

Journal of the Ocean Science Foundation 2013 Volume 9

Randall, J.E., Bogorodsky, S.V., Alpermann, T.J., Satapoomin, U., Mooi, R.D. & Mal, A.O.

Pempheris flavicycla, a new pempherid fish from the Indian Ocean, previously identified as *P. vanicolensis* Cuvier p. 1



Published December 31, 2013 by the Ocean Science Foundation © 2013 OSF, Inc.

ISSN: 1937-7835

Online edition at <http://oceansciencefoundation.org/josf.html>

Printed copies available at UC Libraries and free from OSF, 4051 Glenwood, Irvine CA

Cover photo: *Pempheris flavicycla marisrubri*, Egypt, Red Sea © Laélia Vulot, Paris, France

Printing sponsored by Walsh Paper Distribution, Inc. of Westminster, CA



Journal of the Ocean Science Foundation

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Journal of the Ocean Science Foundation



2013, Volume 9

***Pempheris flavicycla*, a new pempherid fish from the Indian Ocean, previously identified as *P. vanicolensis* Cuvier**

JOHN E. RANDALL

Bishop Museum, 1525 Bernice St., Honolulu, HI 96817-2704 USA. E-mail: jackr@hawaii.rr.com

SERGEY V. BOGORODSKY

Station of Naturalists, Omsk, Russia. E-mail: ic187196@yandex.ru

TILMAN J. ALPERMANN

*Senckenberg Research Institute and Natural History Museum, Senckenberganlage 25, D-60325
Frankfurt a.M., Germany. E-mail: tilman.alpermann@senckenberg.de*

UKKRIT SATAPOOMIN

Phuket Marine Biological Center, P.O. Box 60, Phuket 83000, Thailand. E-mail: ukkrit@yahoo.com

RANDALL D. MOOI*

*Curator of Zoology, The Manitoba Museum,
190 Rupert Ave., Winnipeg MB R3B 0N2, Canada. E-mail: rmooi@manitobamuseum.ca*

AHMAD O. MAL

*Department of Marine Biology, Faculty of Marine Sciences,
King Abdulaziz University, Jeddah, Saudi Arabia. E-mail: aomal@kau.edu.sa*

Abstract

Pempheris flavicycla is described as a new species of sweeper (Perciformes: Pempheridae) from the Indian Ocean, including the Red Sea. It has a bright yellow ring around the pupil of the eye, a black outer border on the anal and caudal fins, a black spot at the base of the pectoral fins, 38–44 anal soft rays, 54–61 lateral-line scales, and 29–33 gill rakers. It is found in clear-water, coral-reef areas not exposed to heavy seas, and usually in less than 15 m. Two subspecies are recognized: *Pempheris flavicycla flavicycla* from Oman, Tanzania (type locality Mafia Island), Kenya (Wasini Island), Seychelles, Republic of Maldives, Lakshadweep, Sri Lanka, and islands of the Andaman Sea; and *Pempheris flavicycla marisrubri* from the Red Sea and the Gulf of Tadjoura off Djibouti. The Red Sea subspecies differs in having a larger eye, longer pectoral fins, more ctenoid scales, the posterior nostril largest, and modally one fewer pectoral-fin rays. Both subspecies have usually been misidentified as *Pempheris vanicolensis* Cuvier in C. & V. (type locality, Vanikoro Island, Santa Cruz Islands), which differs in having a brownish green iris, no black spot at the base of the pectoral fins, 63–68 lateral-line scales, and 26–29 gill rakers. The range of *P. vanicolensis* is extended west to Papua New Guinea, Raja Ampat Islands, Bali, Sumatra, and the island of Phuket, Thailand in the Andaman Sea.

Key words: taxonomy, Pempheridae, Red Sea, sweeper, new species, subspecies, coral reef fishes, biogeography

*Addendum: Dr. Mooi's authorship does not signify his endorsement of the decision to apply subspecies status in this study.

Introduction

The fishes of the family Pempheridae, popularly called sweepers, consist of two genera, *Parapriacanthus* Steindachner, with two Indo-Pacific species, and *Pempheris* Cuvier, with two Atlantic species and 26 currently recognized Indo-Pacific species. *Pempheris* is unique in body shape, compressed and deepest at the origin of the dorsal fin, then strongly tapering posteriorly, mainly on the ventral side, to the narrow caudal peduncle; the dorsal fin is short-based near the middle of the standard length, in contrast to the very long-based anal fin. The eyes are very large, the snout very short, the mouth strongly oblique, and the teeth extremely small. The scales are thin, cycloid to weakly ctenoid, and in two layers, the inner small, the outer much larger; the lateral line is in the inner layer but not completely covered by the outer scales. The dominant coloration is copper, bronze, or silver; most species have a large black spot distally on the dorsal fin. These fishes typically form aggregations in caves or beneath ledges during the day and emerge at night to feed individually on zooplankton.

The classification of the fishes of the genus *Pempheris* has been confused since the first species was named *P. mangula* by Cuvier (1829: 195) in a footnote referring to a fish from the east coast of India with a common name of Mangula Kutti that was inadequately described by Russell (1803: 10, pl. 114). Russell's drawing is reproduced here as Fig. 1. No specimen was saved.

Cuvier in Cuvier and Valenciennes (1831) provided a brief description of *Pempheris mangula* (still with no specimen) and named seven other new species of the genus. One of these, *P. vanicolensis*, was described from specimens collected at Vanikoro Island in the Santa Cruz Islands of the western Pacific. It is represented by four syntypes at the Muséum national d'Histoire naturelle in Paris. The largest and only adult, MNHN A224, 137 mm SL (Fig. 2), here designated the lectotype, has 40 anal rays and about 63 lateral-line scales (many scales missing). It now has no visible black pigment on the margin of the anal fin, whereas the black distal spot on the dorsal fin is still evident.

Rüppell (1836: 36) was the first to report a species of *Pempheris* from the Red Sea. He identified it as *P. mangula* Cuvier, considered *P. nesogallica* Cuvier as a synonym, and questioned the validity of *P. vanicolensis* Cuvier. From his description of the color, including the absence of a black spot at the base of the pectoral fin, and 37 anal soft rays, we conclude that his specimen was *P. rhomboidea* Kossman & Rüber 1877.

Klunzinger (1870: 469) reported *Pempheris mangula* Cuvier from the Red Sea. Kossman and Rüber (1877: 398) recorded *Pempheris otaitensis* Cuvier, a Pacific Ocean species, from the Red Sea, and Dor (1984) included five species of *Pempheris*, among them *P. vanicolensis*, in a checklist of the fishes of the Red Sea, none with a type

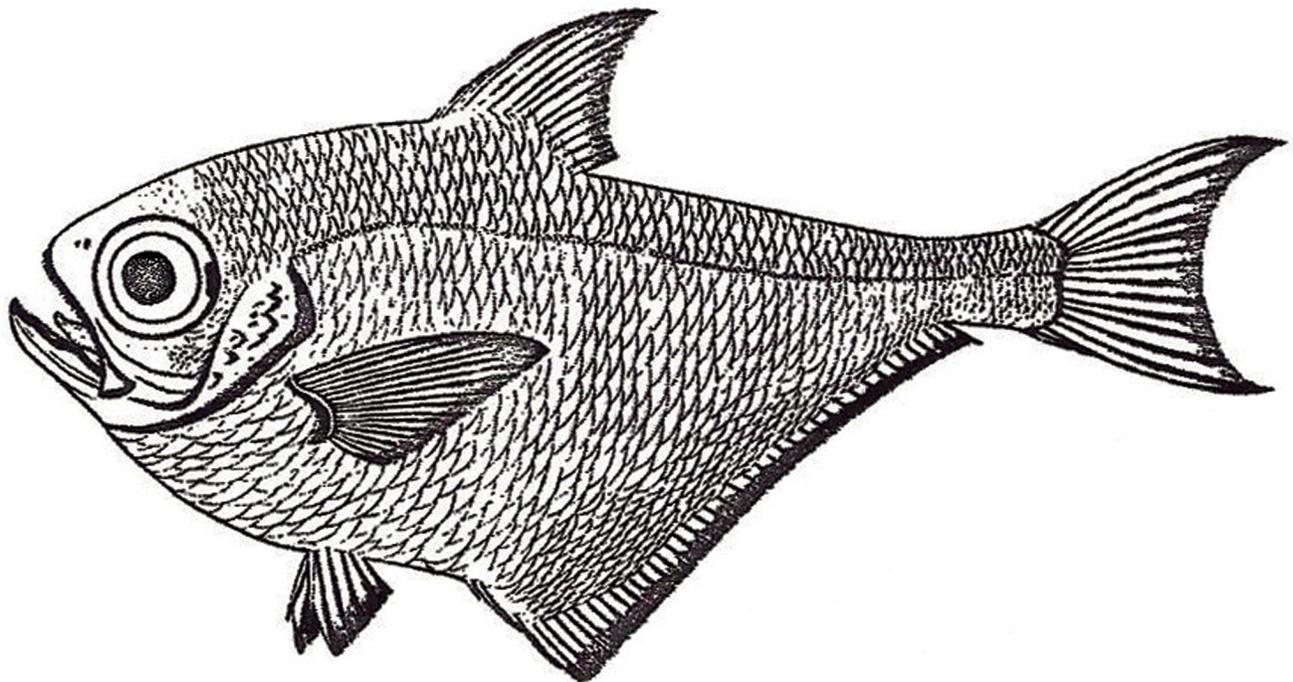


Figure 1. Mangula Kutti (reproduced from Plate 114 of Russell, 1803).



Figure 2. Lectotype of *Pempheris vanicolensis*, MNHN A224, 137 mm, Vanikoro Island, Santa Cruz Islands (R.D. Mooi).

locality in the western Indian Ocean. Allen and Steene (1987: 55, pl. 36, figs. 5 and 6) illustrated what they believed to be *P. vanicolensis* from underwater photos taken in the Red Sea and the Republic of Maldives. Winterbottom *et al.* (1989: 41, fig. 224) reported it from Peros Banhos Atoll, Chagos Archipelago, but their specimen was lost. Randall and Anderson (1993: 29) included *P. vanicolensis* in a checklist of fishes of the Maldives, citing two lots of specimens by Bishop Museum number. Field and Field (1998: 138) illustrated it from an underwater photo taken in the Red Sea. Lieske and Myers (2004: 124) also reported *P. vanicolensis* from the Red Sea, but used an underwater photo from off Kenya. None of these records are correctly identified.

We have concluded that the specimens from the Red Sea, other western Indian Ocean localities, and the Andaman Sea identified as *Pempheris vanicolensis* are instead a new species that is described in the present paper as two new subspecies, one from the Red Sea and Djibouti, and the other wide-ranging from insular localities in the Indian Ocean.

Materials and Methods

Specimens of the genus *Pempheris* for this study have been obtained from, examined at, or deposited in the Bishop Museum, Honolulu (BPBM); California Academy of Sciences, San Francisco (CAS); Central Marine Fisheries Research Institute, Cochin (now Kochi), India (CMFRI); King Abdulaziz University Marine Museum, Jeddah (KAUMM); Muséum national d'Histoire naturelle, Paris (MNHN); Northern Territory Museum, Darwin (NTM); Phuket Marine Biological Center, Phuket, Thailand (PMBC); South African Institute for Aquatic Biodiversity, Grahamstown, South Africa (SAIAB); Senckenberg Museum, Frankfurt (SMF), United States National Museum of Natural History, Washington, D.C. (USNM), and the Zoological Survey of India, Calicut (now Kozhikod), India (ZSI/CLT).

Data in parentheses in the description 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 base of the dorsal fin; body width is measured just posterior to the opercular flap; orbit diameter is the horizontal bony diameter, and interorbital width the least bony width; caudal-peduncle depth is the least depth, and caudal-peduncle length the horizontal distance between verticals at the rear base of the anal fin and base of caudal fin; lengths of spines and rays of median fins are measured to their extreme bases; caudal fin length is measured horizontally from the base to a perpendicular at the end of the longest ray; pectoral-fin length is the length of the longest ray; pelvic-fin length is measured from the base of the pelvic spine to the tip of the longest ray.

Counts of pectoral-fin rays contain the rudimentary upper ray. Lateral-line scale counts are made to the base of the caudal fin (hence do not include one or two pored scales on the base of the fin). Gill-raker counts include rudiments; only the total count is recorded. Proportional measurements are rounded to the nearest .05.

Tissue samples of specimens of *Pempheris* (see Appendix) stored in 96% ethanol were used for extraction of DNA and amplification of a partial sequence of the mitochondrial cytochrome-c-oxidase I (COI) gene for phylogenetic inference. Two sets of universal oligonucleotide primers were used in PCR amplification (“COI-3”; Ward *et al.* 2005; Ivanova *et al.* 2007) and sequencing (“M13”; Messing 1983). Forward and reverse strands were assembled and edited in Geneious Pro 5.4.4. An alignment of resultant COI sequences with sequences of *Pempheris* available from GenBank was generated in the same software package using MAFFT v.7017 (Kato & Kuma 2002). A sequence of *Parapriacanthus ransonneti* Steindachner 1870 was included in the alignment as outgroup (see Appendix). The most likely model of nucleotide substitution was inferred in Modeltest (Posada & Crandall 1998) according to the Akaike Information Criterion (AIC). A gene tree based on the alignment of partial COI sequences of *Pempheris* was then inferred by maximum likelihood (ML) in PhyML (Guindon & Gascuel 2003; Guindon *et al.* 2010). The reliability of tree topology was tested by 100 bootstrap replicates.

***Pempheris flavicycla flavicycla* Randall, Satapoomin & Alpermann, n. subsp.**

Figures 3–6; Tables 1, 3–6.

Pempheris oualensis [*non* Cuvier] Jones & Kumaran 1980: 356, fig. 303 (Lakshadweep); Debelius 1999: 154, middle fig. (Seychelles).

Pempheris vanicolensis [*non* Cuvier] Allen & Steene 1987: 55, pl. 36, no. 6 (Mahé, Seychelles); Winterbottom *et al.* 1989: 41, fig. 224 (Chagos Archipelago; illustrated specimen lost); Randall & Anderson 1993: 29 (Republic of Maldives); Kuitert 1998: 119, upper figs. (Republic of Maldives); Lieske & Myers 2004: 124, middle fig. (Kenya); Imamura in Kimura *et al.* 2009: 177, middle fig. (Andaman Sea); Taquet & Diringer 2012: 133, middle fig. (western Indian Ocean).



Figure 3. *Pempheris flavicycla flavicycla*, holotype, BPBM 17633, female, 138 mm, Mafia Island, Tanzania (J.E. Randall).



Figure 4. *Pempheris flavicycla flavicycla*, North Malé Atoll, Republic of Maldives (J.E. Randall).

Holotype. BPBM 17633, female, 138 mm, Tanzania, Mafia Island, Chole Island, Chole Bay, rocky islet, 0–2 m, rotenone, J.E. Randall, L.G. Westfeldt, and A. Klosser, 11 Dec. 1978.

Paratypes. ZSI/CLT 2465, 120 mm, Sri Lanka, Trincomalee, Dutch Point, large boulder bottom, 5 m, spear, J.E. Randall, April 2, 1975; USNM 410717, 2: 111–120 mm, same data as holotype; BPBM 27210, 2: 106–134 mm, Republic of Maldives, North Malé Atoll, Villingili Island, N side off dock, rock wall, 1–2 m, spear, J.E. Randall, March 8, 1979; SAIAB 189345, 129 mm; North Malé Atoll, Villingili Island, off dock, 2–3 m, spear and quinaldine, J.E. Randall, March 15, 1988; BPBM 36372, 7: 31–130 mm, Arabian Sea, Oman, Raha Bay, W side, rocky point, 16°57'N, 54°49'12"E, tide pools at low tide, 0–2 m, rotenone, J.E. Randall, J.P. Hoover, and I. McLeish, Feb. 8, 1993; SAIAB 77856, 125 mm, Seychelles, Conception, 4.659°S, 55.360°E, coral and sand, 14 m, ichthyocide, P.C. and E. Heemstra, M. Smale, K. Moots, M. Mwale, and A. Bentley, April 23, 2005; SAIAB 77805, 5: 107–130 mm, Seychelles, Mahé, Baie Ternay, 4°38.38'S, 55°22.10'E, coral and sand, 6 m, ichthyocide, P.C. and E. Heemstra, M. Smale, M. Mwale, K. Moots, and A. Bentley, April 25, 2005; SAIAB 187538, 2: 115–118 mm, Republic of the Maldives, Kaafu Atoll, rocky wall of pool opposite power station, 4°10.180'N, 73°30.800'E, O. Gon and G. Gouws, rotenone, Dec. 6, 2010.

Diagnosis. Dorsal rays VI,9, occasionally 10; anal rays III,38–43; pectoral rays 16–18; lateral-line scales 54–61; scales above lateral line to origin of dorsal fin 4; gill rakers 29–33; outer part of paired patch of small teeth anteriorly in lower jaw and narrow band of small teeth of upper jaw exposed when mouth fully closed; body depth 2.35–2.55 in SL; head length 3.35–3.55 in SL; eye small for the genus, 7.9–8.6 in SL; pectoral-fin length 3.55–3.8 in SL; bronze to copper in life, suffused with yellowish green dorsally on head and body; lateral-line scales often with a white dash, one per scale, especially anteriorly; dorsal fin with a large apical black spot (unusual in holotype extending progressively narrower down posterior margin), often with a blackish anterior margin; anal fin whitish with a broad black border, about half the fin-ray length anteriorly, progressively much narrower posteriorly; caudal fin usually with a broad blackish posterior margin, the upper and lower margins often narrowly blackish as well; an elliptical black spot of variable size at base of pectoral fin; iris black with a bright yellow inner ring; color of holotype in alcohol: scales of body below lateral line brassy with a broad dark brown outer border (most specimens more uniform brown); body above lateral line and head darker brown; fins yellowish, the margins broadly blackish; eye with a dull yellow ring around pupil. Largest specimen, the holotype, 138 mm SL.

Description. Dorsal rays VI,9, occasionally 10, the spines slender, the rays branched; anal rays III,38–43, spines stout, rays slender; pectoral rays 16–18, the first rudimentary, the second unbranched, remaining rays

branched; principal caudal rays 17, the median 15 branched; upper procurrent caudal rays 5, the most posterior segmented; lower procurrent caudal rays 3; lateral-line scales 54–61 to base of caudal fin, continuing to end of fin; gill rakers 29–33; branchiostegal rays 7; vertebrae 25.

Body moderately deep, the depth 2.4 (2.35–2.55) in SL, and compressed, the width 2.8 (2.8–3.0) in body depth; head length 3.4 (3.35–3.55) in SL; dorsal profile of head smoothly convex; snout short, 4.75 (4.35–4.65) in head length; eye small for the genus, 8.55 (7.9–8.6) in SL; interorbital slightly convex, the width 3.5 (3.2–3.65) in head length; caudal-peduncle depth 3.35 (3.3–3.65) in head length; caudal-peduncle length 3.75 (3.4–3.85) in head length.

Mouth strongly oblique, forming an angle of about 60° to horizontal axis of head and body, the slender lower jaw slightly protruding when mouth fully closed; maxilla slender anteriorly, expanding posteriorly to a width

TABLE 1

Proportional measurements of type specimens of *Pempheris flavicycla flavicycla* as percentages of the standard length

	holotype		paratypes				
	BPBM 17633	USNM 410717	SAIAB 187538	SAIAB 187538	SAIAB 189345	BPBM 36372	BPBM 27210
Sex	female	female	male	female	female	male	male
Standard length (mm)	138	111	115	118	129	130	134
Body depth	42.0	41.2	41.5	42.5	41.3	40.3	42.4
Body width	14.6	14.9	14.8	13.5	14.3	13.7	14.2
Head length	29.6	29.5	28.2	28.3	29.3	29.0	29.7
Snout length	6.2	6.5	6.5	6.5	6.3	6.6	6.4
Orbit diameter	11.7	12.7	12.4	12.4	12.2	11.6	12.3
Interorbital width	8.4	8.1	8.4	8.8	8.2	8.9	9.0
Caudal-peduncle depth	8.8	8.1	8.7	8.6	8.5	8.8	8.9
Caudal-peduncle length	7.9	7.8	8.4	8.3	7.8	7.5	8.2
Predorsal length	38.5	38.1	38.2	38.3	38.2	38.6	39.1
Preanal length	52.2	53.0	52.4	53.8	51.8	50.4	51.5
Prepelvic length	36.8	37.5	36.8	37.8	36.4	35.0	36.5
Base of dorsal fin	17.5	16.8	16.6	16.5	17.7	16.5	17.4
First dorsal spine	5.6	6.3	6.1	5.8	6.5	5.6	7.4
Fifth dorsal spine	28.1	28.2	22.5	broken	21.8	18.5	20.8
Longest dorsal ray	26.2	27.3	26.6	26.5	26.0	25.7	25.4
Base of anal fin	55.8	55.0	53.8	54.7	54.5	51.2	54.0
First anal spine	5.7	5.5	5.5	5.6	5.4	5.0	5.4
Third anal spine	12.8	11.8	13.4	12.3	13.4	broken	broken
Longest anal ray	18.1	18.5	17.0	18.8	broken	15.2	19.0
Caudal-fin length	24.3	broken	24.8	25.5	23.0	broken	broken
Pectoral-fin length	27.8	27.8	26.9	28.2	27.1	26.4	26.5
Pelvic-spine length	13.3	13.9	13.1	14.4	14.1	14.3	13.9
Pelvic-fin length	17.8	17.6	18.0	18.3	17.1	17.6	17.1

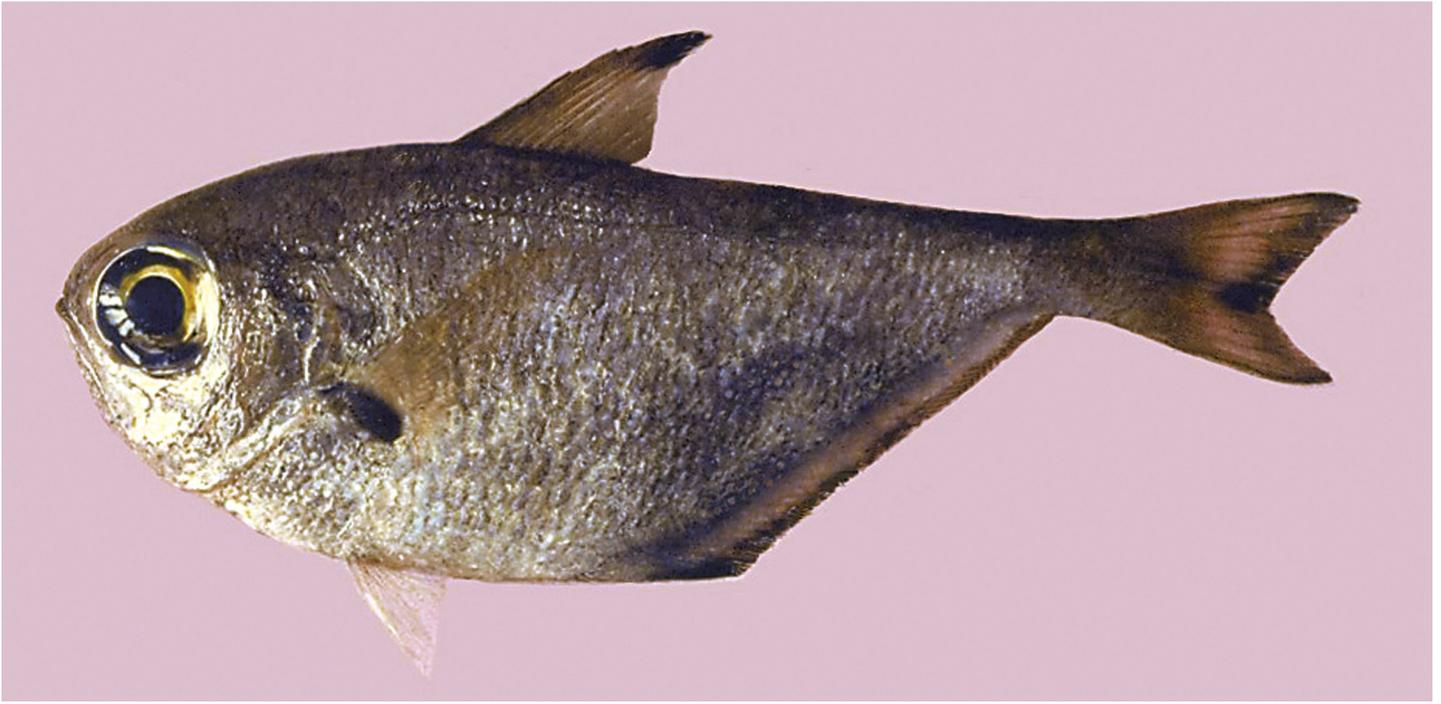


Figure 5. *Pempheris flavicycla flavicycla*, Andaman Islands (P.T. Rajan).

two-thirds to three-fourths pupil diameter, usually reaching to below center of eye, the posterior margin nearly straight, the lower corner broadly round, the upper corner slightly rounded; lower jaw expanding to a slight knob at symphysis; very small, sharp, incurved teeth in two irregular rows anteriorly in upper jaw, narrowing to a single row posteriorly; teeth on each side of nodular symphysis of lower jaw in a patch with at most six irregular rows of small teeth, the outer one or two rows sharply nodular, the inner three or four rows strongly recurved and narrowly sharp; teeth to side of lower jaw narrowing to two rows, ending as a single row; about half of teeth of tooth patches



Figure 6. *Pempheris flavicycla flavicycla*, Rok Island, Krabi, Thailand (U. Satapoomin).

at front of lower jaw and all of teeth of upper jaw exposed when mouth fully closed; vomer with an expanded V-shaped patch of very small nodular teeth in three to four irregular rows; palatines with a long narrow patch of very small nodular teeth in three to four irregular rows anteriorly, narrowing to one or two rows posteriorly; tongue narrowly triangular, the upper surface with small rounded papillae; gill rakers long, the longest twice as long as longest gill filaments.

Gill opening extending dorsally to level of upper edge of orbit, and anteriorly to below anterior edge of orbit. Operculum ending posteriorly in a fleshy obtuse angle; margin of preopercle mostly scaled over, free at broadly rounded corner, with a flat, acutely triangular spine about one-third maximum width of maxilla, separated by a U-shaped notch from a flat, irregular, sharp ridge to ventroanterior end of margin. A slight ridge midventrally on anterior two-thirds of chest.

Anterior and posterior nostrils in front of dorsal edge of pupil, one-third distance to front of snout, the apertures vertically oval, equal in length or the posterior larger, and separated by a narrow septum; anterior nostril with a membranous flap on posterior edge that covers aperture of anterior nostril when folded forward, but not posterior nostril when laid back.

Scales thin, deciduous, and cycloid, except finely ctenoid dorsally on body posterior to dorsal fin and above lateral line; ctenoid scales extend below lateral line on caudal peduncle; scales also ctenoid on chest, strongest ventrally.

Origin of dorsal fin in vertical alignment with rear base of pectoral fin, the predorsal length 2.6 (2.55–2.6) in SL; first dorsal spine short, 5.3 (4.0–5.2) in head length; fifth dorsal spine longest, and variable in length (even when intact) (3.55–5.4) in SL; first or second dorsal soft rays longest, 3.8 (3.65–4.7) in SL; origin of anal fin below middle of dorsal fin, the preanal length 1.9 (1.85–1.95) in SL; first anal spine 5.2 (5.1–5.5) in head length; third anal spine 2.3 (2.2–2.5) in head length; longest anal soft ray 1.65 (1.5–1.9) in head length; caudal-fin length 5.7 (4.6–5.6) in SL; caudal concavity (measured from photographs) 2.6 (2.2–2.4) in orbit diameter; second or third branched pectoral ray usually longest, 3.6 (3.55–3.8) in SL; origin of pelvic fins below middle of base of pectoral fins, the prepelvic length 2.7 (2.65–2.85) in SL; pelvic spine 2.2 (2.1–2.3) in head length; pelvic-fin length 1.65 (1.55–1.75) in head length.

Color of holotype in alcohol bronze overall, remarkably similar to color in life, only lacking the suffusion of green dorsally on head and body; black markings on fins as in life, only more subdued.

Color when fresh as in Figure 3; color in life as in Figures 4 and 6.

Etymology. The name *flavicycla* is from the Latin *flavi* meaning yellow, and *cycla* for ring, in reference to the bright yellow ring encircling the pupil, a color feature often still apparent in recently preserved specimens.

Distribution and Ecology. *Pempheris flavicycla flavicycla* is presently known from Oman, Kenya, Tanzania, Seychelles, Chagos Archipelago, Republic of Maldives, Lakshadweep, Sri Lanka, Andaman Islands (Figure 5 is a photograph of a specimen provided by P.T. Rajan), and Phuket and Rok Island, Thailand, judging from the underwater photograph taken by the fourth author (middle figure on p. 177 of Imamura in Kimura *et al.*, 2009) and a recent photo by him (Fig. 6). However, the caudal fin has no dark margins in both of these photos. Although there is much variation in the dark margins on the caudal fin, both in width and density of pigmentation, the Phuket record should be confirmed by the collection of specimen(s).

The only two records of this species from the east coast of Africa are from islands off the coast, Mafia Island for Tanzania, and Kisiti National Marine Park near Wasini Island, Kenya (record based on underwater photograph taken by Robert F. Myers, published in Lieske and Myers (2004: 124, middle fig.).

Also, we know of no records of *Pempheris flavicycla flavicycla* for the continental coast of India. The only Indian records are from islands with well-developed coral reefs, i.e. the atolls of Lakshadweep and the Andaman Islands.

Although *Pempheris flavicycla flavicycla* may shelter in aggregations in caves or beneath ledges by day, it also may swim in small groups in the open, though close to the shelter of coral reef. All of the type specimens of this study have been collected from less than 11 m, the holotype in less than 2 m.

Remarks. Jones and Kumaran (1980: 356, fig. 303) illustrated a specimen of *Pempheris flavicycla flavicycla* deposited in the Central Marine Fisheries Research Institute (CMFRI, 92/249, 108 mm) from the Laccadive Islands (now Lakshadweep) identified as *Pempheris oualensis* Cuvier in C. & V., type locality Oualan Island in

the Caroline Islands. Their specimen has 42 anal soft rays, 58 lateral-line scales, and 32 gill rakers. The holotype of *P. oualensis* (MNHN A 221, 182 mm SL) has 42 anal soft rays and a black margin on the anal fin, characters shared with *P. flavicycla flavicycla*, but it has 68 lateral-line scales and 28 gill rakers, too different from the respective counts of *P. flavicycla flavicycla*. To our knowledge, *P. oualensis*, wide-ranging in the central and western Pacific, is not yet known from the Indian Ocean. The Lakshadweep specimen is not designated as a paratype of *P. flavicycla flavicycla* because of its poor condition.

Kossman and Räuber (1877: 398) reported *Pempheris otaitensis* Cuvier, type locality Tahiti, from the Red Sea, also similar in color to *P. vanicolensis*. It is known only from islands of the Pacific, and it is even more finely scaled than *P. oualensis* (lateral-line scales 67–79, compared to 62–69 for *P. oualensis*).

***Pempheris flavicycla marisrubri* Randall, Bogorodsky & Alpermann, n. subsp.**

Figures 7–9; Tables 2, 3–6.

Pempheris mangula [non Cuvier] Klunzinger 1870: 469 (Quseir, Red Sea); Klunzinger 1884: 81 (Red Sea); Dor 1984: 165 (Red Sea).

Pempheris otaitensis [non Cuvier] Kossman & Räuber, 1877: 398 (Red Sea).

Pempheris oualensis [non Cuvier] Tortonese 1983: 107 (Jeddah); Dor 1984: 166 (Red Sea); Goren & Dor 1994: 46 (Red Sea).

Pempheris vanicolensis [non Cuvier] Lieske & Myers 2004: 124 (Red Sea); Field & Field 1998: 138 (Red Sea).

Holotype. SMF 33630, 104 mm, Red Sea, Saudi Arabia, Rabigh (22°42'35"N, 39°1'19"E), 30 km N, isolated rock, 10–12 m, rotenone, S.V. Bogorodsky, April 7, 2011.

Paratypes. USNM 402218, 4: 117–130 mm, Red Sea, Gulf of Aqaba, Egypt, just N of Ras Burqa, reef in 0–11 m, rotenone, V.G. Springer, G. Raz, A. Amir, H. Harpaz, and I. Hoselka, July 23, 1969; USNM 402211, 104 mm, Red Sea, Strait of Jubal, southern end of Sinai Peninsula, Ras Muhammed, sand and rock, 0–9 m, rotenone, V.G. Springer, L. Hughes-Gannes, A. Levy, H. Harpaz, and P. Raber, Sept. 26, 1969; SMF 33624: 75 mm, SMF

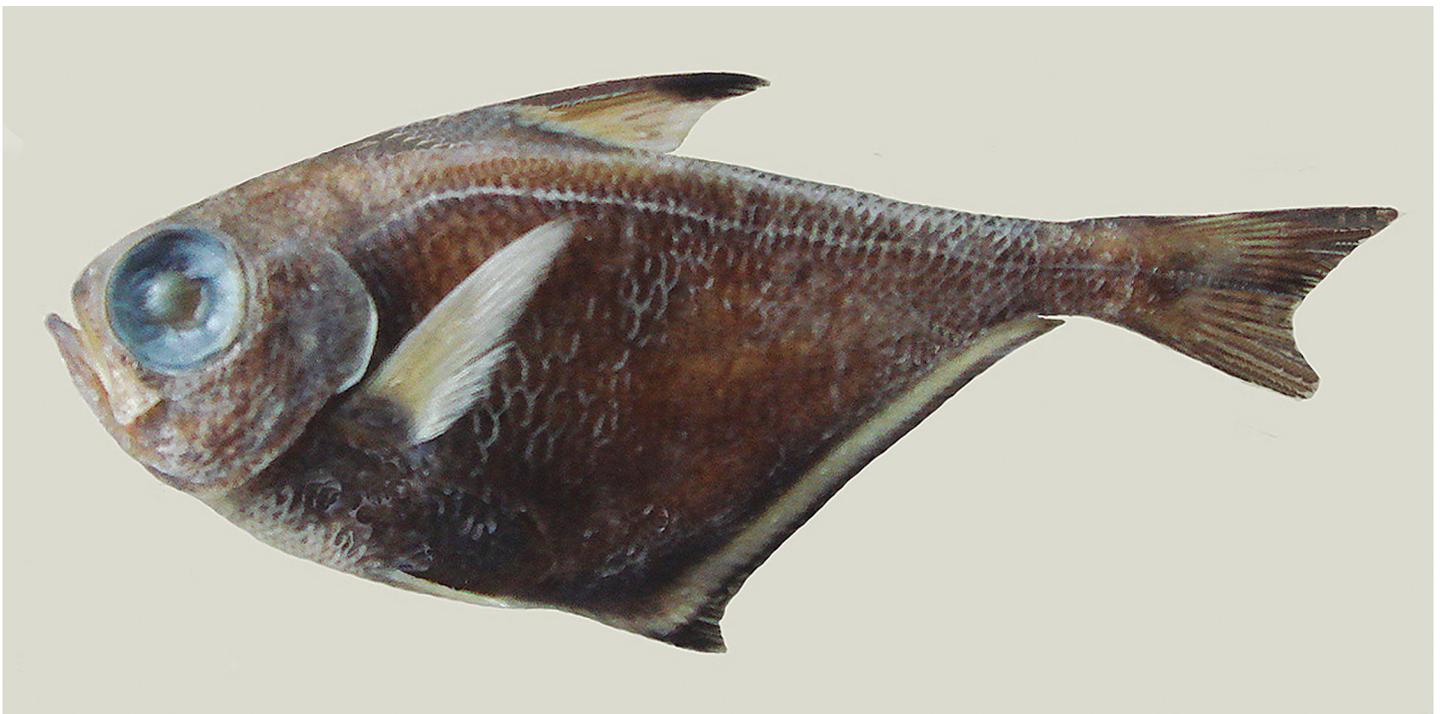


Figure 7. *Pempheris flavicycla marisrubri*, holotype, SMF 33630, female, 104 mm, Rabigh, Saudi Arabia, Red Sea (H.A. Randall).

33625, 80 mm, KAUMM 11, 71 mm, and KAUMM 12, 66 mm, Red Sea, Saudi Arabia, Al Lith, 20°15.111'N, 39°57.825'E, rotenone, S.V. Bogorodsky and T.J. Alpermann, March 28, 2011; BPBM 41159, 107 mm SL; KAUMM 9, 111 mm SL, and SMF 33631, 116 mm SL, all with same collecting data as holotype; CAS 235013, 121 mm, Gulf of Tadjoura, off Djibouti, sunken buoy, 9 m, spear, L.A. Rocha, B.W. Bowen, and J.D. DiBattista, Sept. 27, 2012; CAS 236380, 119 mm, Red Sea, Saudi Arabia, Abulad Island, 16°47.456'N, 42°11.920'E, reef, 5 m, spear, L.A. Rocha, M. Berumen, and J.D. DiBattista, March 10, 2013; KAUMM 10, 118 mm, Red Sea, Saudi Arabia, Duba, 27°20'44.22"N, 35°41'42.12"E, rotenone, S.V. Bogorodsky, June 21, 2013.

Diagnosis. Dorsal rays VI,9, rarely 10; anal rays III,39–44; pectoral rays 17–19; lateral-line scales 54–59; scales above lateral line to origin of dorsal fin 4; gill rakers 29–33; body depth 2.3–2.5 in SL; head length 3.25–

TABLE 2

Proportional measurements of type specimens of *Pempheris flavicycla marisrubri* as percentages of the standard length

	holotype		paratypes				
	SMF 33630	BPBM 41159	KAUMM 9	SMF 33631	KAUMM 10	USNM 402218	USNM 402218
Sex	female	female	female	male	male	female	male
Standard length (mm)	104	107	111	116	118	122	130
Body depth	43.8	43.8	40.8	40.0	42.8	43.7	40.3
Body width	12.3	13.4	12.1	13.2	15.8	15.4	16.4
Head length	28.2	28.8	28.7	28.1	30.7	28.7	29.9
Snout length	6.9	6.7	7.0	6.8	7.2	6.4	7.0
Orbit diameter	13.7	14.0	13.6	13.3	12.7	12.9	12.4
Interorbital width	8.3	8.0	8.3	8.1	8.9	9.0	8.8
Caudal-peduncle depth	8.8	8.1	7.9	7.8	8.0	9.0	8.4
Caudal-peduncle length	7.9	9.1	9.4	8.6	7.3	8.2	8.1
Predorsal length	38.8	39.0	38.2	38.4	36.9	36.3	37.1
Preanal length	53.2	53.4	50.0	53.5	52.8	49.6	49.4
Prepelvic length	36.8	38.0	36.5	37.0	35.9	36.8	36.2
Base of dorsal fin	17.5	16.8	16.5	17.3	17.4	18.1	17.6
First dorsal spine	6.6	6.8	5.9	6.1	5.3	6.5	5.5
Fifth dorsal spine	22.8	23.2	20.1	21.5	24.8	19.7	19.8
Longest dorsal ray	26.2	27.4	27.1	27.2	26.5	25.0	25.3
Base of anal fin	54.1	52.7	51.2	52.8	54.7	56.5	56.0
First anal spine	4.1	3.9	3.9	4.2	5.2	6.2	4.6
Third anal spine	12.5	11.4	12.3	12.7	10.1	10.1	12.3
Longest anal ray	16.2	17.3	17.4	17.1	16.6	broken	15.2
Caudal-fin length	27.0	24.7	25.8	24.8	broken	23.5	broken
Pectoral-fin length	28.2	29.1	28.9	29.8	broken	31.5	27.8
Pelvic-spine length	13.5	13.0	14.4	13.9	14.3	13.9	13.2
Pelvic-fin length	17.3	17.4	16.6	17.5	15.2	14.7	15.5



Figure 8. *Pempheris flavicycla marisrubri*, Ras Mohammed, Red Sea (S.V. Bogorodsky).

3.55 in SL; dorsal profile of head from above eye to origin of dorsal fin straight; orbit diameter 7.15–8.1 in SL; pectoral-fin length 3.45–3.55 in SL; color in alcohol brown, the scale centers paler than margins; dorsal fin pale yellowish, nearly the outer third black, with a broad, dark brown, anterior margin; anal fin broadly dark brown at base, with a middle pale yellowish band, and an outer black border that is half width of fin anteriorly, soon narrowing posteriorly; caudal fin brown, the outer third black; paired fins pale yellowish, the pectorals with an oval black spot covering most of base. Color in life as in Figures 8 and 9 (very similar to *Pempheris flavicycla flavicycla*). Largest specimen, 130 mm SL.

Description. Dorsal rays VI,9, rarely 10, the spines slender, the rays branched; anal rays III,39–44, spines stout, rays slender; pectoral rays 17–19 (mainly 18, one with 19 on one side), the first rudimentary, the second unbranched, remaining rays branched; principal caudal rays 17, the median 15 branched; upper procurrent caudal rays 5, the most posterior segmented; lower procurrent caudal rays 3; lateral-line scales 55 (54–59) to base of caudal fin, continuing to end of fin; gill rakers 31 (29–33), all with 9 upper-limb rakers; branchiostegal rays 7; vertebrae 25.

Body moderately deep, the depth 2.3 (2.3–2.5) in SL, and compressed, the width 2.8 (2.8–3.0) in body depth; head length 3.55 (3.25–3.55) in SL; dorsal profile of head straight from above eye to origin of dorsal fin; snout short 4.1 (4.1–4.3) in head length; orbit diameter 2.05 (2.05–2.1) in head length; interorbital convex, the width 3.4 (3.35–3.6) in head length; caudal-peduncle depth 3.6 (3.55–3.75) in head length; caudal-peduncle length 3.1 (3.05–3.15) in head length.

Mouth strongly oblique, forming an angle of about 75° to horizontal axis of head and body, the slender lower jaw slightly protruding when mouth fully closed; maxilla slender anteriorly, expanding posteriorly to a width equal to pupil diameter, nearly reaching a vertical through center of eye; posterior margin of maxilla nearly straight, the lower corner slightly rounded, the upper corner sharply angular; lower jaw expanding to a slight knob at symphysis; very small, sharp, incurved teeth in two irregular rows anteriorly in upper jaw, narrowing to a single row posteriorly; teeth on each side of symphysis of lower jaw in a patch with at most six irregular rows of small teeth, the outer one or two rows sharply conical, the inner three or four rows strongly recurved and narrowly sharp; teeth to side of lower jaw narrowing to a single row posteriorly; no teeth of tooth patches of lower jaw visible when jaws firmly closed in specimens less than about 110 mm SL; all of teeth of upper jaw exposed when mouth fully closed; vomer with a broad V-shaped patch of very small nodular teeth in three to four irregular rows;



Figure 9. *Pempheris flavicycla marisrubri*, Gulf of Aqaba, Red Sea (J.L. Rose).

palatines with an elongate patch of very small nodular teeth in three to four irregular rows anteriorly, narrowing to a single row posteriorly; tongue narrowly triangular, the upper surface with very small rounded papillae; gill rakers long, the longest nearly twice length of longest gill filaments.

Gill opening extending dorsally nearly to level of upper edge of orbit, and anteriorly to below anterior edge of orbit. Operculum ending posteriorly in a fleshy obtuse angle; margin of preopercle mostly scaled over, free only a short distance at the broadly rounded corner, with a small, flat, acutely triangular spine, separated by a U-shaped notch from a flat, irregular, sharp ridge to ventroanterior end of margin. A slight ridge present midventrally on anterior three-fourths of chest.

Nostrils small, in front of dorsal edge of pupil, one-third distance to front of snout; nostril apertures vertically oval, the posterior larger, separated by a narrow septum; anterior nostril with a membranous flap that covers aperture when folded forward, but does not encroach on posterior nostril when laid back.

Scales thin, deciduous, and cycloid, except finely ctenoid dorsally on body in six longitudinal rows posterior to dorsal fin (hence two longitudinal rows of scales above lateral line are cycloid); scales also ctenoid on chest, strongest ventrally.

Origin of dorsal fin in vertical alignment with mid-base of pectoral fin, the predorsal length 2.6 in SL; first dorsal spine short, 4.25 (4.6–4.85) in head length; fifth dorsal spine longest, 4.4 (4.25–5.8) in SL; second dorsal soft ray longest, 3.8 (3.65–4.0) in SL; origin of anal fin below middle of dorsal fin, the preanal length 1.9 (1.85–2.0) in SL; first anal spine 6.9 (4.65–7.4) in head length; third anal spine 2.25 (2.2–2.95) in head length; longest anal soft ray 1.75 (1.65–1.95) in head length; caudal fin slightly forked, the fin length 3.7 (3.9–4.25) in head length; second or third branched pectoral ray longest, 3.55 (3.2–3.6) in SL; origin of pelvic fins below mid-base of pectoral fins, the prepelvic length 2.7 (2.65–2.75) in SL; pelvic spine length 2.1 (2.0–2.25) in head length; pelvic-fin length 1.65 (1.6–2.0) in head length.

Color in alcohol dark brown, each scale with vertically elongate pale spot; dorsal fin pale yellowish, nearly the outer third black, with a broad dark brown anterior margin; anal fin dark brown at base, with a middle pale yellowish zone, and an outer black border that is half width of fin anteriorly, soon narrowing posteriorly; caudal fin brown, up to the outer third black or blackish, the upper and lower margins usually narrowly blackish; paired fins pale yellowish, the pectorals with an oval black spot covering most of base.

Color in life as shown in Figures 8 and 9.

Etymology. This subspecies is named *Pempheris flavicycla marisrubri* from the Latin for Red Sea, in reference to its principal distribution.

TABLE 3

Pectoral-fin rays of specimens of *Pempheris flavicycla* and *P. vanicolensis*

	16	17	18	19
<i>Pempheris flavicycla flavicycla</i>	3	24	3	
<i>Pempheris flavicycla marisrubri</i>		7	24	1
<i>Pempheris vanicolensis</i>			30	2

TABLE 4

Anal-fin soft rays of specimens of *Pempheris flavicycla* and *P. vanicolensis*

	38	39	40	41	42	43	44	45	46
<i>Pempheris flavicycla flavicycla</i>	1	2	5	3	2	2			
<i>Pempheris flavicycla marisrubri</i>		1	3	2	4	4	2		
<i>Pempheris vanicolensis</i>			2	6	3	2	1		2

TABLE 5

Total gill-raker counts of specimens of *Pempheris flavicycla* and *P. vanicolensis*

	26	27	28	29	30	31	32	33
<i>Pempheris flavicycla flavicycla</i>				1	2	6	4	2
<i>Pempheris flavicycla marisrubri</i>				2	4	6	2	2
<i>Pempheris vanicolensis</i>	2	2	7	5				

TABLE 6

Total lateral-line scale counts of specimens of *Pempheris flavicycla* and *P. vanicolensis*

	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69
<i>Pempheris flavicycla flavicycla</i>	2	1	2	3	2	1	3	1								
<i>Pempheris flavicycla marisrubri</i>	1	3	2	4	4	2										
<i>Pempheris vanicolensis</i>										3	4	3	3	1	1	1

Distribution and Ecology. *Pempheris flavicycla marisrubri* is represented by specimens in the Red Sea from the northern end of the Gulf of Aqaba to the Abulad Islands off the southern end of Saudi Arabia at 16°48'N. We also have one specimen (CAS 235013) from the Gulf of Tadjoura off the city of Djibouti.

Specimens have been collected from coral reefs at depths of 0–12 m; however, the second author observed this subspecies in 30 m in a cave on a reef north of Dahab, east coast of the Sinai Peninsula. This subspecies forms aggregations in caves or crevices in reefs by day, but a few may at times be seen in the open, close to the shelter of reefs. As is known for species of the genus, the fish emerge at night to feed on zooplankton. The second author observed this from the light of the KAU marine station at Sharm Obhur, north of Jeddah. The fish were in small groups in the company of *Myripristis murdjan*, 0.5–1 m below the surface.

Remarks. The four type specimens of *Pempheris flavicycla marisrubri* collected by the second author from near Rabigh, Saudi Arabia proved to be fully mature adults (three females and one male) and unexpectedly small compared to mature fish from other populations. In addition, they have a straighter dorsal profile of the head. This led the first author to suspect these fish might represent an additional undescribed small species until a genetic comparison made by the third author failed to show any sequence difference from other Red Sea populations. Golani and Diamant (1991) reported *Pempheris vanicolensis* as a Lessepsian migrant to the eastern Mediterranean Sea; however, their species is *P. rhomboidea* Kossman & Rüber, type locality Red Sea. We have learned that Azzurro *et al.* (MS) have also made the same correction (Giacomo Bernardi, pers. comm.).

Comparisons. Because we found a modal difference of one in the count of pectoral rays between the Red Sea population of *Pempheris flavicycla* and that of the western Indian Ocean (Table 3), we tried to find other differences. We do not see any obvious difference in color pattern and nothing clearly different in other meristic data of the two populations. However, a comparison of the proportional measurements (Tables 1 and 2) reveals the Red Sea population as having a larger eye and longer pectoral fins. Two other morphological differences were noted. The posterior nostril of fish of the Red Sea population is larger than the anterior nostril; in the Indian Ocean population the anterior nostril is larger or equal in length to the posterior. In addition, the scales are ctenoid on Red Sea fish in six median dorsal, longitudinal rows on the body posterior to the dorsal fin, whereas they are ctenoid on all ten longitudinal rows down to the lateral line on Indian Ocean fish, as well as below the lateral line on the caudal peduncle (scales ctenoid on chest in both species). Our one specimen from the Gulf of Tadjoura off Djibouti (CAS 235013) has the characters of the Red Sea population, whereas our one adult specimen from the south shore of Oman (BPBM 36372) shares the characters of western Indian Ocean *P. flavicycla*.

As may be seen in the synonymy above, both subspecies of *Pempheris flavicycla* have most often been identified as *P. vanicolensis* Cuvier in C. & V., type locality Santa Cruz Islands, which lie about 350 km east of the Solomon Islands that link directly through New Britain and New Guinea to the rest of the East Indies.

The lectotype of *Pempheris vanicolensis* (MNHN A224: 137 mm SL; Fig. 2) was examined by the first and fifth authors. It shares many morphological characters with *P. flavicycla*, such as III,40 anal rays, 57 lateral-line scales, body depth 2.45 in SL, head length 3.3 in SL, and eye diameter 8.2 in SL, as well as some features of color, notably the black margin on the anal fin (this was noted by Cuvier, but is not visible now on the holotype and only faintly on one syntype). However, there are differences in the number of pectoral rays and gill rakers, although not in the number of anal rays (Tables 3–5). *P. vanicolensis* lacks the yellow ring around the pupil of the eye and the black spot at the base of the pectoral fins, as seen in *P. flavicycla*. Also, the black margin on the anal fin becomes more narrow posteriorly on *P. vanicolensis* and may even disappear on the last few rays.

The first author collected three specimens of *Pempheris* from Bali, (BPBM 32253, 113 mm SL, and BPBM 40641, 2: 134–145 mm) and one from Pulau Ular, off Padang, Sumatra (BPBM 39592, 120 mm) that were first misidentified as *P. oualensis* Cuvier in C. & V., but now correctly labeled *P. vanicolensis*. Lateral-line scale counts provide complete separation, 54–61 for *P. flavicycla* and 63–69 for *P. vanicolensis* (Table 6). No photographs were taken of these specimens when collected, but we provide here, as Figure 10, a photograph of the smaller of the two preserved specimens from Bali. We also identify the first author's underwater photos of Figure 11 taken at Sumatra, and Figure 12 from Bali, as *P. vanicolensis*. Dennis Polack provided underwater photographs of *P. vanicolensis* taken at Sulawesi (Figure 13) and the Raja Ampat Islands off the western end of New Guinea (Figure 14), where Mark V. Erdmann (pers. comm.) reports it as the most common species of the genus. We also identified a specimen from the western Pacific collected near Madang, Papua New Guinea (NTM S.13685-014, 131 mm) as *P. vanicolensis*.



Figure 10. *Pempheris vanicolensis*, BPBM 40641, 134 mm, Bali (S. O'Hara).

Pempheris flavicycla flavicycla and *P. vanicolensis* appear to occur together in the Andaman Sea, as may be seen in the review of the pempherid fishes of the Andaman Sea and west coast of southern Thailand by Imamura in Kimura *et al.* (2009: 177). We identify the middle figure as *P. flavicycla*, and the one at the lower right as *P. vanicolensis* (both taken by the fourth author). This would be the most western locality reported for *P. vanicolensis*, and the most eastern for *P. flavicycla*.

To confirm the identification of *P. vanicolensis* at Phuket, the fourth author collected four specimens for deposit at the Bishop Museum as BPBM 41166 (his photograph of one is illustrated here as fig. 15), and two for the Phuket Marine Biological Station as PMBC 21606. Allen and Erdmann (2012: 513, middle figure) illustrate a *P. vanicolensis* from Phuket.

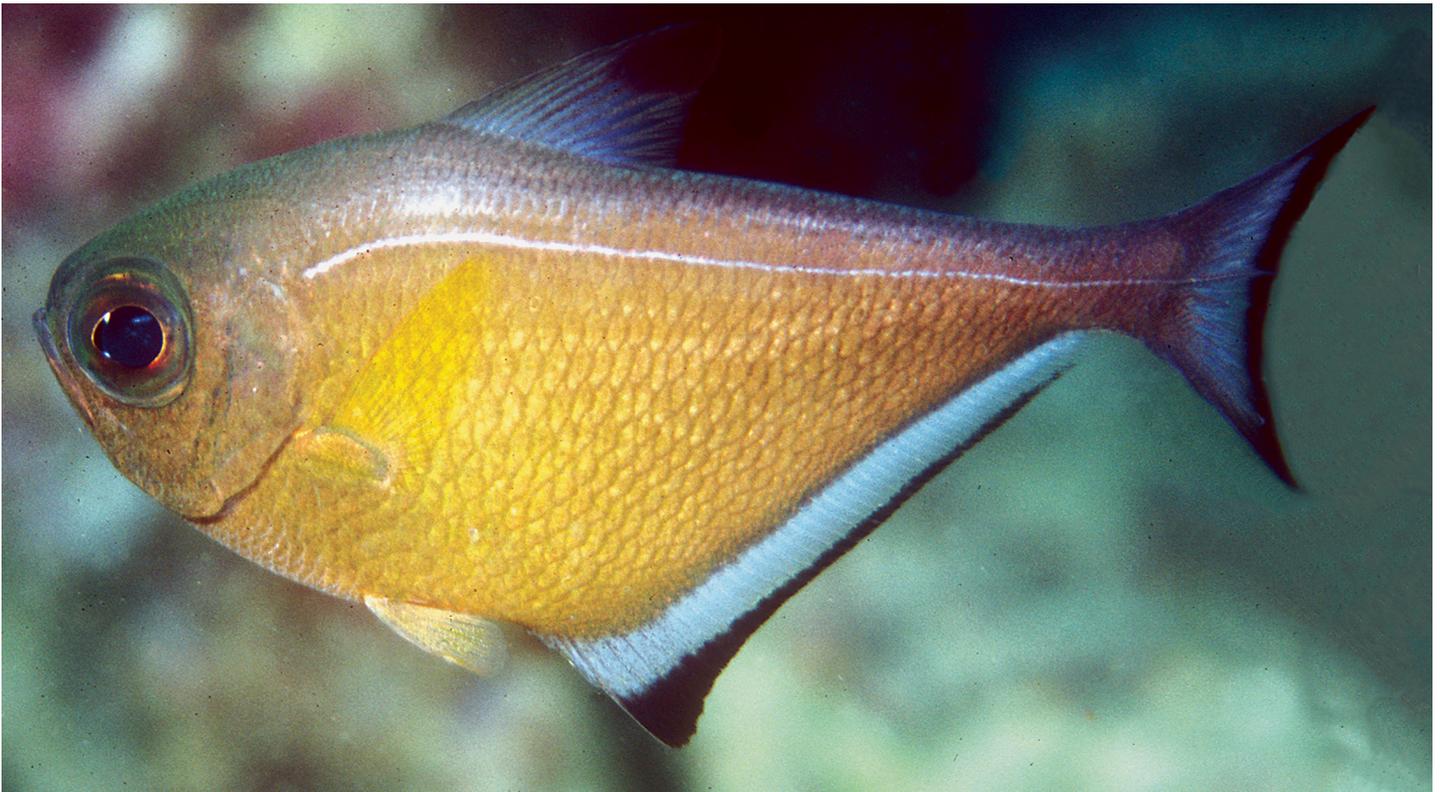


Figure 11. *Pempheris vanicolensis*, off Padang, Sumatra (J.E. Randall).



Figure 12. *Pempheris vanicolensis*, Bali (J.E. Randall).



Figure 13. *Pempheris vanicolensis*, northern Sulawesi (D. Polack).



Figure 14. *Pempheris vanicolensis*, Indonesia, Raja Ampat Islands (D. Polack).

Phylogenetic analysis. The maximum-likelihood phylogenetic analysis conducted herein shows that specimens of *Pempheris flavicycla* n. sp. form a well-supported monophyletic clade, clearly divergent from its closest relative, *P. vanicolensis* (Fig. 16). Within this clade, specimens of *P. flavicycla marisrubri* n. subsp. from the Red Sea form a moderately supported monophyletic subclade, as do the two specimens from the Maldives. The existence of these subclades is interpreted as evidence of evolutionary divergence of geographically isolated populations of *P. flavicycla* n. sp. In view of the morphological differentiation of specimens of *P. flavicycla* n. sp. from the Indian Ocean and Red Sea (including the Gulf of Tadjoura at the western Gulf of Aden), we take the results of the genetic analysis as supportive for the designation of the two subspecies *P. flavicycla flavicycla* and *P. flavicycla marisrubri*. The apparent paraphyly of *P. flavicycla flavicycla* in the COI tree may be resolved in a phylogenetic species tree using multiple nuclear genes. The slight genetic divergence of the Red Sea subspecies



Figure 15. *Pempheris vanicolensis*, BPBM 41166, 111 mm, Phuket, Thailand (U. Satapoomin).

from *P. flavicycla flavicycla* suggests comparatively recent evolutionary separation of the two subspecies. Divergence of the two subspecies may have started not earlier than the end of the last glacial period, as discussed by Klausewitz (1989, and references therein) for pairs of Indian Ocean and Red Sea subspecies. The clade formed by the new species *P. flavicycla* is sister to a clade composed of specimens identified in the present study as *P. vanicolensis* Cuvier that were collected at Phuket, Thailand. Similar specimens fitting the description of *P. vanicolensis* have been collected in Sumatra, Bali, Vanikoro, and Madang, Papua New Guinea and photographed in Sumatra, Bali, Sulawesi, and the Raja Ampat Islands. Interestingly, another rather unrelated monophyletic clade also exclusively contains specimens identified as *P. vanicolensis* that have been collected at Antananarivo, Madagascar (see Appendix). We assume that to be a misidentification of another – presumably undescribed – species of *Pempheris*. Similarly, three distinct clades have been identified as *Pempheris adusta* Bleeker 1877 (type locality, Ambon, Indonesia; holotype illustrated here as Fig. 17) and *Pempheris schwenkii* Bleeker 1855. We expect that each major clade in the tree represents a distinct species of *Pempheris* that can be distinguished by morphology and/or coloration. Specimens in these clades need to be re-examined and identified based on their morphology in order to resolve the taxonomy of the genus *Pempheris*. We believe that *Pempheris schwenkii* Bleeker will prove to be a complex of closely related species or subspecies. *Pempheris mangula* Cuvier, known at present only from the continental eastern and southwest coasts of India that lack well-developed coral reefs, should not be expected at any tropical to subtropical island in the western Indian Ocean, such as the one specimen from Madagascar that forms part of a clade otherwise composed of specimens identified as *P. adusta* Bleeker. To our knowledge, *Pempheris oualensis* remains unknown for any Indian Ocean locality, so material from Réunion identified as this species needs to be re-examined.

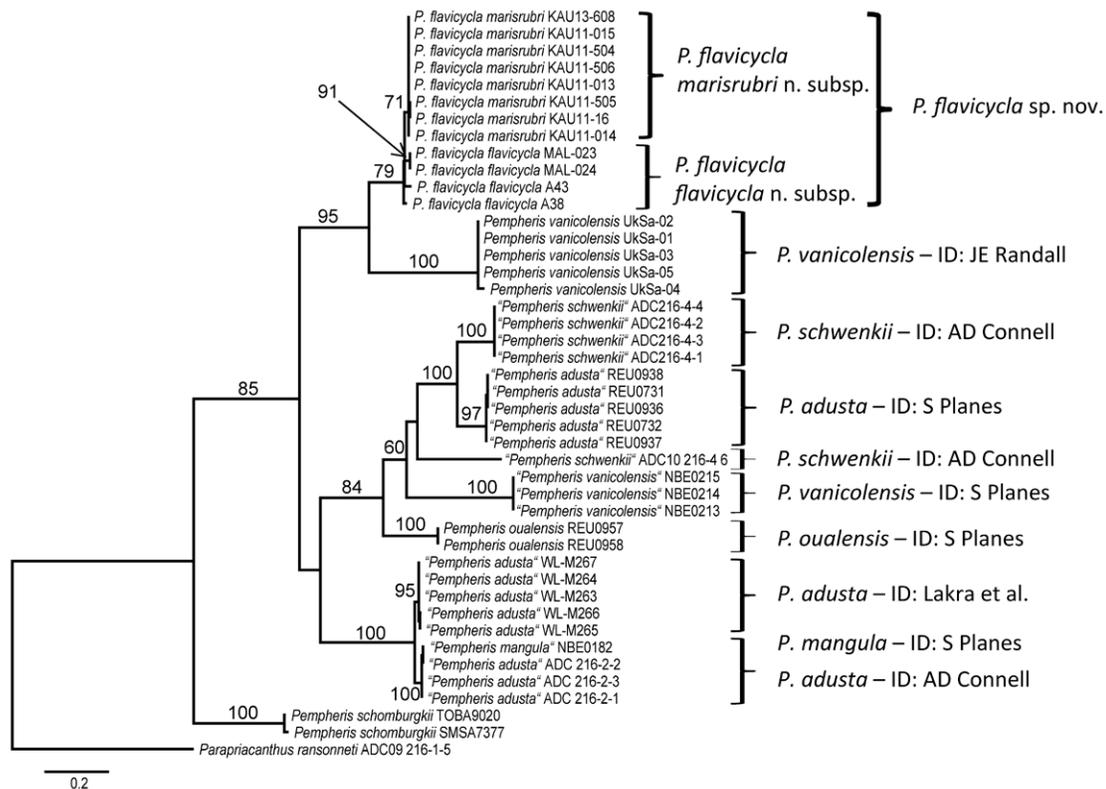


Figure 16. Gene tree as obtained from maximum likelihood analysis of an alignment of partial (652 bp) COI sequences. The tree was derived using a GTR+ Γ +I model of nucleotide substitution as selected by Modeltest according to AIC scores with a proportion of invariant sites of 0.612 and $\alpha = 2.167$ as the shape parameter of the gamma distribution (four rate categories). Base frequencies were estimated as A = 0.22258, C = 0.29628, G = 0.18988, T = 0.29126 and nucleotide substitution ratios were estimated relative against G \leftrightarrow T (= 1.0000) as A \leftrightarrow C = 0.79383, A \leftrightarrow G = 8.54713, A \leftrightarrow T = 1.43056, C \leftrightarrow G = 0.36146 and C \leftrightarrow T = 5.21732. Branch support values from 100 bootstrap replicates are depicted if >50%. Associated data for the sequences are listed in the Appendix.



Figure 17. *Pempheris adusta*, holotype, RMNH 6161, 130 mm, Ambon, Molucca Islands (R.D. Mooi).

Specimens of *Pempheris vanicolensis* examined. BPBM 32253, 111 mm, Indonesia, Bali; BPBM 39592, 120 mm; Sumatra, Pulau Ular (off Padang); BPBM 40641, 2: 124–145 mm, Bali; BPBM 41166, 4: 105–115 mm, Thailand, Phuket. MNHN A-224, 137 mm (lectotype); MNHN A-418, B-2512, and B-2513 (syntypes), Santa Cruz Islands, Vanikoro Island. NTM S.10674-016, 3: 112–127 mm, Thailand, Phuket; NTM S.10732-005, 120 mm, Indonesia, Bali; NTM S.13685-015, 131 mm, Papua New Guinea, Madang, Tab Island. PMBC 21206, 2: 112–129 mm, Thailand, Phuket.

Acknowledgments

We thank the following persons for the loan of specimens of *Pempheris*: David Catania and Mysi D. Hoang of the California Academy of Sciences; Michael Hammer and Gavin Dally of the Museum and Art Galleries of the Northern Territory; Horst Zetzsche of the Senckenberg Museum; Ofer Gon, Roger Bills, and Bafo Konkobe of the South African Institute for Aquatic Biodiversity, Shirleen Smith of the U. S. National Museum of Natural History; and K.K. Bineesh of the Society for Marine Research and Conservation, Kochi (Cochin), Kerala, India. We are also grateful to Sean O’Hara, Dennis Polack, P.T. Rajan, Helen A. Randall, and Jean Louis Rose for the use of their photographs; Ofer Gon for tissue of *P. flavicycla* from the Republic of Maldives; Mongkol Klongsamut and staff of the Phuket Marine Biological Center for collecting specimens of *Pempheris vanicolensis*, and to Loreen R. O’Hara and Arnold Y. Suzumoto of the Bishop Museum for curatorial assistance and x-rays. The authors also acknowledge, with gratitude, the technical and financial support for fieldwork in the Red Sea provided by KAU GRANT NO. “D/1/432-DSR” for the Red Sea Biodiversity Project of the Faculty of Marine Sciences (FMS) of King Abdulaziz University (KAU), Jeddah, Saudi Arabia, and the Senckenberg Research Institute (SRI), Frankfurt, Germany. Special thanks to Drs. Brian W. Bowen, Joseph D. DiBattista, and Luiz A. Rocha for collecting *Pempheris flavicycla marisrubri* from Djibouti for us. The manuscript was reviewed by Giacomo Bernardi, Benjamin Victor, Mark Erdmann, and Helen A. Randall.

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Appendix. Data corresponding to the sequences used in the phylogenetic tree presented in Figure 16.

Species	Collection Location	Field Number of Voucher /Laboratory Identifier	Identified by	Museum Catalog Number	GenBank Accession Number	Sequence Reference
<i>Parapriacanthus ransonneti</i> Steindachner 1870	WIO (Park Rynie, KwaZulu-Natal, South Africa)	ADC09_216.1#5	A.D. Connell	n.a.	GU805108	Steinke <i>et al.</i> (unpublished)
“ <i>Pempheris adusta</i> Bleeker 1877”	EIO (India)	WL-M263	Lakra <i>et al.</i>	n.a.	EU148571	Lakra <i>et al.</i> (2011)
	EIO (India)	WL-M264	Lakra <i>et al.</i>	n.a.	EU148572	Lakra <i>et al.</i> (2011)
	EIO (India)	WL-M265	Lakra <i>et al.</i>	n.a.	EU148573	Lakra <i>et al.</i> (2011)
	EIO (India)	WL-M266	Lakra <i>et al.</i>	n.a.	EU148574	Lakra <i>et al.</i> (2011)
	EIO (India)	WL-M267	Lakra <i>et al.</i>	n.a.	EU148575	Lakra <i>et al.</i> (2011)
WIO (Karridene, KwaZulu-Natal, South Africa)	ADC 216.2-3	A.D. Connell	n.a.	JF494126	Steinke <i>et al.</i> (unpublished)	
WIO (Karridene, KwaZulu-Natal, South Africa)	ADC 216.2-2	A.D. Connell	n.a.	JF494127	Steinke <i>et al.</i> (unpublished)	
WIO (Aliwal Shoal, KwaZulu-Natal, South Africa)	ADC 216.2-1	A.D. Connell	n.a.	JF494128	Steinke <i>et al.</i> (unpublished)	
WIO (St. Gilles, Réunion)	ECOMAR(Fra) REU0731	S. Planes	n.a.	JQ350194	Hubert <i>et al.</i> (2012)	
WIO (St. Leu, Réunion)	ECOMAR(Fra) REU0936	S. Planes	n.a.	JQ350195	Hubert <i>et al.</i> (2012)	
WIO (St. Gilles, Réunion)	ECOMAR(Fra) REU0732	S. Planes	n.a.	JQ350196	Hubert <i>et al.</i> (2012)	
WIO (St. Leu, Réunion)	ECOMAR(Fra) REU0937	S. Planes	n.a.	JQ350197	Hubert <i>et al.</i> (2012)	
WIO (St. Leu, Réunion)	ECOMAR(Fra) REU0938	S. Planes	n.a.	JQ350198	Hubert <i>et al.</i> (2012)	
<i>Pempheris flavicycla flavicycla</i> sp. nov.	WIO (Seychelles)	A38	J.E. Randall	SAIAB77805 or SAIAB77856	EU381029	Thacker (2009)
	WIO (Seychelles)	A43	J.E. Randall	SAIAB77805 or SAIAB77856	EU381030	Thacker (2009)
	EIO (Maldives)	MAL-023	J.E. Randall	SAIAB187538	KF914198	this study
	EIO (Maldives)	MAL-024	J.E. Randall	SAIAB187538	KF914199	this study
<i>Pempheris flavicycla marisrubri</i> sp. nov.	RS (Al Lith, Saudi Arabia)	KAU11-013	J.E. Randall	SMF 33624	KF914190	this study
	RS (Al Lith, Saudi Arabia)	KAU11-014	J.E. Randall	SMF 33625	KF914191	this study
	RS (Al Lith, Saudi Arabia)	KAU11-015	J.E. Randall	KAUMM 11	KF914192	this study
	RS (Al Lith, Saudi Arabia)	KAU11-016	J.E. Randall	KAUMM 12	KF914193	this study
	RS (Rabigh, Saudi Arabia)	KAU11-506	J.E. Randall	SMF 33630	KF914194	this study
	RS (Rabigh, Saudi Arabia)	KAU11-504	J.E. Randall	SMF 33631	KF914195	this study
	RS (Rabigh, Saudi Arabia)	KAU11-505	J.E. Randall	KAUMM 9	KF914196	this study
	RS (Dubai, Saudi Arabia)	KAU13-608	J.E. Randall	KAUMM 10	KF914197	this study

Appendix. cont.

Species	Collection Location	Field Number of Voucher /Laboratory Identifier	Identified by	Museum Catalog Number	GenBank Accession Number	Sequence Reference
<i>Pempheris mangula</i> Cuvier 1829”	WIO (Antananarivo, Madagascar)	ECOMAR(Fra) NBE0182	S. Planes	n.a.	JQ350199	Hubert <i>et al.</i> (2012)
<i>Pempheris oualensis</i> Cuvier 1831	WIO (St. Leu, Réunion)	ECOMAR(Fra) NBE0958	S. Planes	n.a.	JQ350200	Hubert <i>et al.</i> (2012)
	WIO (St. Leu, Réunion)	ECOMAR(Fra) NBE0957	S. Planes	n.a.	JQ350201	Hubert <i>et al.</i> (2012)
<i>Pempheris schomburgkii</i> Müller & Troschel 1848	WA (St. Lucie County, Florida, USA)	SMSA7377	D.G. Smith	n.a.	JQ842644	Weigt <i>et al.</i> (2012)
	WA (Tobago, Trinidad and Tobago)	TOBA9020	C.C. Baldwin	n.a.	JQ843000	Weigt <i>et al.</i> (2012)
<i>Pempheris schwenkii</i> Bleeker 1855 “	WIO (KwaZulu-Natal, South Africa)	ADC10_216.4 #6	A.D. Connell	n.a.	HQ561454	Steinke <i>et al.</i> (unpublished)
	WIO (KwaZulu-Natal, South Africa)	ADC216.4-3	A.D. Connell	n.a.	JF494129	Steinke <i>et al.</i> (unpublished)
	WIO (KwaZulu-Natal, South Africa)	ADC216.4-4	A.D. Connell	n.a.	JF494130	Steinke <i>et al.</i> (unpublished)
	WIO (KwaZulu-Natal, South Africa)	ADC216.4-2	A.D. Connell	n.a.	JF494131	Steinke <i>et al.</i> (unpublished)
	WIO (KwaZulu-Natal, South Africa)	ADC216.4-1	A.D. Connell	n.a.	JF494132	Steinke <i>et al.</i> (unpublished)
<i>Pempheris vanicolensis</i> Cuvier 1831	EIO (Phuket, Thailand)	UkSa-01	J.E. Randall	BPBM 41166	KF914185	this study
	EIO (Phuket, Thailand)	UkSa-02	J.E. Randall	BPBM 41166	KF914186	this study
	EIO (Phuket, Thailand)	UkSa-03	J.E. Randall	BPBM 41166	KF914187	this study
	EIO (Phuket, Thailand)	UkSa-04	J.E. Randall	BPBM 41166	KF914188	this study
	EIO (Phuket, Thailand)	UkSa-05	J.E. Randall	PMBC 21206	KF914189	this study
<i>Pempheris vanicolensis</i> Cuvier 1831 ”	WIO (Antananarivo, Madagascar)	ECOMAR(Fra) NBE0214	S. Planes	n.a.	JQ350202	Hubert <i>et al.</i> (2012)
	WIO (Antananarivo, Madagascar)	ECOMAR(Fra) NBE0213	S. Planes	n.a.	JQ350203	Hubert <i>et al.</i> (2012)
	WIO (Antananarivo, Madagascar)	ECOMAR(Fra) NBE0215	S. Planes	n.a.	JQ350204	Hubert <i>et al.</i> (2012)
	WIO (Antananarivo, Madagascar)	ECOMAR(Fra) NBE0214	S. Planes	n.a.	JQ350202	Hubert <i>et al.</i> (2012)