teeth in two close-set rows to below nostrils, continuing as a single row to end of jaw; teeth in lower jaw in a narrow band, crossed where broadest by six or seven rows of extremely small, recurved, conical teeth that are progressively more retrorse posteriorly; tongue narrowly triangular with slightly incurved sides; predorsal length 2.45 (2.55) in SL; longest dorsal-fin ray 3.75 (3.65) in SL; caudal fin slightly forked, 3.6 in SL in paratype, caudal concavity about 3.5 in HL (estimated, longest rays broken); pectoral-fin length 2.9 (2.95) in SL; prepelvic length 2.5 in SL; pelvic fins just reaching origin of anal fin, 5.65 (5.2) in SL. Color in alcohol (Fig. 21) with dark band at base of anal fin (very broad anteriorly and progressively narrower posteriorly), broad translucent light middle zone of fin, densely stippled with dark brown, and a narrow transparent outer margin; a curved dark purplish brown band at base of pectoral fins; and dorsal fin with a black apical spot, no dark leading edge, and a narrow black band at base. Color in life as shown in Fig. 22.

Etymology. This species is named for the type locality, the Kuriamuria Islands off the south coast of Oman. The specific epithet is a noun in apposition.

Remarks. The underwater photographs of Fig. 22 are identified as *P. kuriamuria* by the long pectoral fins, eye size (equal to postorbital head), body and fin proportions, lateral-line scale count, and color pattern, especially the dark brown band at the base of the anal fin that narrows posteriorly. Although this band is a typical feature of the *schwenkii* complex, *P. kuriamuria* has the stripes along the flank following the scale rows typical of the *rhomboidea*-complex. The holotype is notable for the relatively long pectoral fins distinguishing it from the other species in the complex (shared only with *P. rhomboidea* of the Red Sea which differs by having two scale types on the chest vs. all ctenoid). The barcode mtDNA COI sequence of *P. kuriamuria* is the same as others of the *rhomboidea* complex, including *P. wilsoni*, also from Oman (Fig. 1).



Figure 21. *Pempheris kuriamuria*, holotype, CAS 236521, female, 112.5 mm SL, Oman, Ras Hamar (H.A. Randall). Caudal fin damaged (posterior margin of fin has a uniform dark edge when intact).



Figure 22. *Pempheris kuriamuria*, underwater photographs; **upper:** Raysut, south coast of Oman; **lower:** Kuriamuria Islands, southern Oman (J.E. Randall).

Pempheris leiolepis Randall & Victor, n. sp.

Figure 23, Tables 1–3.

Holotype. SAIAB 200715 (out of SAIAB 51259), male, 100 mm SL, Zanzibar, Chumbe Island, 6.1666° S, 39.1833° E, J.L.B. & M.M. Smith, Aug. 5, 1952.

Description. Dorsal-fin rays VI,9; anal-fin rays III,37; pectoral-fin rays 18; lateral-line scales 53; scales on nape, below dorsal fin, and side of caudal peduncle cycloid; scales on side of chest cycloid, except for two or three ventral ctenoid scales adjacent to operculum; gill rakers 28; body depth 2.4 in SL; body moderately compressed, the width 2.6 in body depth; head length 3.0 in SL; dorsal profile of head nearly straight; eye diameter 7.75 in SL; interorbital width 11.6 in SL; mouth oblique, forming an angle of about 63° to horizontal axis of body; teeth in upper jaw typical of those of lower jaw of the genus, with three or four irregular rows of small conical teeth that are progressively larger and more recurved posteriorly; teeth of lower jaw much smaller and more densely packed, in a maximum of approximately six rows; tip of lower jaw expanded to a small knob that projects slightly forward when mouth firmly closed; tongue triangular with slightly indented sides, the tip rounded and very flexible; predorsal length 2.5 in SL; outer part of dorsal and caudal fins broken; pectoral-fin length 3.15 in SL; prepelvic length 2.4 in SL; pelvic fins just reaching origin of anal fin, their length 6.2 in SL. Color in alcohol as shown in Fig. 23; the body is a nearly uniform orangish brown, except for a reddish hue to the chest and a greenish zone beneath the basal part of the pectoral fin, continuing to the base of pelvic fins; note the absence of a prominent dark spot at the base of the pectoral fins (instead there is a blackish line that nearly crosses the upper part of the fin base). Color in life unknown.

Etymology. This species is named *Pempheris leiolepis*, from the Greek meaning smooth scales, in reference to its having the greatest cover of the body in cycloid scales.

Remarks. The type locality, Chumbe, is a 16-acre, privately-owned island 8 miles SW of Zanzibar, famous for its spectacular coral reefs. Details are lacking for the Smiths' collection of our single specimen. The species is a member of the *schwenkii* complex; it is the only species of the complex we have examined along the African coast north of Mozambique, where there are two other species, *P. ibo* and *P. peza*. The upper-jaw dentition is very similar to that of *P. andilana* and *P. argyrea*, the basis for grouping them in the same part of the identification key. No DNA sequences are available for *P. leiolepis*.

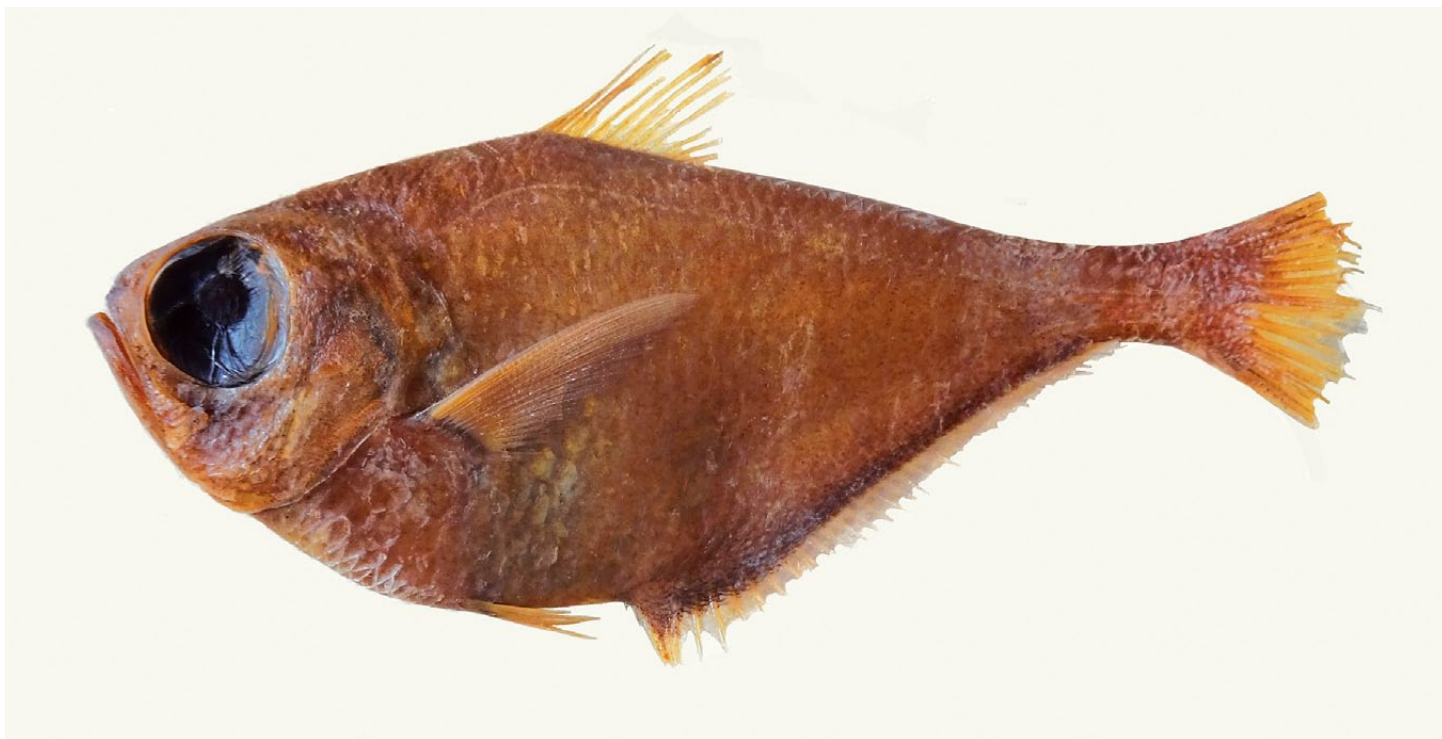


Figure 23. *Pempheris leiolepis*, holotype, SAIAB 200715, male, 100 mm SL, Chumbe Island, Zanzibar (H.A. Randall).

Pempheris megalops Randall & Victor, n. sp.

Figure 24, Tables 1–3.

Holotype. BPBM 41063, female, 121 mm SL, Seychelles, La Digue, North Point, rocky shore, 0–1 m, rotenone, J.E. Randall, H.A. Randall, & D.J. Woodland, June 1, 1977.

Description. Dorsal-fin rays VI,9; anal-fin rays III,42; pectoral-fin rays 17; lateral-line scales 58; outer layer of scales on nape and side of caudal peduncle missing; scales on about ventroanterior half of side of chest ctenoid, those on remaining half cycloid; gill rakers 31; body depth 2.35 in SL; body width 2.9 in body depth; head length 2.95 in SL; eye extremely large, the orbit diameter 6.2 in SL; interorbital width 11.0 in SL; upper jaw with a narrow symphyseal gap, the larger teeth sharply conical and recurved, mainly in two irregular rows, those of the upper row more jutting, narrowing to a single irregular row nearly half way to end of jaw; very small recurved teeth above and interspersed among larger teeth; lower jaw with a band of very small, nodular, recurved teeth in four or five irregular rows where broadest medially; predorsal and prepelvic lengths 2.4 in SL; longest dorsal-fin ray 3.35 in SL; caudal fin damaged; pectoral-fin length 3.0 in SL; pelvic fins just reaching origin of anal fin, 5.8 in SL. Color in alcohol as in Fig. 24; the caudal fin had a broad blackish posterior margin in life, as well as one on the outer margin of anal fin, though not as strongly developed. There is no dark spot at the base or axil of the pectoral fins. Color in life unknown.

Etymology. The species is named *Pempheris megalops* from the Greek meaning large eye, in reference to the type having the largest eye of any species of the genus that we have examined.

Remarks. This species is apparently not a member of the *schwenkii* complex, but its placement is uncertain. Three other *Pempheris* species are found in Seychelles: two in the *schwenkii* complex, *P. ternay* and *P. argyrea* (type specimens of the latter in the same collection as this holotype), and the unrelated *P. flavicycla*. *Pempheris* species typically occur in aggregations, so more than one specimen was probably collected in the rotenone station that resulted in the holotype of *P. megalops*. Not realizing the species was undescribed, only one specimen was preserved, and no photograph was taken. It is odd that this species, with such a large eye, was found by day at a depth of less than one meter. No DNA sequences are available for *P. megalops*.



Figure 24. *Pempheris megalops*, holotype, BPBM 41063, female, 121 mm, La Digue, Seychelles (H.A. Randall).

Pempheris micromma Randall & Victor, n. sp.

Figures 25 & 26, Tables 1–3.

Holotype. BPBM 41157, female, 117 mm SL, Oman, south coast, Rahah Bay, west side, rocky point, 16°57' N, 54°49'12" E, tide pools, 0–1.5 m, rotenone, J.E. Randall & I. McLeish, Feb. 6, 1993.

Description. Dorsal-fin rays VI,9; anal-fin rays III,43; pectoral-fin rays 18; lateral-line scales 56; scales on nape and below dorsal fin cycloid; ctenoid scales on at least ventroanterior two-thirds of chest (missing from rest of chest); scales on caudal peduncle ctenoid; gill rakers 30; body depth 2.35 in SL; body strongly compressed, the width 3.1 in depth; head length 3.6 in SL; eye very small, the orbit diameter 9.45 in SL; interorbital width 13.1 in SL; jaws steeply oblique, the edge of maxilla forming an angle of 67° to horizontal axis of body; dentition of upper jaw typical of the genus; band of teeth in lower jaw broadest medially where crossed by four or five rows of very small conical teeth, progressively more recurved inwardly; predorsal and prepelvic lengths 2.75 in SL; longest dorsal-fin ray 3.65 in SL; caudal fin damaged; pectoral-fin length 3.3 in SL; pelvic fins short, just reaching anus, 6.65 in SL. Color in alcohol as in Fig. 25, the body brown, except for reflection from scale edges, with a greenish gray zone from beneath basal half of pectoral fin to ventral abdomen; each scale with a darker vertical zone from a stippling of dark brown dots; dorsal fin with only a dusky band on the leading edge, but with a typical distal black spot and a narrow blackish band at base; caudal fin with a broad blackish posterior border, but without dark pigment on upper and lower margins; anal fin with three color zones, a very broad basal band a little darker brown than body, strongly narrowing posteriorly, a middle pale yellow zone with brown dots, and a translucent whitish margin; paired fins pale yellowish, the pectoral fins with a narrow dark brown band across most of base where rays end; color in life as shown by the photograph of an aggregation in Fig. 26.

Etymology. This species is named *Pempheris micromma* from the Greek meaning small eye, in reference to the type having the smallest eye for the genus.

Remarks. The holotype was collected from a large tidal channel in Rahah Bay on the south coast of Oman, along with 15 juveniles of what was believed to be the same species. However, the juveniles were later identified, chiefly by meristics, to be the same as an adult specimen of *P. ellipse* speared in the bay at a depth of 8 m. The species of the underwater photograph of Fig. 26 is identified as *P. micromma* by the very small eye, steep angle of the upper jaw, predorsal and prepelvic lengths, and by the locality of the south coast of Oman near Rahah Bay. The eye of the holotype in Fig. 25 appears vertically elliptical, but this is a result of the head not being in the same plane as the body for the photograph. The left eye measures only 0.5 mm higher than broad, and the right eye is a



Figure 25. *Pempheris micromma*, holotype, BPBM 41157, female, 117 mm, Rahah Bay, southern Oman (H.A. Randall).

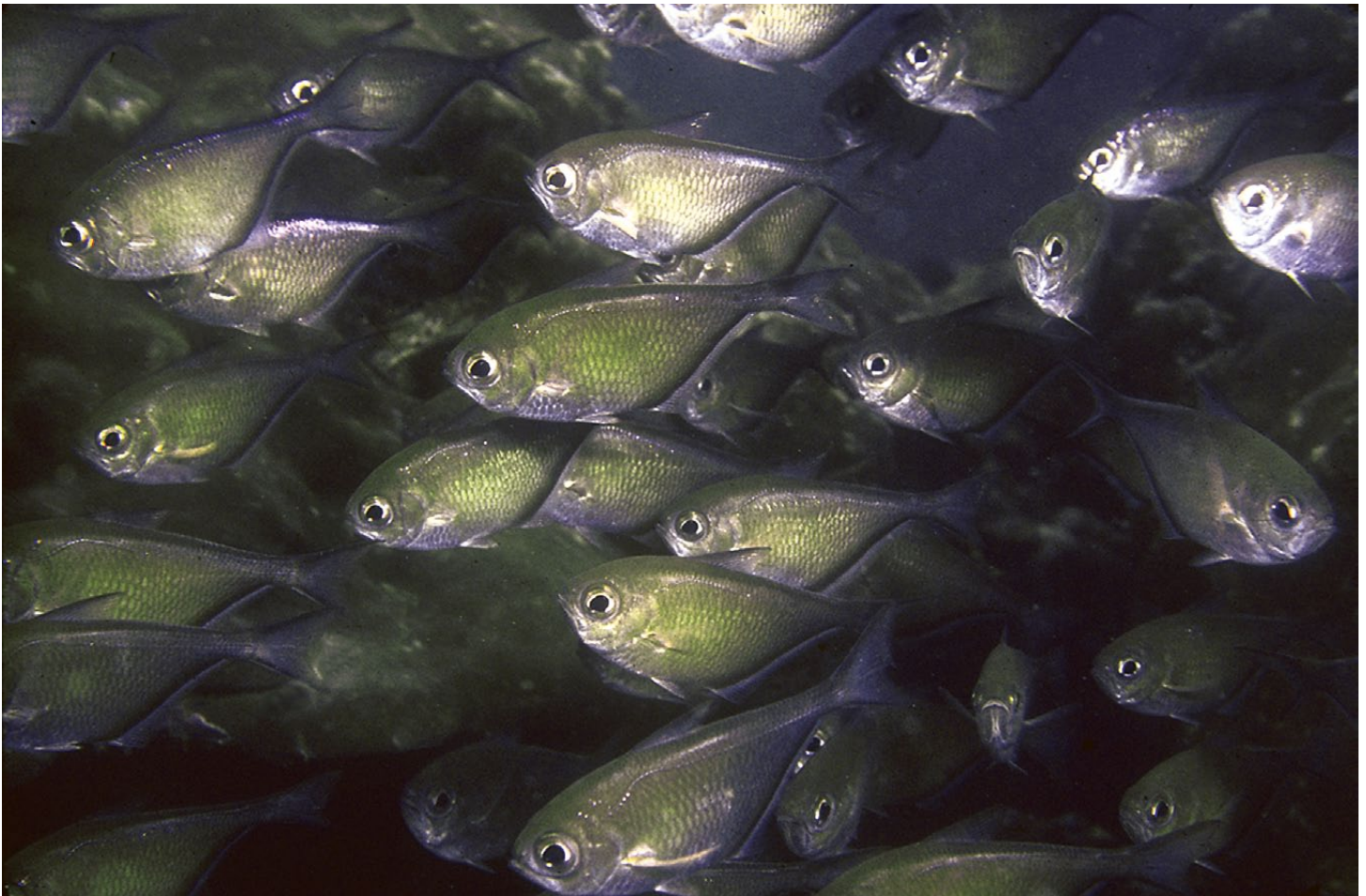


Figure 26. *Pempheris micromma*, underwater aggregation, south coast of Oman (J.E. Randall).

perfect circle, clearly distinguishing this species from *P. ellipse*. The holotype does not have the dark band at the base of the anal fin characteristic of the *schwenkii* complex, but the appearance in the underwater photograph is consistent with *schwenkii*-complex sweepers. Additional material will resolve the status of this species.

Two other species co-occur in Rahah Bay with *P. micromma*: *P. ellipse*, distinguished by elliptical eyes and a highly arched anterior lateral line, and *P. convexa*, diagnosed chiefly by having a pronounced convex head profile and by lacking a dark brown band at the base of the anal fin. *Pempheris rochai*, described from one specimen from Ras Hamar, nearby on the southern coastline of Oman, might be expected from the bay. It differs markedly by having relatively large eyes, only a single row of teeth medially in the upper jaw, and the unusual count of 10 dorsal-fin soft rays. A photograph of the tidal channels of Rahah Bay was published by Randall & Victor (2014: Fig. 2). No DNA sequences are available for *P. micromma*.

***Pempheris muscat* Randall & Victor, n. sp.**

Figure 27, Tables 1–3.

Holotype. BPBM 35845, male, 127 mm SL, Gulf of Oman, Oman, Cat Island, 23°35'8" N, 58°36'34" E, 5–6 m, spear, J.E. Randall, April 28, 1990.

Paratypes. BMNH 1889.4.15.35-38, 3: 124–132 mm SL (a fourth specimen in poor condition, not measured), Gulf of Oman, Oman, Muscat, A. Jayakar, 1889; BPBM 21359, 129 mm SL, Oman, 2–3 miles south of Bandar Sidab, islet about 300 m offshore, depth 3–5 m, spear, J.E. Randall, March 5, 1977.



Figure 27. *Pempheris muscat*, holotype, BPBM 35845, male, 127 mm SL, Cat Island, Gulf of Oman (H.A. Randall).

Description. Dorsal-fin rays VI,9 (one of six with VI,10); anal-fin rays III,40 (35–40); pectoral-fin rays 18 (17–19); lateral-line scales 59 (54–59); outer layer of scales on nape and side of caudal peduncle missing; scales ctenoid on about ventroanterior half of side of chest, those remaining cycloid; gill rakers 31 (30–32); body depth 2.35 (2.2–2.35) in SL; body width 2.95 (2.9–3.5) in body depth; head length 3.15 (3.1–3.25) in SL; eye large, orbit diameter 6.85 (6.8–7.4) in SL; interorbital width 11.7 (11.1–12.4) in SL; jaws moderately oblique, the edge of maxilla an angle of 65° (63 – 68°) to horizontal axis of body; upper jaw dentition similar to that of the generic lower jaw, with a band of 3 to 5 irregular rows of very small, recurved, sharply conical teeth, progressively more sessile inwardly, gradually narrowing posteriorly to side of jaw to a short single row of very small nodules; lower jaw dentition similar to that of upper jaw, the teeth more widely spaced; predorsal and prepelvic lengths 2.5 (2.45–2.55) in SL; longest dorsal and caudal rays broken; longest pectoral ray in paratype with intact fin 3.15 in SL; pelvic fins just reaching anus, 6.8 (6.0) in SL. Color of holotype in alcohol as in Fig. 27, the scales of body gray-brown, each with a vertically elongate orange-brown bar stippled with dark brown dots; dorsal fin with apical black spot, a narrow dark brown band at base, but no darker leading margin; caudal fin with a blackish posterior margin, judging from black pigmentation midposteriorly on remaining fin; anal fin densely stippled with dark brown, darkest anteriorly, except for translucent whitish margin; paired fins pale orangish, the pectoral fins with a faint narrow dark bar across base of rays. Color in life unknown.

Etymology. This species is named for the port city of Muscat, the capital of Oman, the only locality given for the first museum collection of the species. The specific epithet is a noun in apposition.

Remarks. *Pempheris muscat* has as few as 35 anal-fin soft rays, the lowest count for the genus in the region, shared only with two species in the *schwenkii* complex, of which the new species is apparently not a member. The appearance broadly overlaps other *rhomboidea*-complex species, including *P. russellii* Day, a species from the Sind coast of Pakistan, which was our initial identification for these specimens until the dentition was closely examined. The teeth at the front of the lower jaw of *P. muscat* are twice as large as those of *P. russellii*, well spaced, and in regular rows; those of the upper jaw are unique in the genus in being essentially the same as the teeth of the lower jaw. Further comparison revealed that the new species has a larger head, less body depth, and, if specimens of equal size are compared, a larger eye than *P. russellii*. No DNA sequences are available for *P. muscat*.

Pempheris orbis Randall & Victor, n. sp.

Figure 28, Tables 1–3.

Holotype. SMNHTAU P.5284, female, 85 mm SL, Red Sea, Gulf of Aqaba, Dahab, L. Fishelson, Oct. 13, 1968.

Paratypes. HUI 4727, females, 2: 77–77 mm SL, Red Sea, Ras Muhammad, near south tip of Sinai Peninsula, rotenone, E. Clark, Aug. 7, 1968.

Description. Dorsal-fin rays VI,9; anal-fin rays III,39 (38–39); pectoral-fin rays 18 (17–18); lateral-line scales 58 (61–64); scales on nape, below dorsal fin, and on side of chest cycloid; gill rakers 30–31; body depth 2.7 (2.3–2.5) in SL; body width 2.6 (2.55–2.7) in body depth; head length 3.3 (3.2) in SL; dorsal profile of head slightly convex; orbit diameter 7.7 (7.35–7.45) in SL; interorbital width 11.5 (11.3–11.8) in SL; jaws oblique, the edge of maxilla an angle of 63° (62–63°) to horizontal axis of body; tip of lower jaw projecting anterior to upper jaw when mouth fully closed; teeth small, conical and recurved, those medially in upper jaw in three to four irregular rows, soon narrowing to two rows of progressively smaller teeth, and finally to a single row of very small nodules on about posterior fifth of jaw, ending just 2 mm before posterior end of maxilla in holotype; teeth in lower jaw in a band of four to five, irregular, close-set rows (medially where band is broadest) comprising distinctly smaller, more nodular, but still progressively more recurved teeth inwardly; innermost teeth largest and nearly horizontal; lips dark purplish brown with distinct, well-spaced papillae; tongue triangular and straight-sided, except slightly indented near tip; predorsal and prepelvic lengths 2.5 (2.5–2.6) in SL; longest dorsal-fin ray 3.95 (4.1) in SL (longest ray broken in largest paratype); all caudal-fin rays broken; pectoral-fin rays broken on holotype and largest paratype, fin length in smallest paratype 3.5 in SL; pelvic fins reaching or extending slightly posterior to anus, their length 6.3 (6.4–6.8) in SL. Color of holotype in alcohol as in Fig. 28. Scales below the lateral line of the largest paratype with light golden centers and orange margins, brightest in pectoral region; dorsal fin with black membranes distally between last three spines and first four soft rays; broad anterior margin of dorsal fin darker than rest of fin, except distal black part of fin. Color in life unknown.

Etymology. This species is named *orbis*, Latin for circle or ring, for the most striking color feature of this species in alcohol (and presumably also in life), i.e. the bright copper ring around the pupil of the eye. The specific epithet is a noun in apposition.

Remarks. No information is available on the habitat of this species; the collectors of the holotype and paratypes are deceased. Evidently a small species; the smallest paratype is a fully mature female. One of seven *schwenkii* complex species in the Red Sea, distinguished by high lateral-line scale counts, along with more than two rows of teeth medially in the upper jaw, a wide dark band at the base of the anal fin, and the copper ring around the pupil. No DNA sequences are available for *P. orbis*.



Figure 28. *Pempheris orbis*, holotype, SMNHTAU P.5284, female, 85 mm SL, Red Sea, Gulf of Aqaba (H.A. Randall).

Pempheris pathirana Randall & Victor, n. sp.

Figure 29, Tables 1–3.

Holotype. USNM 432500, male, 129 mm SL, Sri Lanka, Trincomalee District, Koddiyar Pattu, Foul Point (on E side of lighthouse base), 8°31'36" N, 81°19' E, 0–2 m, Ceylon – University of Miami & Smithsonian Institution Project 3818, rotenone, T. Iwamoto *et al.*, May 15, 1970.

Paratypes. USNM 402255, female, 125 mm SL, Sri Lanka, North Eastern Province, Trincomalee, outside harbor, large rock outcrop, about 50 yards offshore, 1–5 m, rotenone, W.F. Smith-Vaniz, June 26, 1969; USNM 402235, 9: 104–140 mm SL, same data as holotype; BPBM 41225, 121 mm SL, & SAIAB 200844, 2: 126–127 mm SL (formerly three specimens of USNM 379412), same collection data as USNM 402255 except date is July 1, 1969.

Description. Dorsal-fin rays VI,9 (one paratype with VI,10); anal-fin rays III,43 (38–43); pectoral-fin rays 18 (17–19, strongly modal 18); lateral-line scales 57 (56–62); scales on nape, all of chest, and caudal peduncle ctenoid, those below dorsal fin cycloid; gill rakers 30 (29 or 30); body depth 2.3 (2.1–2.3) in SL; body width 2.8 (2.7–2.95) in depth; head length 3.2 (3.1–3.3) in SL; eye moderate in size, orbit diameter 7.2 (7.0 in 140-mm paratype to 7.9 in 104-mm paratype); interorbital width 11.5 (11.3–12.5) in SL; jaws steeply oblique, the edge of maxilla forming an angle of 63–68° to horizontal axis of body; upper jaw to each side of symphyseal gap with a single row of slender recurved teeth within a narrow zone of very small nodular teeth; main row of teeth smaller laterally, in an irregular row (nearly two rows in places); small slender teeth at front of lower jaw in three to five irregular rows, progressively more recurved inwardly; predorsal length 2.7 (2.65–2.7) in SL; longest dorsal-fin ray 3.7 (3.75–4.15) in SL; pectoral-fin length 3.2 (3.15–3.3) in SL; prepelvic length 2.65 (2.6–2.7) in SL; pelvic fins varying from reaching anus to just reaching origin of anal fin, 5.75 (5.2–6.1) in SL, relatively longest in smallest paratype. Color in alcohol as in Fig. 29; note the absence of black pigment at the base of the pectoral fins (also lacking in axil), no black on base or margin of anal fin, and black pigmentation forming a spot only distally on the dorsal fin. Color in life unknown.

Etymology. This species is named for Yohan Pathirana of Aquamarines International in Sri Lanka, who has provided specimens and photographs of *Pempheris* from the island nation. He also had his divers search for *P. pathirana* at Trincomalee, where it was collected in 1969 and 1970, but they failed to find it.



Figure 29. *Pempheris pathirana*, holotype, USNM 432500, male, 129 mm, Trincomalee District, Sri Lanka (S. O'Hara).

Remarks. *Pempheris pathirana* is presently known only from Sri Lanka, but it might be expected in suitable shallow reef habitat in southern India. Specimens from the 1969 and 1970 collections of this species from Sri Lanka in the U.S. National Museum of Natural History were first identified as *Pempheris nesogallica* Cuvier in C. & V. The two species appear very similar as preserved specimens. *Pempheris nesogallica* was described from the Mascarene Islands and was recently found in KwaZulu-Natal. It has slightly longer predorsal and prepelvic lengths (2.55–2.65 vs. 2.6–2.7 in *P. pathirana*); slightly longer pectoral fins (3.05–3.2 in SL vs. 3.15–3.3 in *P. pathirana*); ctenoid vs. cycloid scales on side of caudal peduncle; a few cycloid scales above ctenoid scales on side of chest of *P. nesogallica* (vs. all ctenoid on *P. pathirana*); a large black spot on base and axil of pectoral fins of *P. nesogallica* (at most dark brown on *P. pathirana*); and 30–34 gill rakers for *P. nesogallica* (vs. 29 or 30 for *P. pathirana*).

Pempheris pathirana is also a close relative of *P. kruppi*, found on the coast of Yemen and Socotra. *Pempheris kruppi* differs in the steeper angle of the jaws, 37–41 anal-fin soft rays (vs. 38–43 in *P. pathirana*), and in dentition. Specimens of *P. pathirana* have a single row of recurved teeth anteriorly in the upper jaw, compared to two in most other species in the *rhomboidea* species complex, followed in *P. pathirana* by many irregular rows of very small teeth. Two related species are found in India: *P. sarayu* and *P. mangula*. *Pempheris sarayu* differs in having a shorter pelvic fin, 6.15 in SL, and a mode of 19 pectoral-fin rays. *Pempheris mangula* has a characteristic dark brown or dark red margin on the anal fin. The representative of the *schwenkii* complex in India is *P. bineeshi*, and in Sri Lanka the local representative is *P. trinco*. The unrelated *P. malabarica* is also found in the region. No DNA sequences are available for *P. pathirana*.

***Pempheris peza* Randall & Victor, n. sp.**

Figure 30, Tables 1–3.

Holotype. SAIAB 50637, male, 107 mm SL, Mozambique, Ponta do Ouro, 26.833° S, 32.8833° E, rotenone, P.C. Heemstra, A. Wood, & A. Paterson, Nov. 9, 1995.

Paratypes. SAIAB 200761, 9: 75–114 mm SL, & BPBM 41192, 6: 91–110 mm SL, same data as holotype.

Description. Dorsal-fin rays VI,9; anal-fin rays III,39 (36–40); pectoral-fin rays 17 or 18; lateral-line scales 51 (50–59); lateral line moderately arched anteriorly, rising slightly more than 1/2 orbit diameter above level of

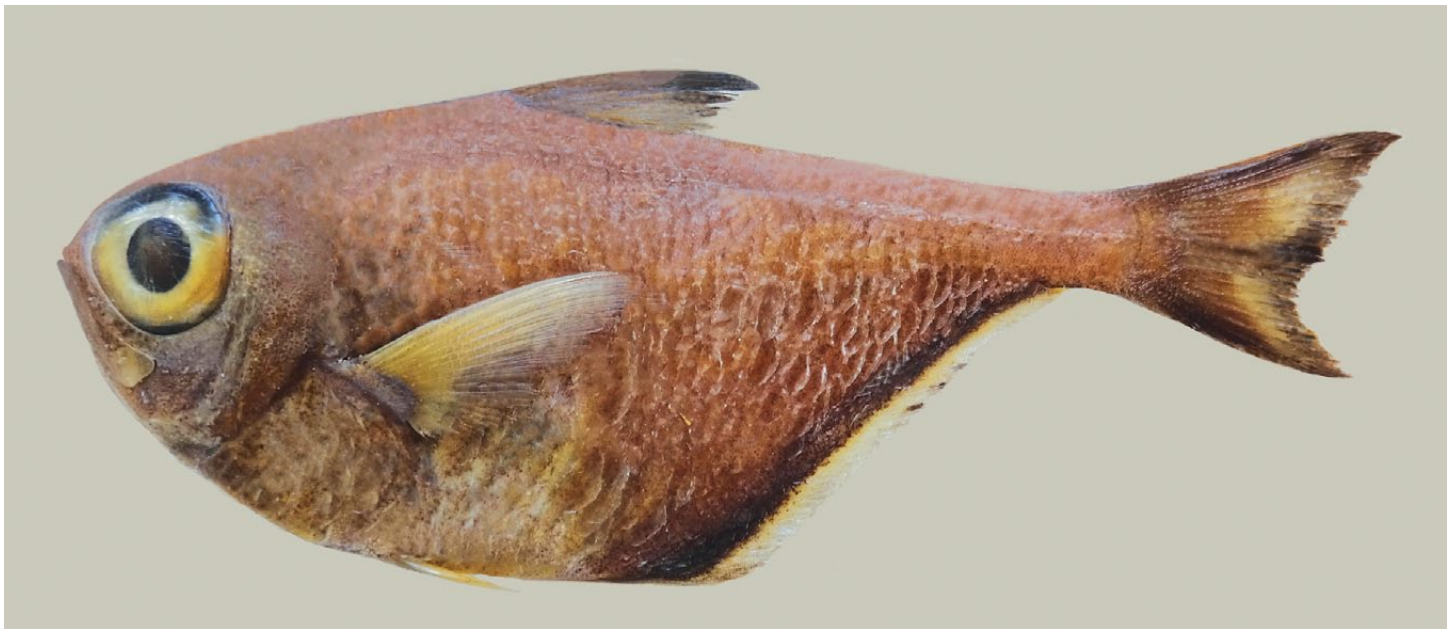


Figure 30. *Pempheris peza*, holotype, SAIAB 50637, male, 107 mm SL, Mozambique (H.A. Randall).

origin of lateral line; scales ctenoid on nape and below dorsal fin, but cycloid on side of caudal peduncle and on chest, except for two or three ventroanterior ctenoid scales; gill rakers 28 (28–30); body depth 2.35 (2.2–2.35) in SL, and compressed, the width 2.9 (2.9–3.2) in body depth; head length 3.2 (3.2–3.35) in SL; orbit diameter 7.5 (7.2–8.1) in SL; interorbital width 10.7 (10.2–12.5) in SL; jaws moderately oblique, angle of maxilla to horizontal axis of body 68° (66 – 69°); no prominent knob at tip of lower jaw; lower jaw slightly to moderately projecting when mouth firmly closed; a single row of sharply conical, recurved teeth anteriorly in upper jaw; a second more anterior and more projecting row of teeth present laterally, reduced to a single row of progressively smaller teeth half way back in jaw, and ending posteriorly as a row of small nodules; a narrow band of small teeth in three or four rows medially in lower jaw, progressively more recurved inwardly, and ending laterally in jaw as a single row of small nodules; tongue triangular with pointed tip; predorsal length 2.7 (2.65–2.7) in SL; no dorsal-fin rays fully intact; caudal concavity about 4 in head length; pectoral-fin length 3.25 (3.0–3.25) in SL; prepelvic length 2.45 (2.4–2.5) in SL; pelvic fins nearly or just reaching anus, 6.3 (6.0–6.8) in SL. Color in alcohol as in Fig. 30; scales brown with whitish edges; dorsal fin with a broad anterior black margin expanding slightly to a distal spot; caudal fin with broad blackish border posteriorly and on dorsal and ventral margins; anal fin with a broad, very dark brown band at base, the outer part of fin pale yellowish and nearly as broad; three blackish spots at margin of fin (one to three such spots on a few paratypes); these are not remnants of a black border, nor are they parasites (though they could be of parasitic origin); iris light yellow, the upper half of the yellow dorsal part of the iris abruptly black (irregular on holotype, but a straight margin on most paratypes). Color in life unknown.

Etymology. This species is named *Pempheris peza* from the Greek meaning border, in reference to the very broad blackish border on all of the outer edge of the caudal fin.

Remarks. The 16 specimens of the new species are all from a single collecting station at Ponta do Ouro, a small coastal town 10 km north of the border of South Africa and Mozambique. Two of the collectors were asked for details of the collection. They only recall that rotenone was used in relatively shallow water. Two other species of the *schwenkii* complex occur along the southern Mozambique coast, *P. ibo* and *P. connelli*: *P. ibo* has many fewer lateral-line scales (43–49), and *P. connelli* has a wider body and less marked caudal fin. No DNA sequences are available for *P. peza*.

***Pempheris rochai* Randall & Victor, n. sp.**

Figure 31, Tables 1–3. BIN AAC6084 (in part).

Holotype. CAS 236522, female, 116.5 mm SL, Oman, south coast, Ras Hamar, $16^\circ 54'$ N, $53^\circ 57'$ E, spear, L.A. Rocha, March 18, 2013.

Description. Dorsal-fin rays VI,10; anal-fin rays III,39; pectoral-fin rays 17 or 18; lateral-line scales 59; lateral line moderately arched anteriorly, rising 1/2 orbit diameter above level of origin of lateral line; outer layer of scales almost totally missing (no cycloid vs. ctenoid scale characters possible); gill rakers 28; body moderately deep, depth 2.25 in SL, and compressed, the width 3.1 in depth; head length 3.15 in SL; eye moderately large, orbit diameter 6.8 in SL; interorbital width 11.6 in SL; jaws moderately oblique, the edge of maxilla forming an angle of about 68° to horizontal axis of body; knob at tip of lower jaw bulges more posteriorly than anteriorly; upper jaw with a single row of sharply conical, recurved teeth that are progressively smaller posteriorly to side of jaw, ending as small nodules; lower jaw with a narrow band of very small conical teeth in three to five rows medially, progressively more recurved inwardly; predorsal length 2.65 in SL; longest dorsal-fin rays broken; pectoral-fin length 3.0 in SL; prepelvic length 2.5 in SL; pelvic fins just reaching anus, 6.15 in SL. Color in alcohol as shown in Fig. 31; the scales silvery with thin brown margin (when wet, they show lavender iridescence; however these are the scales of the inner layer); leading edge of dorsal fin dark brown, broadening to a dark spot distally; dark brown band at base of anal fin broad; tips of heavily abraded anal rays with traces of black pigment, suggesting a blackish margin when intact; caudal fin probably fully bordered in dark brown or black in life; pectoral fins with



Figure 31. *Pempheris rochai*, holotype, CAS 236522, female, 116.5 mm, Ras Hamar, Oman (H.A. Randall). Spear wound below pectoral fin.

a narrow blackish band at base of rays, except lateral two or three rays. Color in life unknown.

Etymology. This species is named for the collector, Dr. Luiz A. Rocha, Curator of Ichthyology at the California Academy of Sciences, in recognition of his broad body of ichthyological research on the phylogenetics of reef fishes.

Remarks. Species of *Pempheris* typically have 9 dorsal soft rays, but one can expect an occasional rare individual of any species of the genus to have 10. The holotype of *P. rochai*, with 10 dorsal soft rays, may be such an individual, or 10 may be the true count for the species. More specimens will provide the answer. It is distinctive for its single row of enlarged curved teeth medially in the upper jaw (vs. two or three in other species), relatively large eye, and the unusually broad dark brown band at the base of the anal fin. The barcode mtDNA COI sequence of the holotype of *P. rochai* is the same as *P. conelli* from South Africa and *P. hollemani* from Madagascar, indicating either a recent split of closely related species or some degree of gene flow across the western Indian Ocean between the three species (Fig. 1).

***Pempheris rubricauda* Randall & Victor, n. sp.**

Figure 32, Tables 1–3. BIN AAI3650 (in part).

Holotype. MNHN 2015-003, 72 mm SL, male, Madagascar, Nosy Be, Nosy Vorona, E side, 13°25'28" S, 48°21'52" E, 3 m, rotenone, H. Bruggemann, N. Hubert, & S. Planes, May 8, 2008.

Paratypes. URUN 2008-4281, 3: 68.5–77 mm SL, & BPBM 41199, 72 mm SL, same data as holotype.

Description. Dorsal-fin rays VI,9; anal-fin rays III,36 (36–41); pectoral-fin rays 17 or 18 (modally 18); lateral-line scales 56 (55–57); gill rakers 28 (28 or 29); body depth 2.3 (2.2–2.45) in SL; body width 2.75 (2.75–2.9) in body depth; head length 3.2 (3.05–3.3) in SL; eye relatively small, orbit diameter 8.1 (7.6–8.2) in SL; interorbital width 11.9 (11.2–12.0) in SL; mouth oblique, forming an angle of 70° to horizontal axis of body; tip of lower jaw slightly anterior to upper jaw when mouth fully closed; teeth in upper jaw in two rows medially, soon narrowing to a single row; teeth in lower jaw very small and densely spaced, in a band of three or four rows medially, progressively more retrorse posteriorly, those of inner row largest and nearly horizontal; outer layer of scales nearly completely absent on most specimens, but enough remain on holotype to determine that those on nape and in first row below dorsal fin are cycloid; side of chest about three-fourths cycloid, the ctenoid scales

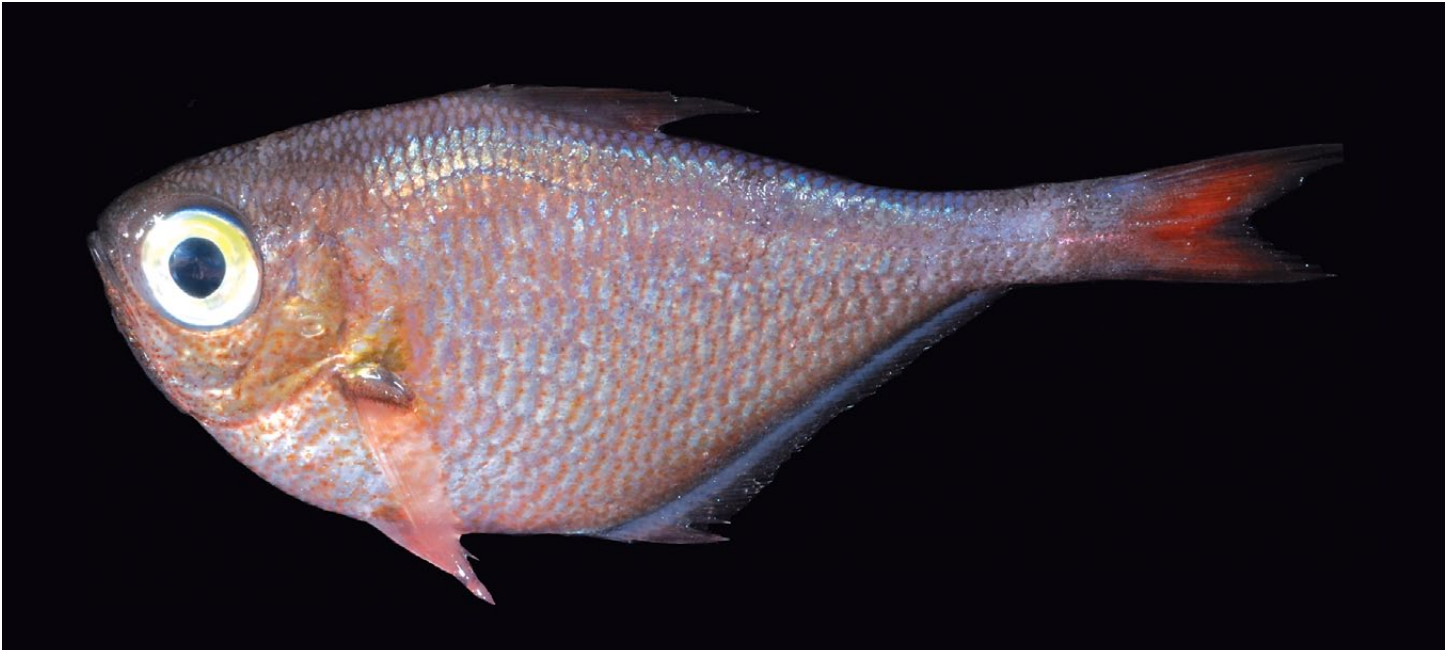


Figure 32. *Pempheris rubricauda*, holotype, MNHN 2015-003, male, 72 mm, Nosy Be, Madagascar (H. Bruggemann).

ventroanteriorly; scales on side of caudal peduncle cycloid, those dorsally and ventrally ctenoid; predorsal length 2.65 (2.7) in SL; dorsal and caudal fins too damaged for measurement; pectoral-fin length 3.45 (3.4–3.6) in SL; prepelvic length 2.4–2.5 in SL; pelvic fins nearly or just reaching origin of anal fin, 5.8 (5.8–6.0) in SL. Color in alcohol light gray-brown below lateral line, the scale edges darker from a concentration of very small dark brown dots; scale edges blackish above lateral line and on snout; dorsal fin dusky yellowish with blackish anterior margin and black apical spot; caudal fin yellowish with blackish outer margin; anal fin pale yellowish with a narrow dark brown band at base and a broad dusky margin; paired fins yellowish, the pectoral fins without a dark spot at base; iris dark bluish gray. Color of holotype when fresh in Fig. 32.

Etymology. This species is named *Pempheris rubricauda* from the Latin for red-tailed, in reference to the bright red-orange coloration of the broad central part of the caudal fin.

Remarks. The new species is presently known only from NW Madagascar. The barcode mtDNA COI sequences of *P. rubricauda* (along with a sequence from *P. ternay* from Seychelles) form a barcode lineage very close, only 0.66% divergent, to the lineage comprising *P. tominagai* from the Red Sea and *P. xanthomma* from Yemen. That set of four species is sister to two other clades of *schwenkii*-complex lineages that occupy non-overlapping ranges in the Indo-Pacific: 3.4% divergent from the lineage that comprises *P. hadra* from Maldives, *P. bineeshi* from India, and probably true *P. schwenkii* from Indonesia (Fig. 1), as well as 3.6% divergent from a lineage of *P. aff. schwenkii* from the Pacific Ocean.

***Pempheris sergey* Randall & Victor, n. sp.**

Figure 33, Tables 1–3.

Holotype. SMF 35717 (KAU 13-671), 103 mm SL, Red Sea, Saudi Arabia, Sharm Obhur, in front of Marine Station, 21°42'34.00" N, 39°05'45.70" E, steep slope, 12–17 m, rotenone, S.V. Bogorodsky, July 1, 2013.

Paratypes. SMF 35718 (KAU 13-672), 85 mm SL, KAUMM 370 (KAU 13-673), 104 mm SL, KAUMM 371 (KAU 13-675), 83 mm SL, & BPBM 41229 (KAU 13-674), 89 mm SL, all same data as holotype.

Description. Dorsal-fin rays VI,9; anal-fin rays III,38 (39–42); pectoral-fin rays 17 (17 or 18); lateral-line scales 51 (53–55); scales on nape, below dorsal fin, and side of caudal peduncle cycloid, scales on side of chest



Figure 33. *Pempheris sergey*, holotype, SMF 35717, 103 mm SL, Sharm Obhur, Saudi Arabia, Red Sea (S.V. Bogorodsky).

cycloid except for a few ctenoid scales ventroanteriorly; gill rakers 27 (26–27); body depth 2.5 (2.5–2.55) in SL; body width 2.65 (2.65–2.8) in body depth; head length 3.4 (3.3–3.35) in SL; eye relatively small, the orbit diameter 7.65 (7.35–7.55) in SL; interorbital width 10.6 (11.2–11.8) in SL; mouth strongly oblique, forming an angle of 60–65° to horizontal axis of body; recurved conical teeth in a double row in upper jaw, those of upper row more projecting, those of lower row more strongly recurved; double row continues progressively smaller, nearly to end of jaw where it ends as tiny teeth in a single row; teeth in lower jaw very small and slender, in a band of four or five, close-set, irregular rows where broadest medially, progressively more recurved inwardly; numerous black dots in spaces between teeth; teeth smaller and in fewer rows posteriorly in jaw, ending in a few extremely small teeth in a single row; tongue narrowly triangular or with sides slightly incurved, the tip pointed to slightly rounded; upper lip appears smooth, but surface consists of small, close-set papillae when viewed by microscope, papillae more evident on lower lip; predorsal length 2.7 (2.65–2.75) in SL; longest dorsal soft ray 4.05 (4.15–4.35) in SL; caudal-fin length 3.55 in SL, the caudal concavity 11.1 in SL (fin damaged in all paratypes); pectoral-fin length 3.1 (3.25–3.35) in SL; prepelvic length 2.6 (2.5–2.6) in SL; pelvic fins nearly or just reaching anus, 5.9 (5.75–6.3) in SL. Color in alcohol yellowish brown, the scales narrowly darker brown; dorsal fin translucent yellowish, the rays edged in dark brown, with a broad blackish anterior margin that expands to a large distal black spot; caudal fin brownish yellow, with a very broad blackish posterior margin, the upper and lower dark margins half as wide and not as strongly pigmented; anal fin pale yellowish with a dark brown basal band that narrows posteriorly (band is narrower when fresh; also there is a darkened border on the anal fin when fresh that is no longer apparent in alcohol); paired fins pale yellowish, pectoral fins with a dark brown band at base; eye with yellow iris when fresh, dark bluish gray when preserved. Color when fresh as in Fig. 33.

Etymology. This species is named for the collector, Sergey V. Bogorodsky, in recognition of his extensive research documenting the fishes of the Red Sea. The specific epithet is a noun in apposition.

Remarks. This species is known from a single collection at Obhur Creek, 36 km north of Jeddah, Saudi Arabia; the topography is a broad tidal channel with steep marginal reefs. S. Bogorodsky observed feeding on zooplankton by this species and *P. flavicycla* near the surface from the light of a nearby boat landing. *Pempheris sergey* is one of seven species of the *schwenkii* complex from the Red Sea; it is distinguished by color in life, having two rows of teeth medially in the upper jaw, and a slender body, i.e. the body depth more than 2.5 in SL. The color is similar to the closely related *P. viridis*; morphological differences include three rows of teeth medially in the upper jaw and a straight dorsal profile in the latter. Both *P. sergey* and *P. viridis* have relatively narrow dark bands at the base of the anal fin, vs. *P. xanthomma* and some others. *Pempheris tominagai* differs by having three rows of teeth in the medial upper jaw, a wider body, and at most dusky edges to the caudal fin. Mitochondrial DNA sequences from the type specimen (obtained during review) match those of *P. tominagai*; more specimens are needed to resolve the genetic relationships in this group.

Pempheris shimoni Randall & Victor, n. sp.

Figure 34, Tables 1–3.

Holotype. SAIAB 51257, female, 133 mm SL, Kenya, Shimoni, 4.6500° S, 39.8333° E, J.L.B. & M.M. Smith, Jan. 1, 1952.

Paratypes. SAIAB 51256, 7: 31–48 mm SL, same data as holotype but Oct. 1, 1950; SAIAB 200843, 3: 41–51 mm SL, same data as holotype; USNM 402231, 65 mm SL, Kenya, Andromache Reef, just south of entrance to Port Kilindini, Mombasa Harbor, off Ras Mwa Kisenge, 4° 5'5" S, 39° 40'39" E, reef flat, 0–1.3 m, dead coral & sand, rotenone, H. Fehlmann *et al.*, *Anton Bruun* Cruise 9, International Indian Ocean Expedition, Nov. 15, 1964.

Description. Dorsal-fin rays VI,9; anal-fin rays III,40 (37–41); pectoral-fin rays 17 (17–19, modally 18); lateral-line scales 56 (53–58); gill rakers 30 (28–31); body depth 2.2 in SL; body width 3.0 in body depth; head length 3.25 in SL; eye diameter 7.3 in SL; interorbital width 11.3 in SL; mouth oblique, forming an angle of 63° to horizontal axis of body; upper-jaw dentition with two irregular rows of sharply recurved teeth on each side of symphyseal gap, reduced to a single row of gradually smaller teeth about half way back in jaw; lower jaw with a close-set band of four or five irregular rows of very small teeth that seem to be only nodular, but microscopic inspection reveals them to be sharply pointed, progressively larger, and more recurved inwardly in mouth; tongue deeply concave on each side, resulting in a narrow, rectangular, anterior part, that ends in a rounded flexible flap; lower jaw projecting when mouth fully closed; scales on nape, below dorsal fin, and on about ventroanterior two-thirds of chest ctenoid; predorsal length 2.7 in SL; dorsal and caudal fins damaged; pectoral-fin length 3.15 in SL; prepelvic length 2.5 in SL; pelvic fins reaching anus, 6.05 in SL. Color in alcohol as in Fig. 34; the reddish brown band across the base of the pectoral fins was probably dark brown in life. Color in life unknown.

Etymology. This species is named for the type locality, the small town of Shimoni, a port near the border of Kenya and Tanzania. The specific epithet is a noun in apposition.

Remarks. Measurements in the above description are from our only adult specimen (the paratypes are all juveniles). We regret not having more information on the fish collection made at Shimoni by the Smiths 63 years ago. No DNA sequences are available for *P. shimoni*.



Figure 34. *Pempheris shimoni*, holotype, SAIAB 51257, female, 133 mm SL, Shimoni, Kenya (H.A. Randall).

Pempheris shirleen Randall & Victor, n. sp.

Figure 35, Tables 1–3.

Holotype. USNM 402228, female, 105 mm SL, Red Sea, Egypt, Hurghada, 300 yards north of pier of Institute of Oceanography & Fisheries, 27°16'38" N, 33°47'1" E, reef pool surrounded by profuse staghorn coral, rotenone, H. Fehlmann *et al.*, Jan. 4, 1965.

Paratype. USNM 436759, female, 103 mm SL, same data as holotype.

Description. Dorsal-fin rays VI,9; anal-fin rays III,37 (38); pectoral-fin rays 17 or 18; lateral-line scales 50 (54); scales on nape, below dorsal fin, and side of caudal peduncle cycloid, scales on side of chest cycloid except for a few ctenoid scales ventroanteriorly; gill rakers 28 (27); body depth 2.35 (2.4) in SL; body width 2.75 (2.85) in body depth; head length 3.25 (3.2) in SL; eye relatively small, the orbit diameter 7.35 (7.45) in SL; interorbital width 11.8 (11.5) in SL; mouth oblique, forming an angle of 66° (63°) to horizontal axis of body; teeth medially in upper jaw small, progressively more recurved inwardly, in three irregular rows (many medial teeth of holotype and nearly all of paratype missing); teeth reduced to a single row about half way to end of jaw; teeth in lower jaw smaller, more slender, in a band of three or four, close-set, irregular rows where broadest, and progressively more recurved inwardly; teeth smaller and in fewer rows posteriorly in jaw, ending in a few extremely small teeth in a single row; tongue triangular with nearly straight sides, the tip pointed to slightly rounded; upper lip appears smooth, but surface consists of small, close-set papillae when viewed by microscope; predorsal length 2.6 (2.7) in SL; all fins except the pelvics too damaged for measurement; prepelvic length 2.5 (2.55) in SL; pelvic fins very short, not reaching anus, 7.45 (7.3) in SL. Color in alcohol as in Fig. 35. Color in life unknown.

Etymology. This species is named for Shirleen Smith of the Division of Fishes, United States National Museum of Natural History, in appreciation of the many loans of *Pempheris* and other fishes that she has prepared for the senior author. The specific epithet is a noun in apposition.

Remarks. This species is known from a single collection at Hurghada in Egypt. *Pempheris shirleen* is one of seven species of the *schwenkii* complex from the Red Sea; it is distinguished by very short pelvic fins, having three rows of teeth medially in the upper jaw, cycloid scales on the nape and most of chest, a thinner body (body width more than 2.7 in body depth), and a moderately deep body (body depth less than 2.4 in SL). No DNA sequences are available for *P. shirleen*.



Figure 35. *Pempheris shirleen*, holotype, USNM 402228, female, 105 mm SL, Hurghada, Egypt, Red Sea (H.A. Randall).

Pempheris smithorum Randall & Victor, n. sp.

Figure 36, Tables 1–3.

Holotype. SAIAB 51259, male, 126.5 mm SL, Tanzania, Zanzibar, Chumbe Island, 6.1666° S, 39.1833° E J.L.B. & M.M. Smith, Sept. 5, 1952.

Paratypes. BPBM 37176, female, 139 mm SL, Tanzania, Mafia Island, Chole Island, rocky islet, 0–2 m, small cave, rotenone, J.E. Randall, L.G. Westfeldt, & A. Klosser, Dec. 11, 1973.

Description. Dorsal-fin rays VI,9; anal-fin rays III,41 (40); pectoral-fin rays 17 (17 or 18); lateral-line scales 59 (56); gill rakers 30 (31); body depth 2.35 (2.3) in SL; body width 2.6 (2.8) in body depth; head length 3.25 (3.3) in SL; eye diameter 7.0 (7.4) in SL; interorbital width 11.7 (11.8) in SL; mouth oblique, forming an angle of 61–66° to horizontal axis of body; upper-jaw dentition typical of the genus, with two irregular rows of recurved teeth on each side of symphyseal gap, one protruding forward, the other strongly recurved, reduced to a single row of gradually smaller teeth nearly half way back in jaw; tip of lower jaw expanded to a distinct knob, extending both anteriorly and posteriorly, and strongly protruding when jaws fully closed; lips with well-developed bristle-like papillae; lower-jaw teeth to either side large for the genus, beginning medially with seven rows, those of outer row erect or slightly recurved, the remaining inner teeth progressively longer and more recurved, teeth smaller and in fewer rows posteriorly in jaw; tongue triangular, straight-sided, with firm pointed tip; scales on nape, below dorsal fin, and on chest ctenoid; scales on side of caudal peduncle cycloid; predorsal length 2.7 in SL; prepelvic length 2.45–2.5 in SL; dorsal, caudal, and pectoral fins damaged; pelvic fins reaching anus, 6.35 in SL. Color of holotype in alcohol as in Fig. 36; large spot at pectoral-fin base probably dark brown in life. Color in life unknown.

Etymology. This species is named in honor of James Leonard Brierly Smith and Margaret Mary Smith, not only for being the collectors of the holotype, but also for the major contributions they have made in pioneering ichthyology in South Africa, describing hundreds of species, and writing numerous publications on the fishes of southern Africa.

Remarks. Two specimens of *Pempheris* were collected at Chumbe Island in 1952 by the Smiths, each the holotype of a new fish, i.e. the present species and *P. leiolepis*, the former with ctenoid scales on the chest and the latter with cycloid scales and three rows of upper-jaw teeth. The paratype of *P. smithorum* was collected by the first author and associates from nearby Mafia Island with no suspicion at the time that it might be an undescribed species. No photographs and no color notes were taken. It is more copper-colored than the holotype. No DNA sequences are available for *P. smithorum*.



Figure 36. *Pempheris smithorum*, holotype, SAIAB 51259, male, 126.5 mm SL, Zanzibar (H.A. Randall).

Pempheris tau Randall & Victor, n. sp.

Figure 37, Tables 1–3.

Holotype. HUI 10979, male, 95 mm SL, Egypt, Gulf of Aqaba, east coast of Sinai Peninsula, Nuweiba, A. Ben-Tuvia, Aug. 3, 1976.

Paratype. BPBM 41232, female, 99 mm SL, same data as holotype; SMNHATAU P.3650, male, 116.5 mm SL, Sharm el Sheikh, Naama Bay (Marsa el At), 27°54'38" N, 34°19'44" E, Egypt, Red Sea, L. Fishelson, Oct. 16, 1968.

Description. Dorsal-fin rays VI,9; anal-fin rays III,39 (38 or 39); pectoral-fin rays 17 (17 or 18); lateral-line scales 50 (52–55); scales on nape, below dorsal fin, and side of caudal peduncle cycloid, scales on side of chest cycloid except for a few ctenoid scales ventroanteriorly; gill rakers 31 (30–33); body depth 2.5 (2.3–2.6) in SL; body width 2.45 (2.55–2.7) in body depth; head length 3.3 (3.2–3.3) in SL; dorsal profile of head slightly convex; eye very small, orbit diameter 7.9 (8.1–8.65) in SL; interorbital width 11.5 (11.3–11.8) in SL; mouth oblique, forming an angle of 63°(62–63°) to horizontal axis of body; tip of lower jaw projecting anterior to upper jaw when mouth fully closed; teeth conical and recurved, those medially in upper jaw in three irregular rows, soon reduced to two rows, and finally to a single row of very small teeth near end of jaw; teeth in lower jaw similar but much smaller, more slender, in three to four irregular rows medially, then progressively fewer and smaller toward end of jaw; lips yellowish brown, densely stippled with small purple papillae; tongue triangular, straight-sided, with pointed tip; predorsal length 2.75 (2.7–2.75) in SL; prepelvic length 2.5 (2.5–2.6) in SL; longest dorsal-fin ray 3.8 (4.0–4.1) in SL; all caudal-fin rays broken; pectoral-fin length 3.05 (3.15–3.3) in SL; pelvic fins reaching or extending slightly posterior to anus, their length 6.3 (6.8–6.85) in SL. Color in alcohol as in Fig. 37. Color in life unknown.

Etymology. This species is named for the acronym of Tel-Aviv University, in appreciation of their large loan of Red Sea specimens of the genus *Pempheris*, including the largest specimen of the present species. The specific epithet is a noun in apposition.

Remarks. The most distinctive morphological character of this species is the small eye, smaller than for the other six members of the *schwenkii* complex in the Red Sea. Only *P. micromma* from Oman has a smaller eye; note that the preserved holotype of *P. micromma* in Fig. 25 has a different body shape and has different tooth row patterns. *Pempheris zajonzi* from Yemen shares the small eye and three tooth rows in the upper jaw, but has a larger head and fewer gill rakers. No DNA sequences are available for *P. tau*.



Figure 37. *Pempheris tau*, holotype, HUI 10979, male, 95 mm SL, near Nuweiba, Gulf of Aqaba, Egypt (H.A. Randall).

Pempheris ternay Randall & Victor, n. sp.

Figure 38, Tables 1–3. BIN AAI3650 (in part).

Pempheris tominagai [non Koeda, Yoshino, Imai & Tachihara] Koeda *et al.* 2014: 317, in part.

Holotype. SAIAB 77935, male, 91 mm SL, Seychelles, Mahé, Ternay Marine National Park, Cape Matoopa, southern end, 4°39.03' S, 55°22.71' E, coral reef, surrounded by sand, 6 m, spear, M. Smale, A. Bentley, E. Heemstra, & M. Mwale, April 21, 2005.

Description. Dorsal-fin rays VI,9; anal-fin rays III,36; pectoral-fin rays 17; lateral-line scales 51; gill rakers 28; body depth 2.45 in SL; body width 2.85 in body depth; head length 3.25 in SL; eye relatively small and precisely circular, the orbit diameter 7.45 in SL; lips smooth; interorbital width 11.3 in SL; mouth oblique, forming an angle of 60° to horizontal axis of body; tip of lower jaw slightly anterior to upper jaw when mouth fully closed; teeth small, pointed, and recurved, those in upper jaw in two rows medially, the teeth of the upper row projecting forward, those of the lower row curving downward; teeth progressively smaller and narrowing to a single row about half way back in jaw; teeth in lower jaw very small and densely spaced, in a band of three or four rows medially, progressively more retrorse inwardly, those of inner row largest and nearly horizontal; outer layer of scales totally missing, and many of inner layer as well; predorsal length 2.65 in SL; longest dorsal-fin ray (from photograph) 2.7 in SL; pectoral-fin length 3.0 in SL; prepelvic length 2.5 in SL; pelvic fins just reaching origin of anal fin, 6.0 in SL. Scaleless color silvery gray with a vertical brown line on each scale pocket; color when fresh as shown in Fig. 38.

Etymology. This species is named for the type location, Ternay Marine National Park on the island of Mahé, where one can no longer collect fishes, but where one can enjoy viewing and photographing them at close range. The specific epithet is a noun in apposition.

Remarks. This species shares the black-bordered red caudal fin with *P. rubricauda* from Madagascar; it is separated by length of the pectoral fins, the number of lateral-line scales, and the angle of the maxilla. *Pempheris ternay* is the second *schwenkii*-complex species identified from Seychelles; *P. argyrea* shares most meristics with *P. ternay*, but does not have the prominent red tail. The barcode mtDNA COI sequence of *P. ternay* is almost the same as for *P. rubricauda*, and the two form a lineage diverging by only 0.66% from the lineage including both *P. tominagai* from the Red Sea and *P. xanthomma* from Yemen (Fig. 1). That set of four species diverges by 3.4% from the lineage comprising *P. hadra* from Maldives, *P. bineeshi* from India, and probable true *P. schwenkii* from Bali, Indonesia.



Figure 38. *Pempheris ternay*, holotype, SAIAB 77935, male, 91 mm SL, Mahé, Seychelles (A. Bentley).

Pempheris tilman Randall & Victor, n. sp.

Figure 39, Tables 1–3.

Holotype. SMF 35779 [ex SMF 23763], male, 96.5 mm SL, Red Sea, Jordan, Aqaba, F. Krupp, 1980.

Paratypes. BPBM 41233, female, 75 mm SL, & SMF 23763, female, 88 mm SL, same data as holotype.

Description. Dorsal-fin rays VI,9; anal-fin rays III,40 (36–41); pectoral-fin rays 17 (17); lateral-line scales 50 (49–52); gill rakers 30 (29–30); body depth 2.45 (2.4–2.55) in SL; body width 2.5 (2.55–2.65) in body depth; head length 3.0 (2.9–3.2) in SL; dorsal profile of head slightly convex; eye small, orbit diameter 7.7 (7.6–7.65) in SL; interorbital width 11.1 (11.4–11.8) in SL; mouth oblique, forming an angle of 64° (65–67°) to horizontal axis of body; tip of lower jaw projecting anterior to upper jaw when mouth fully closed (very slightly on smallest paratype); teeth conical and recurved, those at front of upper jaw in two irregular rows, reduced opposite nostrils to a single irregular row of progressively smaller teeth ending as a row of tiny nodular teeth in lower jaw very small, in three to four irregular rows medially, progressively fewer and smaller toward end of jaw; lips brown with numerous, very small, dark brown papillae; tongue a straight-sided triangle with pointed tip; many outer-layer scales missing from nape, below dorsal fin, and on chest of all type specimens, but enough to conclude that these areas have cycloid scales, except for a few ctenoid scales ventrally on chest near opercle; predorsal length 2.75 (2.75–2.8) in SL; prepelvic length 2.7 (2.7–2.8) in SL; longest dorsal-fin ray 3.85 (broken on paratypes) in SL; all caudal-fin rays damaged; pectoral-fins broken on all but 88-mm paratype, its length 3.6 in SL; pelvic fins just reaching anus, their length 6.2 (6.45–6.8) in SL. Color of holotype in alcohol as in Fig. 39; color in life unknown.

Etymology. This species is named for Dr. Tilman J. Alpermann of the Senckenberg Research Institute and Natural History Museum Frankfurt in recognition of his studies on Red Sea fishes and his assistance with loans and collection data from the Museum. The specific epithet is a noun in apposition.

Remarks. The three known specimens of this species came on loan with the original label only as follows: “*Pempheris vanicolensis*, Roten Meer, Aqaba, 1980”. They represent one of the seven *schwenkii* complex species in the Red Sea, due to their small adult size (the smallest paratype is a fully mature female), slender body, and dark band at the base of the anal fin. They are distinguished from other members of the complex in the Red Sea by having two rows of teeth medially in the upper jaw, a short prepelvic length, and the dark line on the pectoral-fin base at the insertion of the rays (vs. a band lower on the base). No DNA sequences are available for *P. tilman*.



Figure 39. *Pempheris tilman*, holotype, SMF 35779, male, 96.5 mm SL, Aqaba, Jordan, Red Sea (H.A. Randall).

Pempheris tiran Randall & Victor, n. sp.

Figure 40, Tables 1–3.

Holotype. CAS 236818, male, 122 mm SL, Red Sea, Saudi Arabia, Strait of Tiran, 28° 11.051' N, 34° 38.372' E, wreck of metal ferry on reef, small caves on side of reef, 6 m, spear, L. Rocha, M. Berumen, M. Priest, & T. Sinclair-Taylor, Oct. 1, 2013.

Paratype. BPBM 41230, female, 121 mm SL, same data as holotype.

Description. Dorsal-fin rays VI,9; anal-fin rays III,42 (44); pectoral-fin rays 18 (one with 17 on one side); lateral-line scales 62 (64); scales on nape, below dorsal fin, and side of caudal peduncle cycloid, scales on side of chest missing; gill rakers 31 (32); body depth 2.5 (2.45) in SL; body width 2.7 (2.7) in body depth; head length 3.45 (3.4) in SL; eye relatively small, the orbit diameter 7.95 (7.7) in SL; interorbital width 10.8 (10.9) in SL; mouth strongly oblique, forming an angle of 64° (65°) to horizontal axis of body; teeth large for the genus, those of medial third of upper jaw of male in three irregular rows, the upper-row teeth conical and forward-projecting, those of inner rows strongly recurved and inwardly projecting; remaining teeth in jaw in two rows, progressively smaller, except for a few tiny teeth in a single row near end of jaw; teeth of female about half the size of those of male, those of medial third of upper jaw in a single irregular row, the remaining teeth in two irregular rows, except for very small teeth in a single irregular row for last fourth of jaw; band of teeth in lower jaw of both sexes strongly outcurved medial to narrow symphysis, the teeth in four rows, progressively larger and more recurved inwardly in female; largest teeth of male in two outer rows, erect or slightly recurved; outer medial teeth of lower jaw visible in both sexes when mouth fully closed; upper lip relatively smooth, the surface with close-set, low papillae; lower lip with smaller and more widely separated papillae; tongue with sides slightly incurved, the tip rounded and flexible; predorsal length 2.8 (2.75) in SL; longest dorsal-fin soft ray 3.75 (4.05) in SL; tips of caudal lobes broken, but slight curvature of broad middle part of fin indicates a low caudal concavity; prepelvic length 2.8 (2.75) in SL; pelvic fins extending nearly to origin of anal fin, fin length 5.55 (5.65) in SL. Color in alcohol as in Fig. 40, dark brown, scale edges light gray; row of scales above and below lateral line darker than remaining scales of body; dorsal fin grayish brown with a darker brown anterior margin leading to a large black apical spot (nearly half length of anterior edge of fin); caudal fin dark gray-brown with a very broad black posterior margin



Figure 40. *Pempheris tiran*, holotype, CAS 236818, male, 122 mm SL, Strait of Tiran, Saudi Arabia, Red Sea (H.A. Randall).



Figure 41. Collection location on wreck of ferry for type specimens of *Pempheris tiran*, Strait of Tiran, Saudi Arabia, Red Sea (J. DiBattista).

(width nearly equal to pupil diameter) and narrow black dorsal and ventral margins; anal fin dark brown at base, this color merging with dark brown of body, a middle zone of light yellowish gray, and an outer black border more than half fin width anteriorly, progressively narrower posteriorly; paired fins light yellowish gray; iris bluish black, greenish gray lens nearly encircled by two pale yellowish arcs. Color in life brownish gray with red-tinged fin membranes, iris with a golden ring around pupil, anal fin translucent and colorless below black band along fin margin.

Etymology. This species is named for the type location, the Strait of Tiran between the tip of Sinai and Saudi Arabia. The specific epithet is a noun in apposition.

Remarks. The two type specimens were first identified as *P. vanicolensis* (a Pacific species) because of the prominent black border on the anal fin and the fin-ray and lateral-line scale counts (*P. vanicolensis* can be quickly distinguished by lacking the prominent dark spot around the base of the pectoral fin). However, when the dentition was examined, the new species showed a distinctive tooth pattern shared only with *P. malabarica* in the region: an external patch of teeth on the lower jaw that is apparent when the jaws are closed. *Pempheris tiran* can be clearly distinguished from *P. malabarica* by non-overlapping gill-raker counts and very different colors and marking patterns. Both the markings and meristics of *P. tiran* are similar to those of *P. bexillon*, from the southwest Indian Ocean (see Mooi & Randall 2014), in particular the black margin along the anal fin; the main difference is the distinctive external patch of teeth on the lower lip of *P. tiran*. In addition, *P. bexillon* has a predominantly yellow coloration on the fins, not apparent on the fresh photograph of the holotype of *P. tiran*. *Pempheris flavicycla* is found in the Red Sea and also shares the dark margin of the anal fin, but has a bright yellow iris, a lower range of lateral-line scale counts, and no external patch of teeth. No DNA sequences are available for *P. tiran*.

***Pempheris trinco* Randall & Victor, n. sp.**

Figure 42, Tables 1–3.

Pempheris schwenkii [non Bleeker] Randall & Bineesh 2014: 36.

Holotype. BPBM 18771, male, 104 mm SL, Sri Lanka, Trincomalee, Dutch Point, substratum of large boulders, 5 m, spear, J.E. Randall, April 2, 1975.

Paratypes. USNM 343709, 7: 90–107 mm SL, Sri Lanka, Trincomalee, outside harbor, large outcrop about 50 yards offshore, 1–5 m, rotenone, W.F. Smith-Vaniz, July 1, 1969; USNM 343764, 97 mm SL, Sri Lanka, Negombo, P.C. Heemstra, Sept. 15, 1969; USNM 343760, 4: 93–106 mm SL, Sri Lanka, Weligama, 200 yards offshore from rest house, 1–3 m, rotenone, C. Koenig, Feb. 14, 1970; USNM 343765, 91 mm SL, Sri Lanka, Eastern Province, Batticaloa District, Koralu Pattu, Passakudah Bay, reef 500 yards NE of outlet of small stream, 6–8 m, rotenone, T. Iwamoto, June 10, 1970; BPBM 41213, 4: 85–104 mm SL, same data as holotype; BPBM 27196, 2: 81–88.5 mm SL, Sri Lanka, Hikkaduwa, about one-fourth mile offshore, rocky substrate, 10–12 m, rotenone, J.E. Randall, Feb. 24, 1979.

Description. Dorsal-fin rays VI,9; anal-fin rays III,40 (37–41); pectoral-fin rays 17 or 18, modally 18; lateral-line scales 50 (49–58); gill rakers 26 (26–28); body depth 2.45 (2.3–2.5) in SL; body width 2.6 in body depth; head length 3.25 (3.2–3.3) in SL; eye diameter 7.4 (7.1–7.75) in SL; interorbital width 12.6 (12.6–12.9) in SL; mouth oblique, forming an angle of 65° (61–68°) to horizontal axis of body; tip of lower jaw slightly anterior to upper jaw when mouth fully closed; teeth in upper jaw in two rows medially, the outer row slightly recurved, the inner larger and more strongly recurved, narrowing to a single row posteriorly; teeth in lower jaw similar, but smaller, in three irregular rows and more strongly recurved; tongue strongly concave on sides, creating a slender, slightly rounded tip; outer layer of scales nearly completely absent on most specimens, but enough scales remain on holotype to determine that those on nape and in first row below dorsal fin are cycloid; scales on side of chest cycloid, except for a few ctenoid scales ventroanteriorly; scales on side of caudal peduncle cycloid; predorsal length 2.7 (2.6–2.7) in SL; longest dorsal-fin ray 3.85 (3.5–3.95) in SL; caudal fin damaged in all specimens; the fin is intact on photograph of holotype, showing that it is forked, with a caudal concavity about 5 in head length; pectoral-fin length 3.25 (3.0–3.35) in SL; prepelvic length 2.6 (2.55–2.65) in SL; pelvic fins varying from reaching

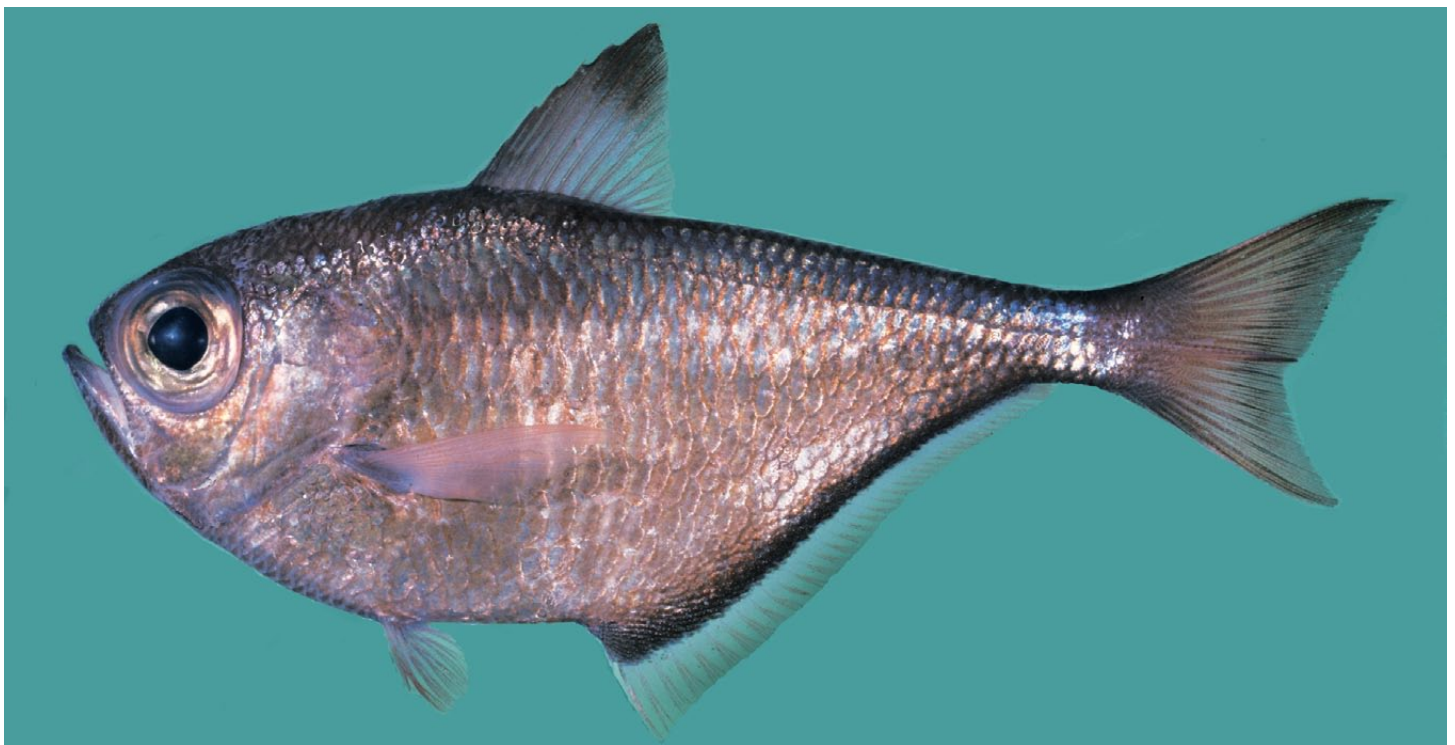


Figure 42. *Pempheris trinco*, holotype, BPBM 18771, male, 104 mm SL, Trincomalee, Sri Lanka (J.E. Randall).

anus to nearly reaching origin of anal fin, their length 6.5 (5.7–6.55) in SL. Fig. 42 of the holotype shows the fresh coloration with the scales intact; note the scale centers are silvery gray, and the scale edges copper-colored. A dark band along the base of the pectoral fin when fresh. Holotype in alcohol orangish brown (the brown from very fine dark brown stippling), the scale edges silvery gray.

Etymology. This species is named for the type location, Trincomalee, which is both a district and a major port city on the east coast of Sri Lanka. It is generally called Trinco by Sri Lankans. The specific epithet is a noun in apposition.

Remarks. *Pempheris trinco* is a relatively small species of the *schwenkii* complex; our largest specimen measures only 107 mm SL. The species is usually encountered on reefs or rocky substrata in small aggregations. Presently known only from Sri Lanka, but the range may extend more widely in the appropriate habitat. The *schwenkii*-complex species in neighboring south India is *P. bineeshi*, which differs by having a shorter predorsal and prepelvic distance, a narrower body, and a lower range of lateral-line scales. Other *Pempheris* species found in Sri Lanka comprise *P. pathirana* of the *rhomboidea* complex, the unrelated *P. malabarica* (see Appendix Fig. 2), and *P. mangula* might be expected on the island as well. No DNA sequences are available for *P. trinco*.

***Pempheris viridis* Randall & Victor, n. sp.**

Figure 43, Tables 1–3.

Holotype. SMF 33629 (KAU11-018), 79.5 mm SL, Red Sea, Saudi Arabia, off Al Lith, 20°15.111' N, 39°57.825' E, fringing reef, 3 m, a large coral block rising to within 0.5 m of surface; rotenone set in cave in coral block, S.V. Bogorodsky, & T. J. Alpermann, March 28, 2011.

Description. Dorsal-fin rays VI,9; anal-fin rays III,37; pectoral-fin rays 17 (one fin removed); lateral-line scales 53; scales on nape, below dorsal fin, and side of caudal peduncle cycloid; scales on side of chest cycloid except for 6 ctenoid scales in two rows on right side, and 12 ctenoid scales in four rows on left side at angle of



Figure 43. *Pempheris viridis*, holotype, SMF 3363, 79.5 mm SL, Al Lith, Saudi Arabia, Red Sea (S.V. Bogorodsky).

opercle; gill rakers 25; body depth 2.65 in SL; body width 2.7 in body depth; head length 3.2 in SL; dorsal profile of head nearly straight; eye diameter 7.25 in SL; interorbital width 11.4 in SL; mouth steeply oblique, forming an angle of 73° to horizontal axis of body; teeth medially in upper jaw small, slender, conical, and recurved in three or four irregular rows, reduced laterally in jaw to two well-separated rows of larger, strongly recurved teeth, and posteriorly to a single row of progressively smaller teeth, ending as small nodules; lower jaw with a band of very small teeth at symphysis, gradually reduced posteriorly to a single row of tiny teeth; tongue triangular in shape with pointed tip; anterior lateral line very highly arched, the vertical height above level of origin of lateral line equal to two-thirds orbit diameter, 11.5 in SL; predorsal length 2.6 in SL; prepelvic length 2.5 in SL; longest dorsal-fin rays broken on holotype, but 4.1 in SL from photograph; caudal-fin length 4.35 in SL; pectoral-fin length 3.4 in SL; pelvic fins reaching posterior margin of anus, their length 6.9 in SL. Color in alcohol: side of body light orangish brown, the margin of scales darker; head and back grayish brown, the head darker; dark brown band at base of anal fin. Color when fresh as in Fig. 43.

Etymology. This species is named for its principal color, i.e. Latin *viridis* for green.

Remarks. *Pempheris viridis* is one of seven species in the *schwenkii* complex in the Red Sea. The unique specimen was first identified by the senior author as *P. tominagai*, but differs from the underwater photograph of the holotype of *P. tominagai* (Fig. 44) by its more slender body (the holotype described in Koeda *et al.* 2014 has body depth 2.35 in SL), a straight dorsal profile (vs. convex in *P. tominagai*), a highly arched anterior lateral line (in *P. tominagai* of equal length, the vertical rise is two-fifths orbit diameter, 17.6 in SL), and in color. *Pempheris viridis* is bright metallic green, has a bright yellow eye, and has a very dark band at the rear margin of the caudal fin. *Pempheris sergey* is similar in color to *P. viridis* but differs by having two rows of teeth medially in the upper jaw and a convex dorsal profile. Mitochondrial DNA sequences from the type specimens of *P. viridis* and *P. sergey* (obtained during review) match those of *P. tominagai*; more specimens are needed to resolve the genetic relationships in this group.



Figure 44. *Pempheris tominagai*, underwater photograph of holotype, Sharm el-Sheikh, Egypt, Red Sea (S.V. Bogorodsky).

Pempheris wilsoni Randall & Victor, n. sp.

Figures 45–48, Tables 1–3. BIN AAD1777 (in part).

Holotype. CAS 236523, male, 123 mm SL, Oman, Gulf of Oman, Fahal Island, 23°40'52" N, 58°30'11.3" E, Station LAR-85, spear, L. Rocha, J. DiBattista, M. Priest, T. Sinclair, & J. Choat, March 28, 2013.

Description. Dorsal-fin rays VI,9; anal-fin rays III,45; pectoral-fin rays 17; lateral-line scales 59; gill rakers 29; body depth 2.35 in SL; body width 2.7 in body depth; head length 3.45 in SL; eye diameter 7.3 in SL; interorbital width 11.7 in SL; mouth oblique, forming an angle of 60° to horizontal axis of body; dentition as described for *P. smithorum*, but teeth of lower jaw smaller; tongue concave-sided with rounded tip; outer layer of scales almost entirely missing; predorsal length 2.7 in SL; prepelvic length 2.85 in SL; longest dorsal-fin ray 3.4 in SL; caudal fin damaged; pectoral-fin length 3.15 in SL; pelvic fins reaching anus, 5.9 in SL. Color in alcohol as in Fig. 45; black pigment on dorsal fin confined to tip; caudal fin with a posterior black border, but none on dorsal and ventral margins of fin. Color in life as in Figs. 46–48.

Etymology. This species is named for Keith D.P. Wilson, an expert on the dragonflies of China, who collected fishes in Oman for our studies on *Pempheris* and took the photographs of Figs. 46 and 48.

Remarks. K.D.P. Wilson and Brian W. Darvell went to Oman at the request of the first author to collect and photograph species of *Pempheris*. Because they were passengers on a commercial dive boat, they had little opportunity to collect fish specimens, succeeding only in three of *P. darvelli* described in Randall & Victor (2014). We were fortunate to find a specimen of *P. wilsoni* in a loan from the California Academy of Sciences for the holotype. It was collected at Fahal Island in the Gulf of Oman, about 4 km from the dive sites of Wilson and Darvell. The label indicates five collectors. All divers were spearing various species of fishes, so no attempt was made to link each specimen to a collector.

The underwater photographs of Figs. 46–48 were identified as *P. wilsoni* by eye size, the 60° angle of the maxilla, predorsal and prepelvic lengths, lengths of the longest rays of the dorsal fin as well as the paired fins, and the dark markings on the fins. Figs. 47 and 48 were first believed to represent different species, but counts and measurements from the photographs fail to show any differences, and the group in Fig. 47 has individuals of intermediate color.



Figure 45. *Pempheris wilsoni*, holotype, CAS 236523, male, 123 mm SL, Fahal Island, Oman (H.A. Randall).



Figure 46. *Pempheris wilsoni*, underwater photograph, Oman (K.D.P. Wilson).



Figure 47. *Pempheris wilsoni*, aggregation, Gulf of Oman (B.W. Darvell).



Figure 48. *Pempheris wilsoni*, underwater photograph, Oman (K.D.P. Wilson).

The barcode mtDNA COI sequence of the holotype of *P. wilsoni* is the same as several other species of the *rhomboidea* complex, mostly species from other locations in the region, i.e. *P. rhomboidea* from the Red Sea and Mediterranean, *P. russellii* from Pakistan, *P. eatoni* from southern Africa, but also *P. kuriamuria* which is described from the southern coast of Oman (vs. *P. wilsoni* from the northern coast in the Gulf of Oman)(Fig. 1).

***Pempheris xanthomma* Randall & Victor, n. sp.**

Figures 49 & 50, Tables 1–3. BIN AAI3650 (in part).

Pempheris tominagai [non Koeda, Yoshino, Imai & Tachihara] Randall *et al.* 2014: 387.

Holotype. SMF 35712, female, 96 mm SL, Gulf of Aden, Yemen, Ras Majdaha, 14°00.868' N, 48°25.572' E, steep rocky slope to 6 m, collected with rotenone from 8–11 m, live coral cover less than 20%, isolated corals, mainly *Porites*, some *Pocillopora*, rotenone, F. Krupp, M. Schneider, & E. Lavergne, May 20, 2005.

Paratypes. SMF 35489, 10: 57–100 mm SL, NHCY-P-10, 9: 58–98 mm SL, BPBM 41227, 74 mm SL, & USNM 436600, 81 mm SL, all with same data as holotype.

Description. Dorsal-fin rays VI,9; anal-fin rays III,38 (36–41); pectoral-fin rays 17 (16–18, strongly modal 17); lateral-line scales 55 (49–57); scales cycloid on nape, below dorsal fin, on side of caudal peduncle, and on chest except from a few scales to as many as one-fourth ctenoid ventroanteriorly; gill rakers 28 (26–29); body depth 2.35 (2.15–2.45) in SL; body width 3.1 (2.45–3.5) in body depth; head length 3.25 (3.05–3.35) in SL; eye relatively small, the orbit diameter 7.5 (7.55–7.75) in SL; interorbital width 12.0 (10.9–13.2) in SL; mouth strongly oblique, forming an angle of 69° (67–70°) to horizontal axis of body; recurved, conical teeth in a double



Figure 49. *Pempheris xanthomma*, holotype, SMF 35712, female, 96 mm SL, Gulf of Aden, Yemen, off Majdaha (H.A. Randall).

row in upper jaw, those of upper row more projecting, those of lower row more strongly recurved; double row continuing nearly to end of jaw where ending in a cluster of very small nodules; teeth in lower jaw much smaller, in four to five rows medially, progressively more recurved inwardly; tongue an equilateral triangle; upper lip with tiny papillae, most separated by a distance two or more times the diameter of the papillae; predorsal length 2.8 (2.7–2.8) in SL; longest dorsal-fin ray 4.0 (3.9–4.4) in SL; caudal fin moderately forked (none fully intact); pectoral-fin length 3.2 (3.15–3.35) in SL; prepelvic length 2.55 (2.5–2.6) in SL; pelvic fins reaching or extending slightly posterior to anus, 6.0 (5.7–6.8) in SL. Color in alcohol as in Fig. 49; dark brown to black band on anterior margin of dorsal fin expanded to a distal spot on only four of the larger type specimens, including holotype; dark band at base of anal fin broad; a narrow dark brown band across base of pectoral fins; scales of pectoral and abdominal region of large adults with light golden centers and brown margins; iris of eye yellow, except for a black linear dorsal rim, the yellow lighter and brighter around pupil. Color in life silvery to brownish with a broad dark band at anal-fin base; orangish caudal fin without a dark posterior margin (Fig. 50).



Figure 50. *Pempheris xanthomma*, underwater photograph, except *P. kruppi* on the far right with tail cropped, Ras Majdaha, Yemen (M.S. Aided).

Etymology. This species is named *Pempheris xanthomma* from the Greek for yellow-eyed, in reference to the dominant color of the iris in both live individuals and preserved specimens.

Remarks. This species was first identified by us as *P. tominagai*. *Pempheris xanthomma* is distinguished from the seven *schwenkii*-complex species in the neighboring Red Sea by having a particularly wide dark band at the base of the anal fin and two rows of teeth medially in the upper jaw. The new species is separated from *P. zajonzi*, the neighboring *schwenkii*-complex species from offshore Socotra Archipelago of Yemen, by having the normal two rows of teeth medially in the upper jaw (vs. three).

The barcode mtDNA COI sequence of *P. xanthomma* is almost the same as the sequences for *P. tominagai* (only 0.16% divergent) and close to *P. ternay* from the Seychelles and *P. rubricauda* from Madagascar. The group of four species diverge by 3.4% from the lineage comprising *P. hadra* from Maldives, *P. bineeshi* from India, and probably true *P. schwenkii* from Bali, Indonesia (Fig. 1).

Pempheris zajonzi Randall & Victor, n. sp.

Figure 51, Tables 1–3.

Holotype. SMF 35713, male, 89 mm SL, ST-024/F4, Yemen, Socotra Archipelago, Socotra Island, Ras Qatanin, 150 m off coast on shipwreck, 12°20'03" N 53°34'26" E, 2–4 m, rotenone, U. Zajonz & M. Khalaf, March 13, 1999.

Paratypes. SMF 35714, juveniles, 4: 41–49 mm SL, same data as holotype.

Description. Dorsal-fin rays VI,9; anal-fin rays III,38 (36–38); pectoral-fin rays 17; lateral-line scales 50 (49–54); scales on nape, below dorsal fin, and side of caudal peduncle cycloid; scales on chest cycloid and about one-fourth ctenoid ventroanteriorly; gill rakers 28 (28–30); body depth 2.4 in SL; body width 2.7 in body depth; dorsal profile from above eye to origin of dorsal fin nearly straight; head length 3.15 in SL; eye relatively small, the orbit diameter 8.0 in SL; interorbital width 11.8 in SL; maxilla forming an angle of 64° to horizontal axis of body; front of upper jaw with three irregular rows of well-developed recurved teeth for two-thirds the length of



Figure 51. *Pempheris zajonzi*, holotype, SMF 35713, male, 89 mm SL, Socotra Archipelago, Yemen (H.A. Randall).

the tooth-bearing part of jaw, the uppers more protruding, and the lowers more strongly recurved; teeth anteriorly in lower jaw very small, in three to four irregular close-set rows, progressively more recurved and larger inwardly; lower jaw not protruding when mouth firmly shut; tongue an equilateral triangle with pointed tip; lips smooth; caudal fin damaged; predorsal length 2.55 in SL; longest dorsal-fin ray 4.45 in SL; pectoral-fin length 3.25 in SL; prepelvic length 2.55 in SL; pelvic fins extending a short distance beyond anus, their length 6.6 in SL. Color in alcohol uniform brown except for paler scale edges (Fig. 51); leading edge of dorsal fin black, expanding slightly distally; caudal fin yellow with a very broad black posterior margin and narrow black upper and lower margins; black band at base of anal fin very broad, about equal in width to the outer ray part of fin; base of pectoral fin only slightly darker than adjacent body; iris very dark bluish gray. Color in life unknown.

Etymology. This species is named for the collector, Uwe Zajonz, of the Senckenberg Museum, Frankfurt, who plans to collect more specimens and obtain photographs of the new species.

Remarks. *Pempheris zajonzi* was first identified by us as *P. tominagai*, but that species differs in having fewer lateral-line scales, and predorsal and prepelvic lengths of about 2.45 in SL. The new species is also separated from *P. xanthomma*, the neighboring *schwenkii*-complex species from the mainland coast of Yemen, by having three rows of teeth medially in the upper jaw (vs. two in *P. xanthomma*). Uwe Zajonz plans to make a special effort to collect more specimens and take photographs when travel to Socotra Archipelago becomes possible. No DNA sequences are available for *P. zajonzi*.

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Appendix A. Specimen data and GenBank accession numbers for the barcode mtDNA COI sequences used to generate the phenogram in Fig. 1, following the order in the tree. Holotypes in bold, paratypes with P in voucher ID.

Species	Collection site	GenBank #	Voucher	BOLD BIN	Collector/Source
<i>Pempheris eatoni</i>	South Africa	JF494126	SAIAB 80038 ADC 216.2-3	AAD1777	A. Connell
<i>Pempheris kruppi</i>	Yemen	KT352048	mot 151115	AAD1777	M.S. Aideed
<i>Pempheris kruppi</i>	Yemen	KT352041	mot 151116	AAD1777	M.S. Aideed
<i>Pempheris kruppi</i>	Yemen	KT352053	mot 151117	AAD1777	M.S. Aideed
<i>Pempheris eatoni</i>	South Africa	JF494127	SAIAB 80038 ADC 216.2-2	AAD1777	A. Connell
<i>Pempheris eatoni</i>	South Africa	KT207966	P BPBM 41191 ADC216.2 #20	AAD1777	A. Connell
<i>Pempheris</i>	Madagascar	JQ350199	NBE0182 “mangula”	AAD1777	S. Planes/N. Hubert
<i>Pempheris eatoni</i>	South Africa	KT207961	SAIAB 189160 ADC2013 216.2-4	AAD1777	P. Eaton/A. Connell
<i>Pempheris eatoni</i>	South Africa	JF494128	SAIAB 80038 ADC 216.2-1	AAD1777	A. Connell
<i>Pempheris</i>	South Africa	KT207952	sa142164c2	AAD1777	A. Connell
<i>Pempheris kruppi</i>	Yemen	KT352044	mot151118	AAD1777	M.S. Aideed
<i>Pempheris russellii</i>	Pakistan	KT207954	BPBM pak14px	AAD1777	P. Psomadakis
<i>Pempheris kuriamuria</i>	Oman	KJ937296	BPBM 41239 JR14po	AAD1777	Darvell & Wilson
<i>Pempheris kuriamuria</i>	Oman	KT352029	CAS236521	AAD1777	L. Rocha/CAS
<i>Pempheris kruppi</i>	Yemen	KT352035	mot 151114	AAD1777	M.S. Aideed
<i>Pempheris eatoni</i>	South Africa	KT207953	P BPBM 41191 ac1421	AAD1777	A. Connell
<i>Pempheris wilsoni</i>	Fahal Is., Oman	KT352058	CAS236523	AAD1777	L. Rocha/CAS
<i>Pempheris</i>	South Africa	KT207965	sa142164c1	AAD1777	A. Connell
<i>Pempheris rhomboidea</i>	Red Sea	KJ609425	PVA_EIL_091017	AAD1777	G. Bernardi
<i>Pempheris rhomboidea</i>	Red Sea	KJ609479	PVA_HAI_091043	AAD1777	G. Bernardi
<i>Pempheris rhomboidea</i>	Red Sea	KJ609414	PVA_EIL_091001	AAD1777	G. Bernardi
<i>Pempheris rhomboidea</i>	Red Sea	KJ609433	PVA_ALE_061005	AAD1777	G. Bernardi
<i>Pempheris rhomboidea</i>	Red Sea	KJ020196	NBFGR PE1	AAD1777	K.K. Bineesh
<i>Pempheris rhomboidea</i>	Red Sea	KJ020197	NBFGR PE2	AAD1777	K.K. Bineesh
<i>Pempheris rhomboidea</i>	Red Sea	KJ020198	NBFGR PM1	AAD1777	K.K. Bineesh
<i>Pempheris rhomboidea</i>	Red Sea	KJ020199	NBFGR PM2	AAD1777	K.K. Bineesh
<i>Pempheris mangula</i>	Bali, Indonesia	JN313327	BW-A11176 “adusta”	AAD1777.1	W. White/R. Ward
<i>Pempheris mangula</i>	Bali, Indonesia	JN313328	BW-A11177 “adusta”	AAD1777.1	W. White/R. Ward
<i>Pempheris mangula</i>	India	EU148571	WL-M263 “adusta”	AAD1777.1	W.S. Lakra <i>et al.</i>
<i>Pempheris mangula</i>	India	EU148572	WL-M264 “adusta”	AAD1777.1	W.S. Lakra <i>et al.</i>
<i>Pempheris mangula</i>	India	EU148574	WL-M266 “adusta”	AAD1777.1	W.S. Lakra <i>et al.</i>
<i>Pempheris mangula</i>	India	EU148573	WL-M265 “adusta”	AAD1777.1	W.S. Lakra <i>et al.</i>
<i>Pempheris mangula</i>	India	EU148575	WL-M267 “adusta”	AAD1777.1	W.S. Lakra <i>et al.</i>
<i>Pempheris bineeshi</i>	India	KJ020182	ZSI/CLT 2492	AAM9396	K.K. Bineesh
<i>Pempheris bineeshi</i>	India	KJ020183	NBFGR-CH-1143	AAM9396	K.K. Bineesh
<i>Pempheris bineeshi</i>	India	KJ020184	ZSI/CLT 2492	AAM9396	K.K. Bineesh
<i>Pempheris bineeshi</i>	India	KJ020185	ZSI/CLT 2492	AAM9396	K.K. Bineesh
<i>Pempheris bineeshi</i>	India	KJ020186	ZSI/CLT 2492	AAM9396	K.K. Bineesh
<i>Pempheris bineeshi</i>	India	KJ020187	ZSI/CLT 2492	AAM9396	K.K. Bineesh
<i>Pempheris bineeshi</i>	India	KJ020188	ZSI/CLT 2492	AAM9396	K.K. Bineesh
<i>Pempheris schwenkii</i>	Bali, Indonesia	pending	BW-A10192 CSIRO KD677	AAM9396	W. White/R. Ward
<i>Pempheris schwenkii</i>	Bali, Indonesia	JN312883	BW-A10194 CSIRO KD678(S)	AAM9396	W. White/R. Ward
<i>Pempheris hadra</i>	Maldives	pending	SAIAB 187537 MAL-022	AAM9396	O. Gon/G. Gouws
<i>Pempheris tominagai</i>	Red Sea	pending	PVA EIL 091005 0.82	AAM9396	G. Bernardi
<i>Pempheris tominagai</i>	Red Sea	pending	PVA EIL 091012 0.82	AAM9396	G. Bernardi
<i>Pempheris tominagai</i>	Red Sea	pending	PVA EIL 091020 0.66	AAM9396	G. Bernardi

<i>Pempheris tominagai</i>	Red Sea	pending	PVA EIL 091023 0.82	AAM9396	G. Bernardi
<i>Pempheris</i>	Chagos Arch.	KT352037	Chagos-702	AAI3650	M. Gaither/CAS
<i>Pempheris</i>	Chagos Arch.	KT352037	Chagos-703	AAI3650	M. Gaither/CAS
<i>Pempheris xanthomma</i>	Yemen	KT352036	mot151113	AAI3650	M.S. Aided
<i>Pempheris ternay</i>	Seychelles	KF930243	P SAIAB 77935 KUT 6867	AAI3650	P. Heemstra et al.
<i>Pempheris rubricauda</i>	Madagascar	JQ350203	NBE0213 “vanicolensis”	AAI3650	S. Planes/N. Hubert
<i>Pempheris rubricauda</i>	Madagascar	JQ350202	NBE0214 “vanicolensis”	AAI3650	S. Planes/N. Hubert
<i>Pempheris rubricauda</i>	Madagascar	JQ350204	NBE0215 “vanicolensis”	AAI3650	S. Planes/N. Hubert
<i>Pempheris bexillon</i>	Réunion	JQ350200	REU0958 “oualensis”	AAU3528	S. Planes/N. Hubert
<i>Pempheris bexillon</i>	Réunion	JQ350201	REU0957 “oualensis”	AAU3528	S. Planes/N. Hubert
<i>Pempheris ibo</i>	South Africa	KT207950	ac14p9	AAF8820	A. Connell/SAIAB
<i>Pempheris ibo</i>	South Africa	HQ561454	P SAIAB 189165 ADC10_216.4 #6	AAF8820	A. Connell/SAIAB
<i>Pempheris ibo</i>	South Africa	KT207959	ac14p7	AAF8820	A. Connell/SAIAB
<i>Pempheris hollemani</i>	SE Madagascar	pending	P SAIAB 97406 AV2010-027	AAC6084	P. & E. Heemstra
<i>Pempheris connelli</i>	South Africa	KT207957	P SAIAB 194783 sa142164b2	AAC6084	A. Connell/SAIAB
<i>Pempheris connelli</i>	South Africa	KF930242	RUSI 65242 UKFBJ655-08	AAC6084	A. Bentley/KU Tissue
<i>Pempheris connelli</i>	South Africa	KT207967	P SAIAB 194782 ac14p5	AAC6084	A. Connell/SAIAB
<i>Pempheris connelli</i>	South Africa	KT207962	P SAIAB 194782 ac14p6	AAC6084	A. Connell/SAIAB
<i>Pempheris connelli</i>	South Africa	KT207951	P SAIAB 194782 ac14p8	AAC6084	A. Connell/SAIAB
<i>Pempheris connelli</i>	South Africa	KT207956	P SAIAB 194782 ac14p10	AAC6084	A. Connell/SAIAB
<i>Pempheris connelli</i>	South Africa	KT207964	P SAIAB 194782 ac14p11	AAC6084	A. Connell/SAIAB
<i>Pempheris connelli</i>	South Africa	KT207958	P SAIAB 194782 ac14p12	AAC6084	A. Connell/SAIAB
<i>Pempheris connelli</i>	South Africa	JF494131	P SAIAB 75850/1 ADC216.4-2	AAC6084	P. Heemstra/SAIAB
<i>Pempheris connelli</i>	South Africa	JF494130	P SAIAB 75850 ADC216.4-4	AAC6084	P. Heemstra/SAIAB
<i>Pempheris connelli</i>	South Africa	JF494132	P SAIAB 75776 ADC216.4-1	AAC6084	A. Connell/SAIAB
<i>Pempheris connelli</i>	South Africa	KF489699	ADC12_216.4A #3	AAC6084	A. Connell/SAIAB
<i>Pempheris connelli</i>	South Africa	KT207960	P SAIAB 194783 sa142164b1	AAC6084	A. Connell/SAIAB
<i>Pempheris connelli</i>	South Africa	KT207949	P SAIAB 194783 sa142164b3	AAC6084	A. Connell/SAIAB
<i>Pempheris rochai</i>	Oman	KT352045	CAS236522	AAC6084	L. Rocha/CAS
<i>Pempheris</i> sp. 1	South Africa	KT207963	L II A2 #1.1 egg DSLAF019-07	pending	A. Connell
<i>Pempheris bruggemanni</i>	Réunion	JQ350194	P REU0731 URUN 2007-1208	AAT9853	S. Planes/N. Hubert
<i>Pempheris bruggemanni</i>	Réunion	JQ350195	P REU0936 BPBM 41198	AAT9853	S. Planes/N. Hubert
<i>Pempheris bruggemanni</i>	Réunion	JQ350198	P REU0938 URUN 2007-1209	AAT9853	S. Planes/N. Hubert
<i>Pempheris bruggemanni</i>	Réunion	JQ350196	P REU0732 URON 2007-1419	AAT9853	S. Planes/N. Hubert
<i>Pempheris bruggemanni</i>	Réunion	JQ350197	REU0937 MNHN 2015-0002	AAT9853	S. Planes/N. Hubert
<i>Pempheris malabarica</i>	Karachi, Pakistan	KT207955	pak14pm	ACR6962	P. Fanning/FAOPK
<i>Pempheris flavicycla</i>	Al Lith, Red Sea	KT352052	CAS PVA02 995	AAE7117	L. Rocha/CAS
<i>Pempheris flavicycla</i>	Djibouti	KT352054	CAS 235013	AAE7117	L. Rocha/CAS
<i>Pempheris flavicycla</i>	Red Sea	KF914197	KAU13-608	AAE7117	S. Bogorodsky
<i>Pempheris flavicycla</i>	Red Sea	KF914196	KAU11-506	AAE7117	S. Bogorodsky
<i>Pempheris flavicycla</i>	Red Sea	KF914195	KAU11-505	AAE7117	S. Bogorodsky
<i>Pempheris flavicycla</i>	Red Sea	KF914193	KAU11-016	AAE7117	S. Bogorodsky
<i>Pempheris flavicycla</i>	Red Sea	KF914194	KAU11-504	AAE7117	S. Bogorodsky
<i>Pempheris flavicycla</i>	Red Sea	KF914192	KAU11-015	AAE7117	S. Bogorodsky
<i>Pempheris flavicycla</i>	Red Sea	KF914190	KAU11-013	AAE7117	S. Bogorodsky
<i>Pempheris flavicycla</i>	Red Sea	KF914191	KAU11-014	AAE7117	S. Bogorodsky
<i>Pempheris flavicycla</i>	Seychelles	EU381029	SAIAB 77856	AAE7117	A. Bentley <i>et al.</i>
<i>Pempheris flavicycla</i>	Seychelles	EU381030	SAIAB 77805	AAE7117	A. Bentley <i>et al.</i>
<i>Parapriacanthus</i>	Tonga	KF930232	USNM 336802	AAC7602	J.T. Williams <i>et al.</i>

Appendix

Pempheris malabarica x *Pempheris russellii*

Appendix Figure 1; Appendix Table 1

A project of the Food and Agriculture Organization of the United Nations to document the fishery resources of the Sind Coast of Pakistan provided us with the opportunity to request specimens of *Pempheris* from the region. Dr. Peter Psomadakis of FAO and Hamid Badar Osmany of the Marine Fisheries Department in Karachi sent specimens, tissue samples, and photographs of *P. malabarica* C. & V. and *P. russellii* Day from the sea off Karachi. While making routine counts of fin rays and scales of the specimens, one that looked like *P. malabarica* (BPBM 41183, male, 125 mm SL) was noted to have the unusual low number of 59 lateral-line scales (60 on the other side)(Appendix Fig. 1). *Pempheris malabarica* has the highest lateral-line scale count (65–75) for the genus. Other meristic data of the specimen are within the range for *P. malabarica*. The eye size is precisely the same as that of *P. malabarica* for the standard length, and the upper-jaw angle of 65° is the same; also it has a dark anterior margin on the dorsal fin like *P. malabarica*, instead of a large distal black spot found on most species of *Pempheris*, including *P. russellii*. However, it has a deeper body like that of *P. russellii* and is intermediate to the two species in its pectoral-fin length (Appendix Table 1). Appendix Fig. 2 of a specimen of *P. malabarica* and Appendix Fig. 3 of a specimen of *P. russellii* are provided for comparison.

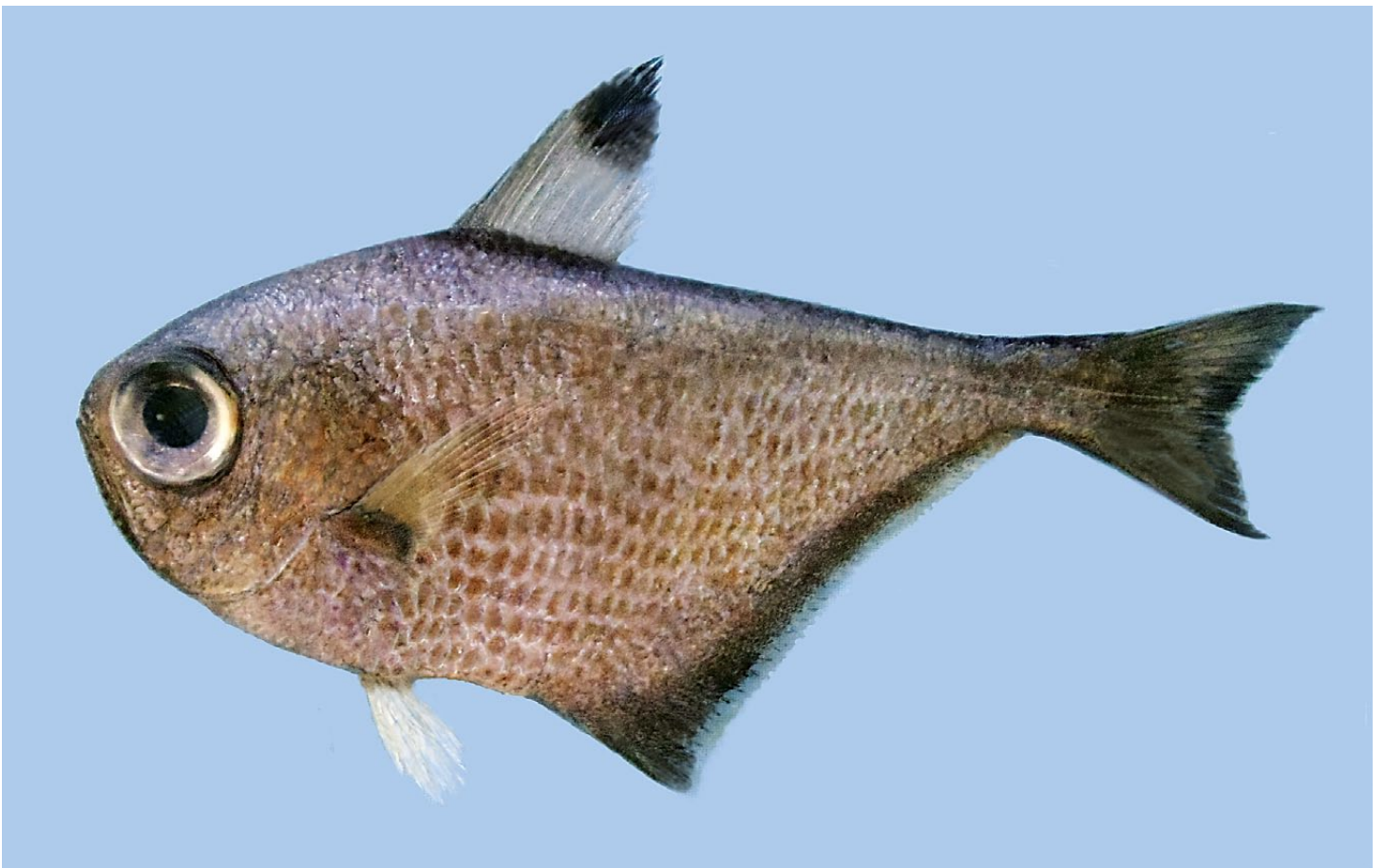
Suspecting the specimen to be a hybrid, the dentition was carefully compared. *P. malabarica* has the most distinctive dentition of the genus: the teeth in the usual two rows anteriorly in the upper jaw are nearly three times larger than those of *P. russellii* and project horizontally forward instead of obliquely downward. The teeth anteriorly in the lower jaw are in a pair of patches shaped like a comma, separated by a narrow medial gap. The patches are half exposed when the jaws are fully closed. The teeth are progressively larger anteriorly (the reverse is typical of the genus), the five or six teeth at the front are stoutly conical, twice as large as remaining teeth,



Appendix Figure 1. *Pempheris malabarica* x *Pempheris russellii*, BPBM 41183, male, 125 mm SL, Karachi, Pakistan (H.A. Randall).



Appendix Figure 2. *Pempheris malabarica*, BPBM 36185, 157 mm SL, Masirah Island, S. Oman (J.E. Randall).



Appendix Figure 3. *Pempheris russellii*, 137 mm SL, Sind coast of Pakistan (H. Badar Osmany).

APPENDIX TABLE 1

Comparison of characters of *Pempheris russellii*,
P. malabarica, and the hybrid *P. malabarica* x *P. russellii**

	<i>P. russellii</i>	hybrid	<i>P. malabarica</i>
Standard length (mm)	124	125	122
Sex	male	male	male
Lateral-line scales	55	59	65
Body depth	2.2	2.2	2.4
Eye diameter	7.4	8.35	8.35
Angle of maxilla	70°	65°	65°
Pectoral-fin length	3.05	3.2	3.3
Dorsal-fin marking	spot	band	band

*Measurements of depths and lengths are times in standard length; band refers to the dark anterior border on the dorsal fin, spot to an isolated large apical black marking on the dorsal fin.

and project directly forward. The remaining teeth in the patches are well separated, progressively smaller, more slender, and recurved. There are two rows of small, slender, recurved teeth to the side of the jaw, narrowing to a single row posteriorly. The dentition of *P. russellii* is typical of the genus *Pempheris*, in general; that of the hybrid is intermediate.

The underwater photograph of Appendix Fig. 4 shows a mixed aggregation of *P. malabarica* (orangish and no dorsal-fin spot) and *P. russellii* (grayish brown with black-tipped dorsal fin) on a reef off Karachi, Pakistan. In view of the proximity of the two species, it is not difficult to predict that the ova of one might at times be fertilized by the sperm of the other.



Appendix Figure 4. Mixed aggregation of *Pempheris malabarica* and *P. russellii*, Karachi Reef, Pakistan (M. Farooq).



Appendix Figure 5. *Pempheris* sp. USNM 343770, 98.5 mm SL, St. Brandon's Shoals (H.A. Randall).

St. Brandon's Shoals Fish Collections. Large fish collections were made, mainly with rotenone, in the St. Brandon's Shoals (Cargados Carajos) of the Indian Ocean, from a sailing vessel in April 1976. The expedition was sponsored by Lewis H. Strauss and included the ichthyologists Victor G. Springer, Thomas H. Fraser, and C. Lavett Smith. Among the many species of fishes collected are what seemed to be a single small species of *Pempheris* of the *schwenkii* complex from three stations: USNM 343769, 35: 70–107 mm, SE side of Grande Passe (16°28' S, 59°40' E) at 0–20 feet on April 5, 1976; USNM 343770, 44: 44–114.5 mm SL, 0.5 miles S of Île Raphael (16°27' S, 59°36' E) at a depth of 0–30 feet, April 12, 1976; and USNM 343768, 8: 101.5–110.5 mm SL, off NW shore of Albatross Island (16°15' S, 59°15' E), at 0–18 m, April 14, 1976. Appendix Fig.5 illustrates a 98.5-mm specimen from the second collection.

Routine measurement and meristic data were taken of the three St. Brandon's collections in the expectation that all would be essentially the same. They are for body and fin proportions and within one count for anal-fin rays (38–43) and lateral-line scales (49–60). However, a surprise came with gill-raker counts. The fish of the first collection have 27–29 gill rakers, while the next two collections have 28–30. We then searched for other characters that might show differences. The angle of the maxilla averaged about 65° for all the specimens. Whether scales on the side of the chest are cycloid or ctenoid is a valuable character for species of *Pempheris*. Unfortunately there are usually at least some scales missing. When the chest scales are fully present or nearly so, the fish of the first collection have all or nearly all cycloid scales, while those of the second and third collections are mainly or all ctenoid. Unexpectedly, we found fish of all three St. Brandon's collections that clearly had too many of the wrong kind of chest scales, suggesting hybridization.

To determine the status of the species of *Pempheris* of these three collections is beyond our present capability, in view of the time frame to complete the manuscript. A future expedition to St. Brandon's Shoals, with observations on habitat, underwater photographs, and taking tissue samples for genetic analysis, should be able to resolve this interesting complex of species.

Unidentified species of *Pempheris*. Many species of *Pempheris* are difficult to positively identify from underwater photographs. However, there are a few photographs that are sufficiently distinct to suggest undescribed species. Appendix Figs. 6 and 7, the former from Madagascar, the latter from Sri Lanka, are examples of new species for which specimens are needed. We also believe Appendix Figs. 8 through 15, taken by Dawn Goebbels in the Watamu Marine National Park in Kenya, represent undescribed species of *Pempheris*.



Appendix Figure 6. *Pempheris* sp., 60 km north of Tuléar, Madagascar (G.R. Allen). Koeda *et al.* (2014: fig. 7a) mistakenly identified this photograph as *P. tominagai*.



Appendix Figure 7. *Pempheris* sp., with dark edge on anal fin and truncate caudal fin, resembles *P. flavicycla*, but is missing the characteristic dark oval at the pectoral-fin base, Sri Lanka (J.E. Randall).



Appendix Figure 8. *Pempheris* sp. 1. In addition to color pattern, distinct in the deep body and slightly forked caudal fin, Watamu Marine National Park, Kenya (D. Goebbels).



Appendix Figure 9. *Pempheris* sp. 1: apparent subadult, Watamu Marine National Park, Kenya (D. Goebbels).



Appendix Figure 10. *Pempheris* sp. 2. Note the very long anterior part of the anal fin, the black membranes of the pelvic fins, and the copper and green striped color pattern, Watamu Marine National Park, Kenya (D. Goebbels).



Appendix Figure 11. *Pempheris* spp., all of the fish in this aggregation are the same species except for the striped reddish brown fish at the lower right edge. The color difference is mainly from the angle of the light reflected from the scales; all of the fish share a reddish caudal fin with dark brown dorsal and ventral margins, Watamu Marine National Park, Kenya (D. Goebbels).



Appendix Figure 12. *Pempheris* spp., two species of *Pempheris* with the cleaner wrasse *Labroides dimidiatus*, one with the black-tipped dorsal fin probably *P. nesogallica*, the other probably undescribed, Watamu Marine National Park, Kenya (D. Goebbels).



Appendix Figure 13. *Pempheris* of the *schwenkii* complex, distinct in its yellow-green color pattern. Cropped from a dense aggregation, mainly of this species, Watamu Marine National Park, Kenya (D. Goebbels).



Appendix Figure 14. *Pempheris* sp., a reddish species, its small size apparent by the size of the blades of *Thalassia* and the associated apogonid fishes, Watamu Marine National Park, Kenya (D. Goebbels).



Appendix Figure 15. *Pempheris* sp., the small eye and unique color pattern of the anal fin indicate another probable new species, Watamu Marine National Park, Kenya (D. Goebbels).