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FULL PAPER

Pterois paucispinula, a new species of lionfish (Scorpaenidae: Pteroinae) from the western Pacific Ocean

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Abstract A new species of lionfish (Scorpaenidae: Pteroinae), *Pterois paucispinula* sp. nov., is described on the basis of 37 specimens from the western Pacific Ocean. The new species is closely related to and has been previously confused with *Pterois mombasae* (Smith 1957), both species sharing usually XIII, 10 dorsal-fin rays, usually more than 18 pectoral-fin rays, numerous black blotches on the pectoral-fin membrane, and several bands on the posterior portion of the pectoral-fin rays (free from membrane). However, *P. paucispinula* differs from similarly sized *P. mombasae* in having a lesser body depth at the anal-fin origin, head width, postorbital length, and caudal-peduncle depth, in addition to a slightly higher number of scale rows below the lateral line. *Pterois paucispinula* also differs from the typical form of *P. mombasae*, occurring off the east coast of Africa and in the central Indian Ocean and Andaman Sea, by having usually 18 pectoral-fin rays (vs. usually 19 in the latter) and relatively long dorsal-fin spines, with the longest dorsal-fin spine length 42.9–51.7 % of standard length (SL) (vs. 35.1–44.8 % of SL). Although a Sri Lankan population of *P. mombasae* is similar to *P. paucispinula* in the above characters (usually 18 pectoral-fin rays and longest dorsal-fin spine length 37.5–51.1 % of SL), such differences among *P. mombasae* are regarded as intra-specific geographical variations. Additionally, young and adult *P. mombasae* have ctenoid scales on the pectoral-fin base, ventrolateral portion of the body (below the lateral line) and laterally on the caudal peduncle. These regions in all examined *P. paucispinula* usually have only cycloid or at most a few ctenoid scales, thereby providing a consistent basis for identification of both species, including the Sri Lankan population of *P. mombasae*. *Pterois mombasae* is distributed in the Indian Ocean from the east coast of Africa to the Andaman Sea, whereas *P. paucispinula* is recorded from the western Pacific Ocean, from northern Australia to southern Japan and eastward to the Wallis and Futuna Islands.

Keywords *Pterois mombasae* · *Pteropterus* · Geographic variation · Distribution

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Introduction

The Indo-Pacific genus *Pterois* Oken 1817 (Scorpaenidae: Pteroinae) has been characterized as having a combination of three anal-fin spines, all pectoral-fin rays unbranched, the parietal spine of males not elongated, and the mandible lacking a spine or ridge (Eschmeyer and Randall 1975; Poss 1999). Although Smith (1957) and Mandrytsa (2001, 2002) regarded *Pteropterus* Swainson 1839 as valid, being distinguished from *Pterois* by several characters, including

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pectoral-fin ray and body scale number, scale morphology and eye position, a comprehensive phylogenetic study of Pteroinae is yet to be made, and the relationships among *Pterois*, *Pteropterus* and related genera remain unclear. The treatment of *Pteropterus* as a junior synonym of *Pterois* by most recent studies (e.g., Herre 1952; Eschmeyer and Randall 1975; Poss 1999) is tentatively followed here (see also Matsunuma and Motomura, 2011, 2013b).

Pterois mombasae, originally described by Smith (1957) (as *Pteropterus mombasae*) from a single specimen from Mombasa, Kenya, has since been widely recorded in the Indo-West Pacific, ranging from the east coast of Africa to Wallis and Futuna Islands, and from northern Australia to southern Japan (Eschmeyer 1986; Poss 1999; Matsunuma and Motomura 2011; Motomura et al. 2011a; Allen and Erdmann 2012). However, careful examination has recently shown that western Pacific and Indian Ocean specimens can be separated on the basis of meristics, morphometrics and scale morphology. The western Pacific specimens are therefore described herein as a new species of *Pterois*.

Materials and methods

Measurements generally followed Motomura (2004b, c), with head width and maxillary depth following Motomura et al. (2005b, 2006a) and Motomura et al. (2006b), respectively. Body depth at the anal-fin origin and first to ninth pectoral-fin ray length measurements followed Matsunuma and Motomura (2013b). The length of the supraocular tentacle was taken as the distance from the flap base to the extreme distal point on the flap. Counts generally followed Motomura et al. (2005a–c) and Motomura and Johnson (2006), with counts of pre-dorsal-fin scale rows and scales above the lateral line following Motomura et al. (2006b) and Matsunuma and Motomura (2013b), respectively. The last two soft rays of the dorsal and anal fins were counted as single rays, each pair being associated with a single pterygiophore. Counts and measurements were made on the left side whenever possible, except for pectoral-fin rays (counted on both sides). The numbers of scale spinules in each of the following regions were represented as the mean numbers of spinules counted on 3–10 scales (Fig. 1): dorsolateral scales (Fig. 1a), 4–6 scales along the scale row between the first pored lateral line scale and the dorsal-fin base, not including the small uppermost scale; cheek scales (Fig. 1b), 3–6 scales along a more or less horizontal row, beginning from the second scale above that located at the posteroventral corner of the cheek (junction of suborbital and postorbital ridges), not including small anterior scales (much smaller than posterior scales); preopercular scales (Fig. 1c), 4–10 scales along a horizontal scale row, beginning from the posteriormost scale just below the upper posterior-most scale, not including small anterior scales; ventrolateral scales (Fig. 1d), 5–6 scales along a row below the pored lateral-line scale below the last dorsal-fin spine base; caudal-peduncle scales (Fig. 1e), 4–6 scales surrounding the pored lateral-line scale located at the approximate midportion of the caudal peduncle; pectoral-fin base scales (Fig. 1f), 4–6 scales along a row on the pectoral girdle, beginning from the scale located at the most laterally expanded point on the girdle and running posteroventrally.

The mitochondrial DNA (mtDNA) cytochrome *b* gene was examined, and DNA extraction from a single specimen of *P. paucispinula* (KAUM–I. 48423, Okinawa Prefecture, Japan) was performed with the Gentra Puregene Tissue Kit (QIAGEN) following the manufacturer's protocols. Using total DNA and the primer pair AJG15 (Akihito et al. 2000) and Simt12-Fb (Kuriiwa et al. 2007), approximately 2.3 kbp fragments, including the cytochrome *b* gene and control region of mtDNA, were amplified under the following PCR conditions. Thirty amplification cycles were performed at 94 °C for 45 sec, 56 °C for 30 sec and 72 °C for 2 min. Sequencing reactions were carried out using the BigDye Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems) with the primer L15369-CYB (Miya and Nishida 2000), following the manufacturer's protocols and utilizing the automated genetic analyzer model 3500 (Applied Biosystems). The obtained DNA sequences were subjected to multiple alignment using Clustal X (Thompson et al. 1997). A sequence is available on DDBJ/EMBL/GenBank accession number AB986281. Comparative sequences of *P. mombasae* from Kenya were also available (DDBJ/EMBL/GenBank accession numbers AJ429427–429428) (Kochzius et al. 2003). The sequence difference (*p*-distance) was calculated using MEGA 6 (Tamura et al. 2013).

Head spine terminology generally followed Randall and Eschmeyer (2002: fig. 1), Motomura (2004c: fig. 1), and Matsunuma and Motomura (2013b). Supplemental preopercular spine and lateral lacrimal spine terminology followed Eschmeyer (1965) and Motomura and Senou (2008: fig. 2), respectively.

A principal component analysis (PCA) was conducted for the following nine measurements considered to influence interspecific and intraspecific differences: body width, head width, maxillary depth, postorbital length, sixth–eighth and twelfth dorsal-fin spine lengths, and caudal-peduncle depth. All measurements were standardized by log transformation and taken from the following 12 specimens of *P. paucispinula*, including the holotype, and 13 specimens of *P. mombasae*. *P. paucispinula*: AMS I. 37179-002 (Australia); BSKU 61061, BSKU 61062, BSKU 72569, BSKU 86402, BSKU 86404, CMNH–ZF 15450, NSMT-P 110789 (two specimens), URM-P 4265, URM-P

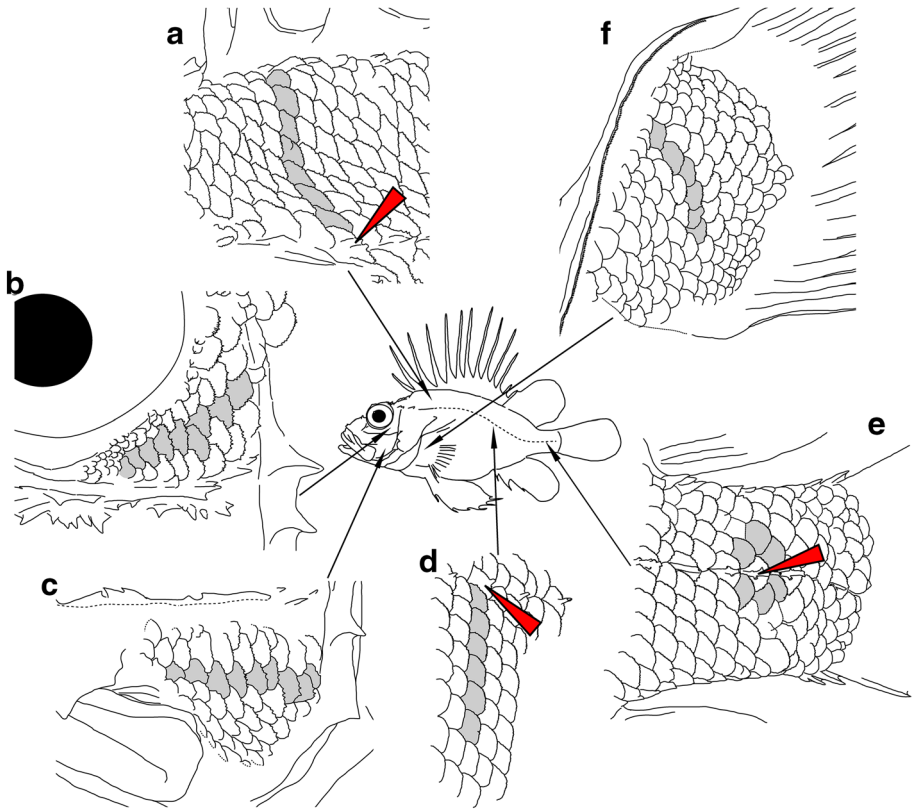

Fig. 1 Positions of head and body scales (shown as shaded) utilized for spinule counts in this study (see Materials and methods). **a** Dorsolateral scales; **b** cheek scales; **c** preopercular scales; **d** ventrolateral scales;**e** caudal-peduncle scales; **f** pectoral-fin base scales. Arrowheads in **a**, **d** and **e** indicate first pored lateral-line scale, pored lateral-line scale below last dorsal-fin spine base and pored lateral-line scale at midpoint of caudal peduncle, respectively. Schematic drawings of scales based on *Pterois mombasae*, MNHN 1992-494, 112.7 mm SL

4266, URM-P 4268 (Japan); and *P. mombasae*: PMBC (uncataloged; one of two specimens) (Andaman Sea coast of Thailand); CAS 75355 (India); AMS I. 33775-001 (three specimens), SMF 4209, SMF 4322 (Sri Lanka); BPBM 36050 (Oman); SMF 10692, 12797, 12818 (Tanzania); SMF 4210, MNHN 1992-494 (Madagascar). Damaged specimens, including the holotype of *P. mombasae*, were eliminated from the analysis, because they lacked one or more aforementioned measurements, such as dorsal-fin spine length. The first two components (PC1 and PC2) were obtained using the software package R 3.1.0 (R Core Team 2014) based on the function *prcomp*.

A distributional map was prepared using Quantum GIS 2.2 (Quantum GIS Development Team 2014), with data from Natural Earth. Standard length is abbreviated as SL. In the description, features of the holotype are presented first, followed by paratype data (if different) in parentheses. Institutional codes followed Sabaj Pérez (2014), with the following addition: NSMT, National Museum of Nature and Science, Tsukuba.

Pterois paucispinula sp. nov.

(Japanese name: Mizuhiki-minokasago) (Figs. 2, 3a–d, 4, 5, 6–10, 11a; Tables 1–3)

Pterois antennata (not of Bloch): Masuda et al. 1975: 339, pl. 144, fig. C (Japan; in part; short description); Shimizu 1984: 302, pl. 282, fig. C [Japan; in part; figure from Masuda et al. (1975); short description]; Randall et al. 1997: 79, unnumbered fig. (Coral Sea; short description); Randall 2005: 116, unnumbered fig. [South Pacific; in part; figure from Randall et al. (1997); short description]; Hirata 2010: 34, left unnumbered fig. (Ehime, Japan; in part).

Pterois mombasae (not of Smith): Gloerfelt-Tarp and Kailola 1984: 112, unnumbered fig. (northwestern Australia; short description); Eschmeyer 1986: 467, fig. 149.9; pl. 25, fig. 149.9 (Indo-West Pacific; in part; short description); Allen and Cross 1989: 446 (northwest coast of Western Australia; list); Randall 1995: 109, unnumbered fig. (Indo-West Pacific; in part; short description); Kuiter 1996: 90, unnumbered fig. (Australia; short description); Allen 1997: 76, pl. 19, fig. 4 (Indo-West Pacific; in part; short description); Poss 1999: 2330, unnumbered fig. (Indo-West Pacific; in part; keys); Hutchins 2001: 27 (Western Australia; list); Allen and Adrim 2003: 29 (Flores to Sumatra, Indonesia; list); Allen et al. 2003: 370, unnumbered fig. (Indo-West Pacific; in part; shot description); Allen et al. 2006: 879 (northwest coast of Western Australia); Kuiter and Debelius 2006: 193, unnumbered figs. (Indo-Pacific; in part); Fricke et al. 2011: 378 (New Caledonia; list); Matsunuma and Motomura 2011: 27,

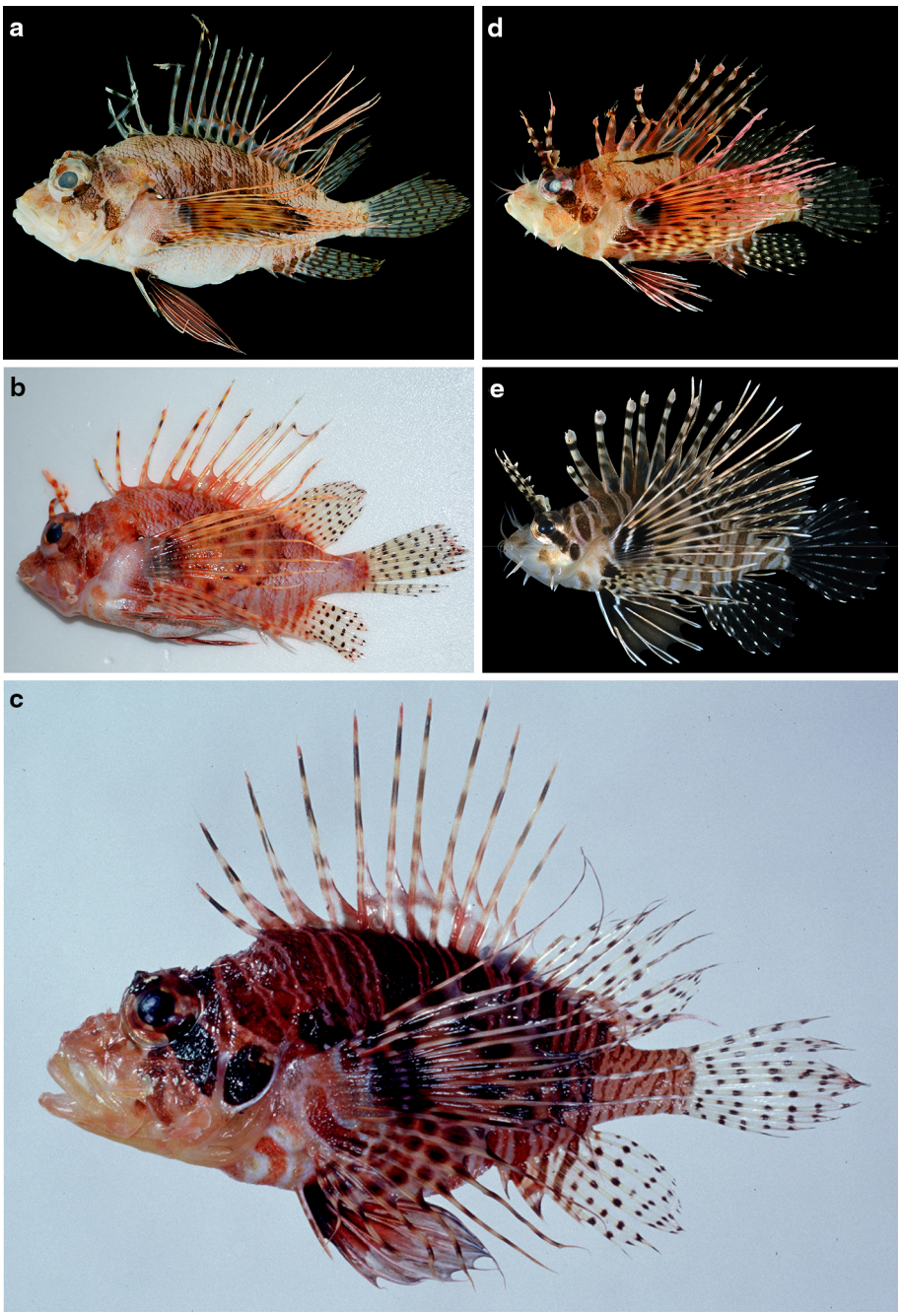

Fig. 2 Fresh specimens of *Pterois paucispinula* sp. nov. at different stages. **a** KAUM–I. 6588, 103.1 mm SL, paratype, Okinawa-jima island, Ryukyu Islands, Japan; **b**KAUM–I. 39268,98.3 mm SL, paratype, southwestern Taiwan (Photo: H.-C. Ho); **c** BSKU 61062, 90.2 mm SL, holotype, Kashiwa-jima island, Kochi Prefecture, Japan (Photo: BSKU); **d** KAUM–I. 48423, 39.3 mm SL, paratype, Okinawa-jima island, Ryukyu Islands, Japan; **e** CMNH–ZF 15450, 30.9 mm SL, paratype, Yaku-shima island, Kagoshima Prefecture, Japan (Photo: M. Aizawa)

figs. 1–2, 3A, 4 (Japan; description); Matsunuma et al. 2011: 3, figs. 1, 2A (Japan; description); Motomura et al. 2011b: 98, fig. 1 (Taiwan; description); Kubota et al., 2011: 14 (Japan; list); Allen and Erdmann 2012: 221, unnumbered fig. (Indonesia, Philippines, Papua New Guinea, and Solomon Islands; short description, ecological note).

Holotype. BSKU 61062, 90.2 mm SL, Kashiwa-jima Island, Kochi Prefecture, Japan, S. Manabe, hand net, 21 November 2002.

Paratypes. Thirty-six specimens of 22.7–143.5 mm SL. JAPAN: BSKU 61061, 82.3 mm SL, collected with holotype; BSKU 72569, 79.3 mm SL, Irino, Kochi Prefecture, bottom trawl, 16 January 2004; BSKU 86402, 59.4 mm SL, Saga, Kochi Prefecture, bottom trawl, 22 March 1999; BSKU 86404, 56.3 mm SL, Saga, Kochi Prefecture, bottom trawl, 31 March 1999; BSKU 100149, 22.7 mm SL, Okino-shima Island, Kochi Prefecture, hand net, 25 September 2009; CMNH–ZF 15450, 30.9 mm SL, Isso, Yaku-shima Island, Kagoshima Prefecture

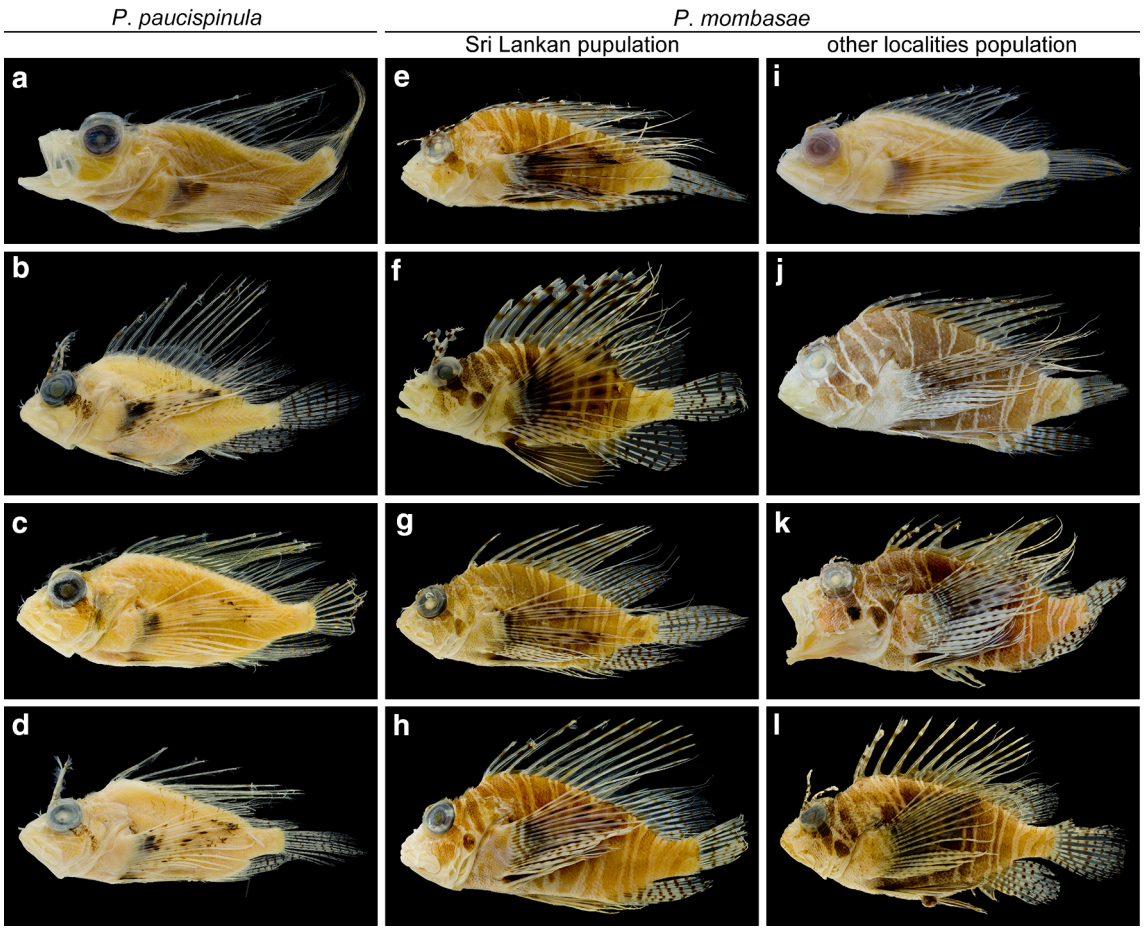

Fig. 3 Preserved specimens of *Pterois paucispinula* sp. nov. (**a**–**d**) and Sri Lankan (**e**–**h**) and other (**i**–**l**) specimens of *P. mombasae* showing differences in overall appearance between the two species and within *P. mombasae*. **a** USNM 265918, 53.7 mm SL, paratype, Macclesfield Bank, South China Sea; **b** AMS I. 39038-030, 59.5 mm SL, paratype, Nemya Island, Solomon Islands; **c** URM-P 4268, 84.1 mm SL, paratype, Okinawa-jima islands, Ryukyu Islands, Japan; **d** AMS I. 37179-002, 102.1 mm SL, paratype, Timor Sea, Australia; **e** SMF 10728, 47.5 mm SL, Sri Lanka; **f** AMS I. 33775-001 (one of three), 60.6 mm SL, Kalpitya, Sri Lanka; **g** SMF 10055, 84.5 mm SL, Sri Lanka; **h** SMF 4322, 99.7 mm SL, Trincomalee, Sri Lanka; **i** SAIAB 46315, 38.4 mm SL, Cathedral Reef, South Africa; **j** SMF 12793, 78.1 mm SL, Seychelles; **k** SMF 12797, 82.4 mm SL, Dar es Salaam, Tanzania; **l** MNHN 1992-494, 112.7 mm SL, Madagascar

(30°27′28″N, 130°29′21″E), hand net, 13 July 2006; FAKU 26425, 143.5 mm SL, Makurazaki, Kagoshima Prefecture, 2 September 1956; FAKU 98973, 40.0 mm SL, FAKU 98976, 46.3 mm SL, FAKU 99044, 124.0 mm SL, Shirahama, Wakayama Prefecture, washed ashore; FAKU 99087, 89.1 mm SL, Shirahama, Wakayama Prefecture, washed ashore, 20 February 2011; KAUM–I. 6582, 82.2 mm SL, KAUM–I. 6588, 103.1 mm SL, Nakagusuku, Okinawa-jima Island, Ryukyu Islands, Y. Sakurai, washed ashore, 13 July 2007; KAUM–I. 22824, 52.3 mm SL, Okinawa-jima Island, Ryukyu Islands, before October 2008; KAUM–I. 48423, 39.3 mm SL, Zanpa, Yomitan, Okinawa-jima Island, Ryukyu Islands (26°26′08″N, 127°42′45E), 1–3 m, K. Matsuzaki, hand net, 28 October 2011; KPM-NI 26919 (formerly IOP-1103), 26.2 mm SL, Futo, Ito, Shizuoka Prefecture, H. Masuda, 7 January 1990; KPM-NI 26930 (formerly IOP-3210), 49.5 mm SL, Futo, Ito, Shizuoka Prefecture, H. Masuda; NSMT-P 54352, 38.3 mm SL, Susaki, Chiba Prefecture, 25 m, K. Utsuki; NSMT-P 110789 (formerly KSHS 22471 and KSHS 22473), two specimens, 83.6–112.1 mm SL, Kashiwa-jima Island, Kochi Prefecture, 22 April 1995; URM-P 4264, 134.7 mm SL, URM-P 4265, 101.1 mm SL, URM-P 4266, 90.3 mm SL, URM-P 4267, 92.7 mm SL, URM-P 4268, 84.1 mm SL, URM-P 4269, 63.3 mm SL, west of Sesoko-jima Island, Okinawa-jima Islands, Ryukyu Islands, 14 April 1977; URM-P 41467, 73.6 mm SL, Okinawa-jima Island, Ryukyu Islands, washed ashore, 17 October 2001.

TAIWAN: KAUM–I. 39268,98.3 mm SL, off southwestern Taiwan (obtained at Hsin-Da Port, Kaohsiung), H.-C. Ho., 3 April 2011.

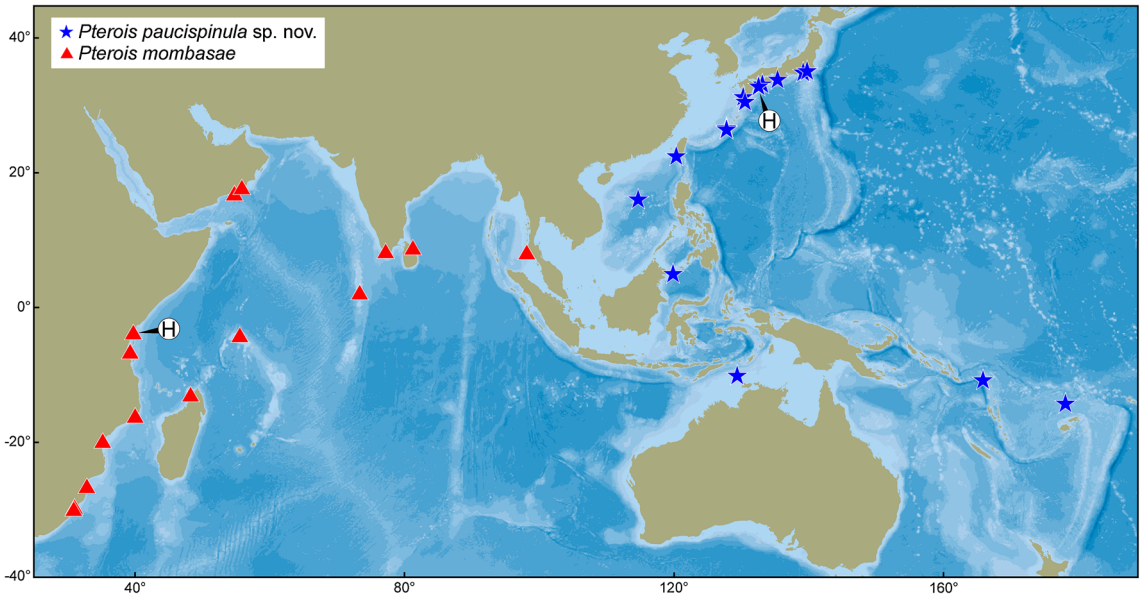

Fig. 4 Distributional map of *Pterois paucispinula* sp. nov. (*stars*) and *P. mombasae* (*triangles*) based on specimens examined in this study. *H* indicates holotype

Fig. 5 Holotype of *Pteropterus mombasae*, SAIAB 117, 128.8 mm SL, reef near Mombasa, Kenya (Photo: T. Yoshida)

PHILIPPINES: SMF 12808, 70.6 mm SL, 1972; USNM 99920, 58.4 mm SL, Observation Island, Tawi Tawi Group, Sulu Archipelago (4°59′10″N, 119°51′00″E), 51 m, R/V *Albatross*, 24 February 1908.

SOUTH CHINA SEA: USNM 265918, 53.7 mm SL, Macclesfield Bank (16°03′42″N, 114°40′00″E), 82.3–84.1 m, W. Chan on board of R/V *Cape St. Mary*, 21 June 1964.

AUSTRALIA: AMS I. 37179-002, 102.1 mm SL, Timor Sea (10°07′49″S, 129°19′55″E), 85 m, J. Lloyd, trammel net, 2–3 October 1995.

SOLOMON ISLANDS: AMS I. 39038-030, 59.5 mm SL, mouth of Nemya Bay, just north of Nemya Island, Sanra Cruz Islands, AMS Team; USNM 382904, 66.5 mm SL, deep channel just north of Nemya Island at mouth of Nemya Bay, Ndendo Island, Santa Cruz Islands (10°49′30″S, 165°49′48″E), 5–35 m, J. Williams et al., 28 September 1998.

WALLIS AND FUTUNA ISLANDS: MNHN 1995-737, 96.3 mm SL, Futuna Island (14°19′05″S, 178°04′05″E), 245–440 m, R/V *Alis*, trawl, 11 May 1992.

NO DATA: ZUMT 46873, 138.4 mm SL.

Diagnosis. A species of *Pterois* distinguished from other species of the genus by the following combination of characters: dorsal-fin rays XIII, 10 (rarely XIII, 11); pectoral-fin rays 17–19 (modally 18); scales below lateral line 11–15 (13); body depth at anal-fin origin 26.0–32.8 (mean 30.2) % SL; head width 12.6–15.6 (14.4) % SL; postorbital length 15.4–20.0 (18.1) % SL; longest dorsal-fin spine length 42.9–51.7 (47.8) % SL; caudal-peduncle depth 9.9–11.9 (11.0) % SL; pectoral fin with 14–28 relatively large (subequal to pupil diameter) black blotches on membrane, several bands on posterior portion of rays (not attached to membrane); several narrow to wide vertical bands laterally on body and caudal peduncle; area of ctenoid scales on body relatively small (usually dorsolateral region only at ca. 90 mm SL, sometimes extending below lateral line onto ventrolateral region, and on pectoral-fin base and laterally on caudal peduncle in adults >80 mm SL).

Description. Morphometrics and selected meristics are shown in Tables 1–3. Meristics given in Diagnosis are not repeated here. Anal-fin rays III, 6; pelvic-fin rays with I, 5. Branchiostegal rays 7.

Body oblong, moderately compressed posteriorly; depth moderate, subequal to (or slightly less than) length of longest dorsal-fin spine. Three barbels on snout tip, their

Table 1 Morphometrics, expressed as percentages of standard length, of *Pterois paucispinula* sp. nov. and *P. mombasae*

	Pterois paucispinula sp. nov.			*Pterois mombasae*			
	Holotype	Paratypes	Mean	Holotype	Other specimens		Mean
Locality	Japan (BSKU 61062)	western Pacific ($n = 36$)		Kenya (SAIAB 117)	India and Sri Lanka ($n = 13$)	other Indian Ocean ($n = 19$)	
SL (mm)	90.2	22.7–143.5		128.8	47.5–136.5	26.1–128.8	
Body D (% SL)	43.0	33.0–44.6	39.9	40.1	36.8–46.6	36.1–43.6	40.1
Body D[a]	32.8	26.0–32.5	30.2	33.5	31.7–34.8	27.4–35.2	32.2
Body W	28.0	18.2–29.3	25.2	26.6	22.8–30.1	20.1–32.3	27.0
Head L	45.1	39.9–46.5	43.1	45.5	40.7–44.9	41.6–47.1	43.6
Head W	14.0	12.6–15.6	14.4	15.2	14.2–16.1	14.4–16.4	15.2
Snout L	14.2	11.0–14.3	12.3	14.1	10.9–12.8	11.4–14.2	12.2
Orbit diameter	14.0	11.7–17.1	14.3	12.9	13.0–15.6	12.4–16.2	14.3
Interorbital W[b]	7.8	7.2–10.1	8.4	9.9	7.0–8.9	7.0–9.9	8.1
Interorbital W[c]	7.5	6.6–9.4	8.0	9.4	6.7–9.4	5.3–9.6	8.0
Upper-jaw L	20.6	18.0–22.3	20.2	21.1	18.5–21.7	19.1–22.4	20.4
Maxillary D	8.1	7.1–8.9	8.0	7.8	6.4–7.5	6.5–8.9	7.5
Postorbital L	18.5	15.4–20.0	18.1	20.0	18.7–20.9	17.7–21.3	19.6
Suborbital D	1.9	0.4–1.9	1.2	2.0	0.5–2.1	0.4–2.4	1.3
Pre-dorsal-fin L	39.7	33.7–42.0	37.8	36.5	33.7–37.9	35.0–39.9	36.1
Pre-anal-fin L	75.5	70.5–79.7	75.1	76.2	70.4–81.1	71.3–76.2	74.0
Pre-pelvic-fin L	42.6	35.2–43.2	39.7	47.4	36.3–41.2	37.7–47.4	39.6
1st DS L	16.6	14.4–19.7	17.0	14.8	18.4–23.6	14.8–21.2	18.9
2nd DS L	25.6	21.2–30.0	26.0	21.0	24.2–34.1	21.0–28.7	26.6
3rd DS L	30.7	27.6–36.8	31.7	broken	27.3–37.8	23.3–32.7	30.4
4th DS L	35.3	31.4–43.0	36.7	broken	31.8–41.6	26.2–35.1	33.8
5th DS L	40.0	34.4–48.2	42.2	broken	38.6–46.0	30.7–38.3	37.8
6th DS L	42.4	37.9–54.1	45.5	32.0	35.1–49.0	32.0–42.1	39.9
7th DS L	42.5	39.2–53.8	46.5	33.9	37.1–51.1	33.8–45.0	41.8
8th DS L	43.5	41.6–51.5	46.8	broken	37.5–50.6	35.1–44.2	42.0
9th DS L	42.7	39.0–51.7	45.7	33.5	41.9–50.0	33.5–44.0	41.2
10th DS L	38.1	33.2–48.9	41.8	30.9	34.5–46.2	29.2–42.2	38.3
11th DS L	28.9	16.8–45.4	29.5	26.7	24.4–38.7	17.9–35.5	29.9
12th DS L	12.2	10.2–18.5	13.4	12.4	12.9–18.2	12.4–22.9	16.0
13th DS L	13.9	13.1–17.8	15.1	12.3	12.4–18.6	12.3–19.2	15.4
Longest DS L	43.7	42.9–51.7	47.8	unknown	37.5–51.1	35.1–44.8	42.1
1st DSR L	20.5	18.8–26.2	22.8	broken	19.6–25.9	17.3–26.4	22.4
Longest DSR L	27.8	26.5–33.0	29.5	broken	24.6–31.8	24.3–32.9	27.4
1st AS L	6.9	6.3–11.0	8.3	6.3	7.0–10.8	6.3–9.8	8.9
2nd AS L	14.0	13.0–19.3	15.5	10.5	10.5–19.1	10.5–19.0	15.4
3rd AS L	18.1	14.5–22.6	18.4	14.4	15.7–22.5	14.4–22.3	18.5
1st ASR L	26.4	25.0–31.7	28.4	broken	24.9–33.3	22.4–31.1	27.6
Longest ASR L	28.4	28.7–34.3	31.0	broken	27.2–35.7	26.1–32.6	30.1
1st P1 L	66.3	49.0–87.6	67.9	broken	43.5–82.0	57.2–76.6	66.7
2nd P1 L	71.1	59.6–85.4	74.8	broken	68.6–88.9	65.7–82.0	75.9
3rd P1 L	72.0	63.1–89.6	75.6	broken	58.6–90.1	68.5–79.5	77.3

Table 1 continued

	Pterois paucispinula sp. nov.			*Pterois mombasae*			
	Holotype	Paratypes	Mean	Holotype	Other specimens		Mean
Locality	Japan (BSKU 61062)	western Pacific ($n = 36$)		Kenya (SAIAB 117)	India and Sri Lanka ($n = 13$)	other Indian Ocean ($n = 19$)	
4th P1 L	76.6	65.3–89.3	76.2	broken	64.8–90.7	70.5–82.5	77.5
5th P1 L	76.3	58.2–87.1	74.9	broken	70.6–88.0	69.1–83.2	76.4
6th P1 L	73.2	60.7–85.2	73.4	broken	70.1–87.8	66.6–81.9	76.0
7th P1 L	69.8	56.1–84.8	71.8	52.7	62.1–86.7	52.7–79.7	71.6
8th P1 L	68.6	56.3–82.5	69.1	53.7	69.3–83.2	53.7–76.6	70.0
9th P1 L	62.2	55.1–81.6	65.5	broken	61.1–73.0	57.2–73.1	66.3
Longest P1 L	76.6	65.7–89.3	77.2	broken	76.2–90.7	71.4–83.2	74.3
P2S L	19.5	17.6–23.9	21.1	17.5	17.0–23.4	17.5–23.1	20.3
Longest P2SR L	46.0	36.4–53.9	45.0	broken	40.1–52.5	38.2–52.4	45.9
Caudal-fin L	34.8	32.6–42.4	37.3	broken	32.0–41.4	32.5–43.0	36.9
Caudal-peduncle L	16.1	13.8–17.8	15.9	16.5	14.1–17.2	13.4–16.9	15.7
Caudal-peduncle D	11.1	10.2–11.9	11.0	11.6	11.1–13.0	11.0–12.8	11.9

AS anal-fin spine; *ASR* anal-fin soft ray; *D* depth; *DS* dorsal-fin spine; *DSR* dorsal-fin soft ray; *L* length; *P1* pectoral-fin ray; *P2S* pelvic-fin spine; *P2SR* pelvic-fin soft ray, *W* width

[a] At the anal-fin origin

[b] At the vertical midline of the eye

[c] At the posterior end of the preocular spine base

length subequal to anterior nasal tentacle length. Short simple tentacle on posterior edge of low, membranous tube associated with anterior nostril, its tip extending beyond posterior margin of posterior nostril when depressed posteriorly. Supraocular with a low skin flap (long tentacle with 2–4 lateral branches in juveniles; low skin flap in large adults). Anteroventral portion of lacrimal with a short tentacle, its length subequal to that of barbels on snout tip. A relatively large fan-like skin flap on tip of posterior lacrimal spine, its tip extending slightly beyond posterior margin of maxilla when laid flat. Two small fan-like flaps on posterior margin of preopercle, their tips just reaching or extending slightly beyond posterior margin of interopercle when laid flat. Small fan-like flap usually present on ventral portion of third preopercular spine in large adults > ca. 130 mm SL (absent in juveniles). A small skin flap anterodorsally on orbit surface, its length slightly greater than diameter of posterior nasal pore. No other skin flaps on head or body.

Ctenoid scales covering preopercle, suborbital area (exposed or embedded cycloid scales in juveniles < ca. 30 mm SL), cheek, suprapostorbital region between tympanic and sphenotic spine bases, occipital region (exposed or embedded cycloid scales in juveniles) and anterodorsal portion of opercle. Dorsal surface of postocular and frontal portion of preocular with mostly cycloid scales, sometimes with weakly ctenoid scales possessing 1–4 spines (cycloid scales only or scales absent in juveniles). Scales generally absent from middorsal interorbital area, interorbital canal (sometimes a row of small cycloid scales in adults > ca. 100 mm SL), snout, lacrimal (several small scales, mostly cycloid but a few poorly developed ctenoid scales possessing 1–4 spines, on posterior lacrimal spine plate in largest adults > ca. 130 mm SL), maxilla [ZUMT 46873, 138.4 mm SL (largest examined specimen) with a patch of small cycloid scales on posterodorsal corner], lips, mandibular and interopercle. Other regions of head covered with cycloid scales [all head scales cycloid in BSKU 100149, 22.7 mm SL (smallest examined specimen)]. Anterodorsal portion of body mostly above lateral line and anterior to level of last dorsal-fin spine base, with ctenoid scales; remainder of body with cycloid scales (all scales cycloid in BSKU 100149, area of body with ctenoid scales increasing with increasing SL). Soft-rayed portions of dorsal and anal fins, pectoral-fin and caudal-fin bases with small cycloid basal scales.

Mouth moderately large, slightly oblique, forming angle of ca. 30° (30–40°) to horizontal axis of head and body; upper edge of posterior maxilla swollen laterally, forming

Table 3 Frequency distribution of selected meristics in *Pterois paucispinula* sp. nov. and*P. mombasae*, showing interspecific differences and geographical variations in *P. mombasae*

	Pectoral-fin rays						
	17/17	17/18	18/18	18/19	19/19	19/20	20/20
P. paucispinula	1	2	28[H]	2	4		
P. mombasae							
Sri Lanka and northern India		1	9	2			
Andaman Sea (Thailand)					1	1	
Maldives and Seychelles					2		
Oman			2				
east Africa and Madagascar			4	1	9[H a]		1

	Scales between last DS and LL				Scales between 6th DS and LL				Pre-dorsal-fin scale rows				
	6	7	8	9	6	7	8	9	4	5	6	7	8
P. paucispinula	4	18	8[H]		3	5	11[H]		4	8	12[H]	6	1
P. mombasae													
Sri Lanka and northern India	1	2	8	2		4	7	2	2	3	6	2	
Andaman Sea (Thailand)		1	1			2			1		1		
Maldives and Seychelles		1				2			1				
Oman		1	1				2			1	1		
east Africa and Madagascar		5	5			7	3		2	4	2	2	

DS and *LL* indicate dorsal-fin base and lateral line, respectively

[H] includes holotype

[a] from original description of *Pteropterus mombasae*; right pectoral fin of holotype removed

low ridge; posterior margin of maxilla just reaching mid-orbit level. Symphyseal gap separating premaxillary teeth bands distinctly broader than width of each band; upper jaw with band of small, slender conical teeth; ca. 8 (8–10) tooth rows at front of upper jaw; ca. 3–5 tooth rows at front of lower jaw; small teeth in ca. 6 (6–15) rows forming blunt V-shaped patch on vomer; no palatine teeth. Three sensory pores on underside of each dentary, one small pore on each side of symphysial knob.

Dorsal profile of snout relatively steep, forming angle of ca. 40° (30–40°) to horizontal axis of head and body. Nasal spine with 1 (1 or 2) spinous point. Preocular spine with 2 (1–4) spinous points directed upward. Supraocular with 1 spinous point covered by skin. Postocular with 7 (1–13) small spines directed laterally. Interorbital ridge not developed, reduced posteriorly, connected to coronal spine base. Coronal spine with a single point. Tympanic spine with a single point (absent in BSKU 100149). Anterior margin of occipital region sloped transversely from between bases of coronal spines, slightly curved posteriorly in dorsal view. Parietal spine with 2 (0–4) spinous points; its base relatively long, diverging posteriorly and not connected to coronal spine base. Nuchal spine with 1 (1–3) spinous point, its base completely conjoined with that of parietal spine. Postorbital spine and exposed sensory canal absent. Sphenotic with 5 (0–10) small spines. Pterotic with 3 (0–7) small spines. Lower post-temporal spine with a single (1 or 2) small spine. Cleithrum with short upper and long lower ridges; upper ridge with a single (0–2) somewhat flattened spine posteriorly; lower ridge with 2 (1–4) spinous points posteriorly (single ridge without spine in BSKU 100149).

Lateral lacrimal spine with 3 (0–3) spinous points (upper and lower ridges with 2–3 and 1–4 spines in large adults > ca. 130 mm SL); other ridges on lacrimal mostly smooth (strongly spinous in large adults). Suborbital with upper main and lower supplemental spines; upper ridge with 11 (2–18) small spines; lower spines 8 (0–14) (ridge only without spines in BSKU 100149). Anterior lacrimal spine absent. Posterior lacrimal spine broad, plate-like, with a single (1–5) spinous point on distal margin, tip covered by skin (if more than two spines present, all spinous points exposed, except for a point situated at posterior lacrimal skin flap base). Preopercle with 3 distinct similar-length spines; uppermost spine directed posterodorsally, middle spine directed posteroventrally, lowermost spine directed posteriorly; spine bases lacking supplemental spines (1 or 2 supplemental spines in ZUMT 46873,

138.4 mm SL); lowermost spine broad, plate-like. Exposed opercular spine absent.

Origin of first dorsal-fin spine above lower post-temporal spine; bases of first and second dorsal-fin spines closer than those of subsequent adjacent spines; eighth (sometimes seventh or ninth) spine longest; sixth to ninth spines almost same length; twelfth [rarely thirteenth (last)] spine shortest, its length 42 % (36–73 %) and 88 % (64–107 %) that of antepenultimate and posteriormost spines, respectively; membrane of spinous portion of dorsal fin strongly incised. Dorsal-fin soft rays all branched; fifth (usually fourth or fifth, sometimes sixth, rarely third) ray longest, but distinctly shorter than longest dorsal-fin spine; posteriormost ray joined by extremely low membrane to caudal peduncle. Origin of first anal-fin spine below posteriormost dorsal-fin spine base (sometimes below first soft-ray base); third spine longest; length of first spine 49 % (45–63 %) and 38 % (38–60 %) of that of second and third spines, respectively. Anal-fin soft rays all branched; third (sometimes second) ray longest, its length subequal to that of longest dorsal-fin soft ray; posteriormost ray free from caudal peduncle. Pectoral fin relatively long, all rays unbranched, lower 7 (7–8) rays weakly thickened; fourth (variably second to seventh) ray longest, tip of longest ray extending beyond caudal-fin base, not reaching posterior margin of caudal fin. Pelvic-fin spine base below third (or fourth) dorsal-fin spine base; all pelvic-fin soft rays branched; third soft ray longest, its tip extending slightly beyond third (second to fifth) anal-fin soft ray base when depressed, not reaching posteriormost anal-fin soft ray base (tip of longest ray just reaching first anal-fin spine base in URM-P 4265); posteriormost soft ray with membranous connection to abdomen for ca. one-fourth of ray length. Caudal fin rounded, with 3 procurrent rays, 2 segmented unbranched rays and 5 segmented branched rays in dorsal series, and 3 procurrent rays, 3 segmented unbranched rays and 4 segmented branched rays in ventral series (usually 3 procurrent, 2 segmented unbranched and 5 segmented branched rays in both series; rarely with 4 procurrent rays in ventral series). Caudal peduncle moderately short, deep, its depth 69 % (63–88 %) of caudal-peduncle length.

Color of fresh specimens (based on Fig. 2). Ground color of head and body pinkish creamy-white (or white). A poorly defined dark red (or light brown) band on snout reaching from anteroventral portion of eye to anteroventral margin of lacrimal. A poorly defined dark red (or light brown) band with narrow white margin extending from below eye, across posterodorsal corner of maxilla to posteroventral margin of preopercle. A relatively broad (broadest on head) reddish-black (or black) band with narrow white margin from supraocular tentacle base, obliquely crossing eye and reaching posterior margin of preopercle (uppermost and middle preopercular spine bases); indistinct connection with a large black blotch (slightly smaller than eye) on subopercle. Three bands saddling nape; first band reddish-black (or black), just behind eye, at level between coronal spine and origin of parietal spine; second band at level of parietal spine, reaching central posterior margin of opercle at level of upper origin of pectoral-fin base; third band at level between nuchal spine and dorsal-fin origin, reaching upper origin of gill opening. Numerous (ca. 18) reddish-brown (or pale red to light brown) bands on side of body, narrow

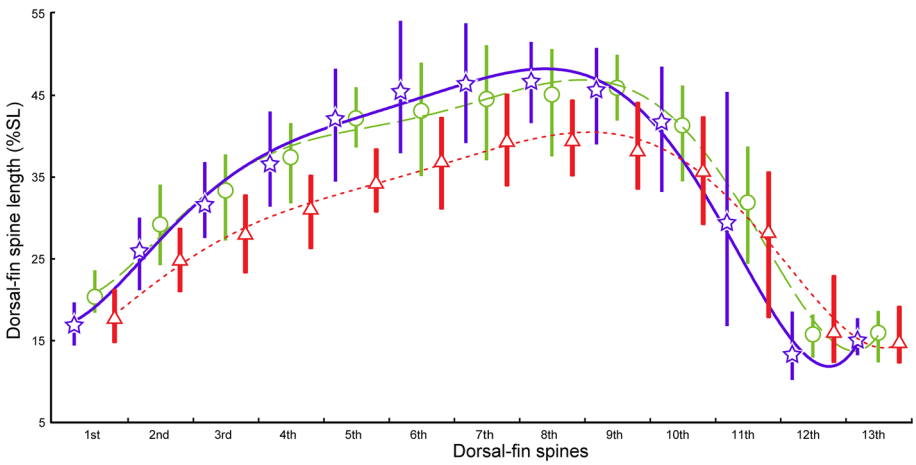

Fig. 6 Comparisons of dorsal-fin spine length (as % of standard length) between *Pterois paucispinula* sp. nov. and Sri Lankan and other specimens of *P. mombasae*. Symbols indicate means of each dorsal-fin spine length (*stars*, *P. paucispinula*; *circles*, Sri Lankan population of *P. mombasae*; *triangles*, other *P. mombasae*). *Vertical bars* indicate ranges of each dorsal-fin spine length (top and bottom indicate maximum and minimum values, respectively). Polynomial trendlines for means of each dorsal-fin spine length (*solid line*, *P. paucispinula*; *dashed line*, Sri Lankan population of *P. mombasae*; *dotted line*, other *P. mombasae*)

bands inserted between each relatively broad band running transverse and obliquely in anterior and posterior portions of trunk region; a band below fourth to sixth dorsal-fin spine bases broadest; caudal peduncle with ca. 6 (2–6) poorly defined narrow bands running obliquely. Body bands extending slightly onto dorsal-fin rays and membrane; more so onto anal-fin, a posteriormost trunk band reaching from penultimate dorsal-fin soft ray base to middle of third anal-fin spine. A moderately large black blotch (slightly smaller than iris) situated just above pectoral-fin base, partly (partly or mostly) behind pectoral fin, with a small white inner spot (ca. one-fourth to one-third of iris diameter). Two (or one) white margined reddish bands on chest. Dorsal-fin membrane and soft rays translucent, spines creamy-white; 2–6 reddish-brown (or, pale red to light brown) (lower portion) to black (upper portion) bands on each dorsal-fin spine; ca. 70 (37–74) small black spots on soft rays [juveniles (CMNH-ZF 15450, 30.9 mm SL and KAUM–I. 48423, 39.3 mm SL) with numerous small white spots on soft rays between each black spot]. Anal-fin membrane and rays translucent; ca. 44 (26–50) small black spots on soft rays (juveniles with numerous small white spots on soft rays between each black spot). Pectoral-fin membrane translucent (or pale red), a poorly defined narrow black line marginally, and a poorly defined broad black band basally on inner surface; ca. 21 (14–28) relatively large reddish-black (to black) blotches (subequal to pupil diameter) on membrane associated with non-thickened rays (first to tenth or eleventh rays); 2–3 (1–4) relatively small black blotches (slightly smaller than half pupil diameter) on each membrane between thickened rays (below eleventh ray); posterior portion of rays (free from membrane) creamy-white (or somewhat yellowish to reddish) with numerous brown to reddish-black bands [ca. 10 (5–13) bands on first ray]; pectoral-fin base with 2 white marginal dark red bands. Pelvic-fin membrane dark reddish, becoming gradually blackish toward base; rays creamy-white. Caudal-fin membrane translucent with ca. 86 (48–98) small black spots on ray (juveniles with numerous small white spots on soft rays marginally between each black spot). Images of live specimens (KPM-NR 1425, 25926, 35565, 62458–62460, 63160, and 82854) registered in the Image Database of Fishes in the Kanagawa Prefectural Museum of Natural History (KPM-NR; http://fishpix.kahaku.go.jp/fishimage-e/index.html).

Color of preserved specimens (Fig. 3a–d). Head and body creamy-white with brown to black markings; ca. 70 (26–71) small spots on soft-rayed portion of dorsal fin, 44 (26–47) on that of anal fin, 86 (41–96) on caudal fin.

Distribution. *Pterois paucispinula* is distributed in the western Pacific Ocean from northern Australia (Timor Sea) to southern Japan; eastwards to Wallis and Futuna Islands (Fig. 4). Collection depth data from seven specimens indicated a depth range of *P. paucispinula* between 1 and 440 m. However, the deepest collected specimen (MNHN 1995-737, 96.3 mm SL, collected by trawl from off Wallis and Futuna Islands in depths of 245–440 m) was most likely taken in a shallow water layer. The species has been photographed underwater several times (KPM-NR) at Pacific coast locations in central Japan (Matsunuma and Motomura 2011).

Etymology. The specific name *paucispinula* is derived from Latin for "few spines" in reference to the small number of spinules on the head and body ctenoid scales, in contrast to its closely related congener, *P. mombasae*.

Pterois mombasae (Smith 1957)

Pteropterus mombasae Smith 1957: 80, fig. 7, pl. 6, fig. D (type locality: Mombasa, Kenya); Mandrytsa 2001: 16 (phylogenetic material).

Pterois antennata (not of Bloch): Jones and Kumaran 1980: 637, fig. 544 (Kavarathi, Laccadive Islands, India; short description).

Pterois mombasae: Kotthaus 1979: 21, fig. 473 (Gulf of Aden and off Somalia; short description); Poss and Rama-Rao 1983: 24, unnumbered fig. (Sri Lanka, India, east coast of Africa; sort description, ecological note); Eschmeyer 1986: 467, fig. 149.9; pl. 25, fig. 149.9 (Indo-West Pacific; in part; short description); Randall 1995: 109, unnumbered fig. (Indo-West Pacific; in part; short description); Allen 1997: 76, pl. 19, fig. 4 (Indo-West Pacific; in part; short description); Poss 1999: 2330, unnumbered fig. (Indo-West Pacific; in part; keys); Allen et al. 2003: 370, unnumbered fig. (Indo-West Pacific; in part; short description); Kochzius et al. 2003: 396 (Kenya; molecular analysis material); Kuiter and Debelius 2006: 193, unnumbered figs. (Indo-Pacific; in part; figures taken in Indonesia); Motomura 2009: 65, unnumbered fig. (Andaman Sea; short description); Satapoomin 2011: 53 (Andaman Sea; list).

Holotype. SAIAB117, 128.8 mm SL, reef near Mombasa, Kenya.

Other specimens examined. Thirty-two specimens of 26.1–136.5 mm SL. THAILAND (ANDAMAN SEA): PMBC (uncatalogued), two specimens, 70.3–75.0 mm SL, Phuket.

SRI LANKA: AMS I. 33775-001, three specimens, 53.5–60.6 mm SL, Kalpitya (8.22N, 79.82E), P. Pethiyagodo; CAS 75358, 102.0 mm SL, Trincomalee (8°33′24″N, 81°14′42″E), 5–15 feet (ca. 1.5–4.6 m), T. Iwamoto, 17 May 1970; FMNH 75819, 83.4 mm SL, L. Woods et al., 4 March 1964; SMF 4209, 60.1 mm SL, 10 May 1957; SMF 4322, 99.7 mm SL, Trincomalee, R. Jonklaas, 21 May 1958; SMF 10055, three specimens,

Table 2 Frequency distribution of selected meristics in *Pterois paucispinula* sp. nov. and *P. mombasae*

	Dorsal-fin rays		Scale rows in longitudinal series											
	XIII, 10	XIII, 11	43	44	45	46	47	48	49	50	51	52	53	54
P. paucispinula	35[H]	2		1	1		3	2	2	14[H]	2			
P. mombasae	30[H]	3	1		2		1	3	3[H]	3	6	2	2	3

	Pored lateral-line scales				Scales above lateral line				Scales below lateral line				
	24	25	26	27	6	7	8	9	11	12	13	14	15
P. paucispinula	2	5[H]	3	2		8[H]	16	5	1	5	12	6	2[H]
P. mombasae	2	17[H]			2	6[H]	17	4	4	17[H]	3	3	

	Upper gill rakers		Lower gill rakers				Total gill rakers			
	4	5	9	10	11	12	13	14	15	16
P. paucispinula	21	14[H]	1	20	14[H]		1	13	15	6[H]
P. mombasae	18	15[H]		21	11[H]	1		10	16	4[H]

[H] includes holotype

84.5–108.2 mm SL, 1958; SMF 10728, 47.5 mm SL, 1968; SMF 11887, 75.8 mm SL, Trincomalee, October 1972.

INDIA: CAS 75355, 136.5 mm SL, Wadge Bank (8°01′60″N, 77°12′00″E), 27–33 fathoms (ca. 49–60 m), C. Koenig, 23 December 1969.

MALDIVES: BMNH 1901.12.31.26, 48.7 mm SL.

SEYCHELLES: SMF 12793, 78.1 mm SL, August 1969.

OMAN: BPBM 34447, 115.3 mm SL, Eagles' Retreat, near Mirbat (16°58′00″N, 54°42′50″E), 6–8 m, J. Randall and J. Mee, rotenone, 25 April 1990; BPBM 36050, 134.3 mm SL, off southwest side of Sawda Island, 21 m, J. Randall et al., rotenone, 7 November 1993.

KENYA: SMF 10056, 87.0 mm SL, Mombasa, 21 February 1966.

TANZANIA: SMF 10692, 128.0 mm SL, Dar es Salaam, 7 August 1969; SMF 12797, 82.4 mm SL, Dar es Salaam, 7 August 1969; SMF 12818, 111.1 mm SL, Dar es Salaam, 1973.

MOZAMBIQUE: CAS 65996, 53.7 mm SL, southeast of Beira, 3 October 1964; SAIAB 82480, 81.6 mm SL, off Mozambique (16°23.4′S, 40°02′E), P. Heemstra and E. Heemstra, bottom trawl, 4 November 2007.

MADAGASCAR: MNHN 1992-494, 112.7 mm SL, 16 August 1972; SMF 4210, 79.2 mm SL, Nosy Be (13°15′S, 48°15′E), February 1922.

SOUTH AFRICA: SAIAB 10741, 102.4 mm SL, off Durban, Oceanographic Research Institute; SAIAB 40285, two specimens, 26.1–27.6 mm SL, 2 km south of Kosi Bay mouth (26°53′S, 32°52′E), C. Buxton and P. Heemstra, 9 August 1992; SAIAB 46315, 38.4 mm SL, Aliwal Shoal, near Cathedral Reef (30°25′S, 30°49′E), C. Buxton and P. Heemstra, 19 June 1994; SAIAB 58553, 37.2 mm SL, Aliwal Shoal, near Hospital Road (30°18′S, 30°49′E), A. Bentley and P. Heemstra, 14 June 1998.

Diagnosis. A species of *Pterois* distinguished from other species of the genus by the following combination of characters: dorsal-fin rays XIII, 10 (rarely XIII, 11); pectoral-fin rays 17–20 [modally 18 in Sri Lankan population; 19 elsewhere (typical form; see under Geographic variations)]; scales below lateral line 11–14 (modally 12); body depth at anal-fin origin 27.4–35.2 (mean 32.2) % SL; head width 14.2–16.4 (15.2) % SL; postorbital length 17.7–21.3 (19.6) % SL; longest dorsal-fin spine length 35.1–51.1 (42.1) % SL; caudal-peduncle depth 11.0–13.0 (11.9) % SL; pectoral-fin with 6–48 relatively large (subequal to pupil diameter) black blotches on membrane, and several bands on posterior portion of rays (not attached to membrane); several narrow to wide vertical bands laterally on body, including caudal peduncle; ctenoid scale-covered area of body relatively extensive (entire body except for abdomen at ca. 90 mm SL; pectoral-fin base, ventrolateral, and caudal-peduncle portions almost always covered with ctenoid scales in young and adults greater than 50 mm SL).

Distribution. Although Matsunuma and Motomura (2011) and Matsunuma et al. (2011) recently recorded *P. mombasae* from Japan, the former stating that the species is widely distributed in the Indo-West Pacific Ocean, *P. mombasae* is now considered to be restricted to the Indian Ocean, from the east coast of Africa to the Andaman Sea (Fig. 4). Depth collection data for two specimens indicated a depth range 1.5–60 m. Kotthaus (1979) recorded the species from the Gulf of Aden and off Somalia in depths of 55–65 m, and Jones and Kumaran (1980) recorded it (as *P. antennata*) from the Laccadive Islands (off the west coast of India).

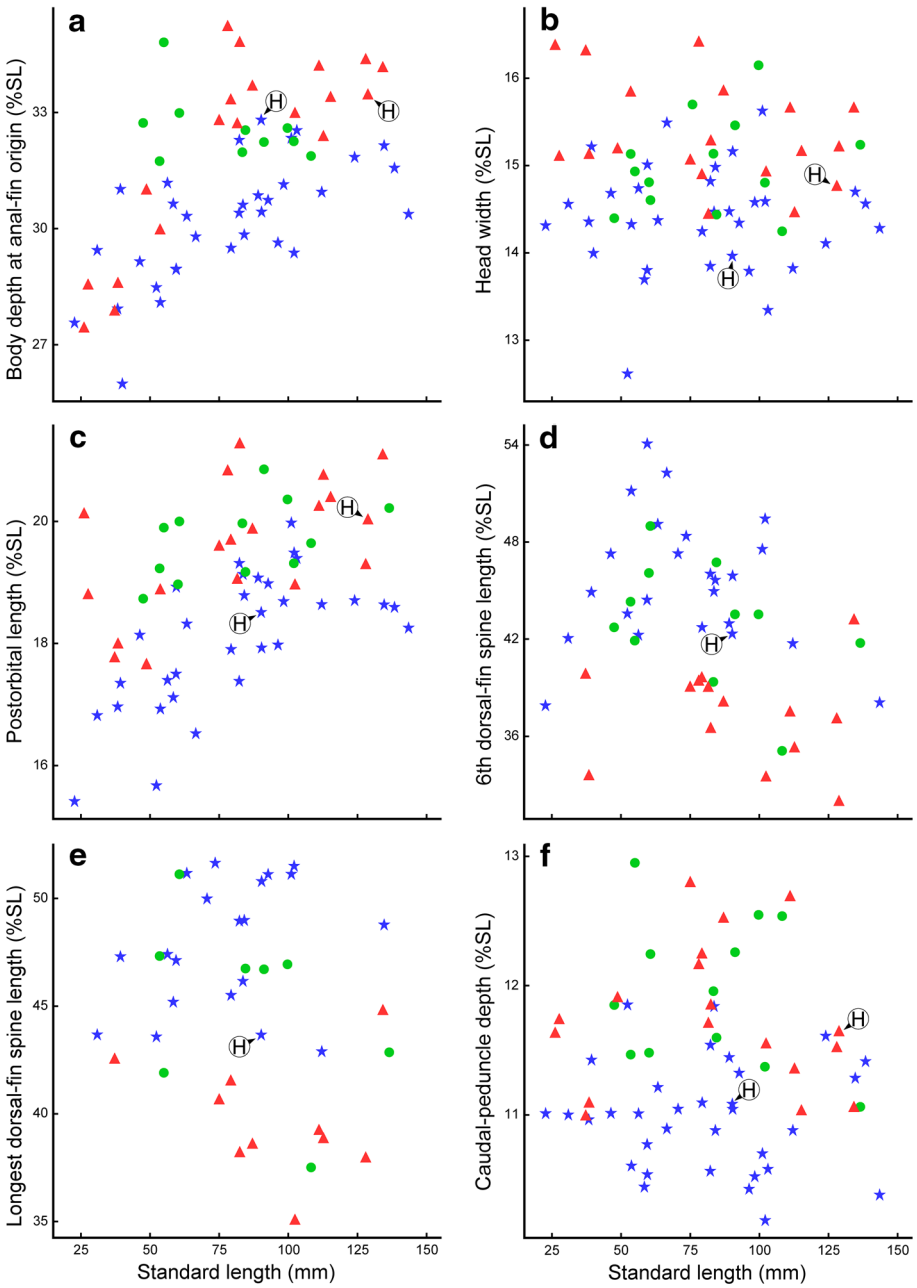

Fig. 7 Relationships of: **a** body depth at anal-fin origin; **b** head width; **c** postorbital length; **d** sixth dorsal-fin spine length; **e** longest dorsal-fin spine length; and **f** caudal-peduncle depth (all as % of standard length) to standard length (mm) in *Pterois paucispinula* sp. nov. (*stars*), Sri Lankan population of *P. mombasae* (*circles*) and other *P. mombasae* (*triangles*). *H* indicates holotype

Remarks. A description and illustration of the so-called *P. antennata* from the Laccadive Islands in Jones and Kumaran (1980) clearly shows the typical form of *P. mombasae* [19 pectoral-fin rays and relatively short dorsal-fin spine length (length of the longest dorsal-fin spine ca. 35.7 % SL; estimated from illustration)]. Although the specimens recorded by Kotthaus (1979) from the Gulf of Aden and off Somalia were not examined in the present study, his photograph of the Gulf of Aden specimen (fig. 374) is clearly identifiable as a typical example of *P. mombasae*.

Geographical variations. Morphological variations evident between specimens of *P. mombasae* from Sri Lanka and the remaining localities justified recognition of a distinct geographical (Sri Lankan) population [including CAS 75355 (Wadge Bank, off the northern tip of the Indian subcontinent) due to the close distributional proximity and morphological similarity to the latter]. The Sri Lankan specimens ($n = 13$, 47.5–136.5 mm SL; Fig. 3e–h) differed from other conspecifics ($n = 20$, 26.1–134.3 mm SL; Fig. 3i–l) in having relatively longer dorsal-fin spines - longest dorsal-fin spine length 37.5–51.1 (mean 45.1) %

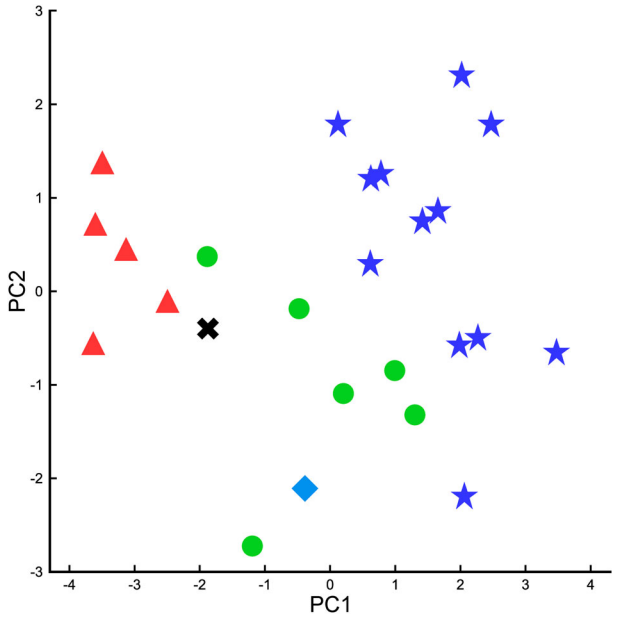

Fig. 8 Plots of principal component (PC) scores based on nine measurements for *Pterois paucispinula* sp. nov. (*stars*) and *P. mombasae* from Sri Lanka and India (*circles*), Andaman Sea (*cross*), Oman (*diamond*) and other Indian Ocean localities (*triangles*)

SL [vs. 35.1–44.8 (39.8) % SL] (Figs. 6, 7d–e); usually one less pectoral-fin ray 17–19 (modally 18) [vs. 18–20 (19)]; a slightly higher number of scales between the last dorsal-fin spine base and the lateral line 6–9 (8) (vs. 7 or 8); scales between the sixth dorsal-fin spine base and lateral line 7–9 (8) [vs. 7–8 (7)]; and pre-dorsal-fin scale rows 4–7 (6) [4–7 (usually 4 or 5)] (Table 3). Although the relative lengths of the dorsal-fin spines of the Sri Lankan specimens were variable, the range overlapping those of other material, several examples of the former had clearly longer dorsal-fin spines.

The results of PCA conducted for 9 measurements (see above) indicated subtle differences between the Sri Lankan and remaining specimens of *P. mombasae* (Fig. 8). The first two principal components (PC1 and PC2) accounted for 68.9 % of the variance of the original data, PC1 being loaded at similarly low levels on all measurements, and PC2 relatively heavily loaded on head width and postorbital length [factor loadings are shown in Electronic Supplemental Material (ESM) Table S1]. Plots for the Sri Lankan and remaining *P. mombasae* slightly overlapped. Although two specimens of *P. mombasae* from the Andaman Sea appeared typical of the species in having relatively short dorsal-fin spines (longest dorsal-fin spine length 40.7 % SL; $n = 1$) and 19–20 pectoral-fin rays, PCA located them between the Sri Lankan and remaining specimens. Two Omani specimens, similar to the Sri Lankan specimens in having 18 pectoral-fin rays and relatively long dorsal-fin spines (longest dorsal-fin spine length 44.8 % SL; $n = 1$), were equivocal, one falling into the grouping of Sri Lankan specimens (Fig. 8).

The Sri Lankan specimens of *P. mombasae* were similar to *P. paucispinula* in having usually 18 pectoral-fin rays (Table 3) and relatively long dorsal-fin spines (Fig. 7; Table 1), the number of pectoral-fin rays usually being considered as a useful diagnostic character for several Pteroinae species (Matsunuma et al. 2013b; Matsunuma and Motomura 2013a–b), whereas dorsal-fin spine lengths were variable within species and populations. In any case, with the exception of pectoral-fin ray numbers and dorsal-fin spine lengths, the diagnostic characters separating Sri Lankan *P. mombasae* from *P. paucispinula* were consistent with those of *P. mombasae* elsewhere. Therefore, the Sri Lankan specimens were identified herein as *P. mombasae* and the aforementioned differences between the two groups regarded as intraspecific geographic variations. The non-Sri Lankan specimens were regarded as the typical form of *P. mombasae* because of their close agreement with the holotype of the species. Additional specimens from eastern distributional borders, characterized by having a form intermediate between *P. mombasae* and *P. paucispinula*, should be examined in greater detail, including genetic appraisal, with the prospect of further clarification of the phylogeography and relationships of the two species.

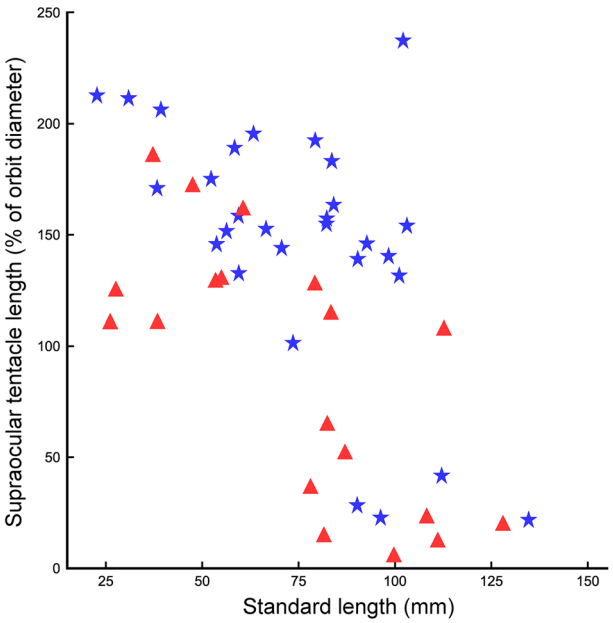

Fig. 9 Relationship of supraocular tentacle length (as % of orbit diameter) to standard length (mm) in *Pterois paucispinula* sp. nov. (*stars*) and *P. mombasae* (*triangles*), showing relative decreases in supraocular tentacle length with growth

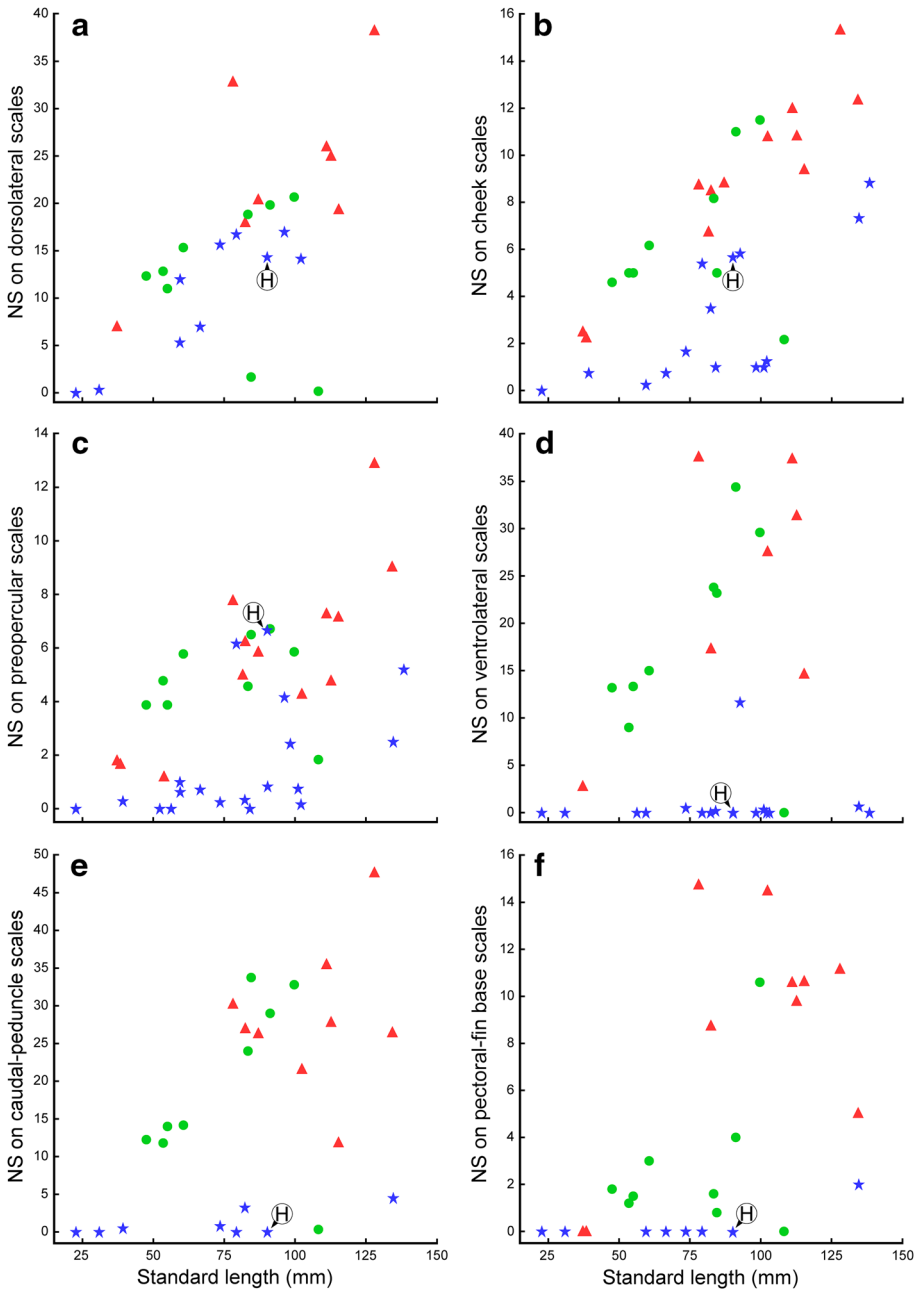

Fig. 10 Relationships of number of spinules (NS) on: **a** dorsolateral scales; **b** cheek scales; **c** preopercular scales; **d** ventrolateral scales; **e** caudal-peduncle scales; and **f** pectoral-fin base scales to standard length (mm) in *Pterois paucispinula* sp. nov. (*stars*), Sri Lankan population of *P. mombasae* (*circles*) and other *P. mombasae* (*triangles*). *H* indicates holotype

Discussion

Morphological changes with growth. Almost all head spine numbers increase with growth in both *Pterois paucispinula* and *P. mombasae*, the number of nasal spines in *P. paucispinula*, for example, being one in juvenile and young specimens, but sometimes two in specimens more than ca. 100 mm SL, as in *Parapterois* (see Motomura 2004a; Matsunuma et al. 2013a) and *Pterois brevipectoralis* (Mandrytsa 2002) (see Matsunuma and Motomura 2013b). In contrast, the numbers of supraocular, coronal, tympanic and preopercular spines remained unchanged with growth, following complete development of the head spines.

Growth-related changes in the proportions of some body parts were also recognized in *P. paucispinula* and *P. mombasae*, as in several other members of the subfamilies Pteroinae (Matsunuma et al. 2013b; Matsunuma and Motomura 2013b) and Scorpaeninae (e.g., Motomura et al. 2005b, c, 2011b). Analysis of 54 measurements of *P. paucispinula* indicated that relative lengths of the orbit diameter and almost all fin rays, except for the first dorsal-

fin spine, first anal-fin spine, first pectoral-fin ray and longest pelvic-fin soft ray, tended to decrease as a percentage of SL with growth (only the sixth dorsal-fin spine shown in Fig. 7d). In contrast, body depth at the anal-fin origin, postorbital length and suborbital depth became relatively greater with growth (body depth and postorbital length shown in Fig. 7a, c). Other growth-related changes in *P. mombasae* included positive correlations in body depth at the anal-fin origin and body width, and negative correlations in orbit diameter, first dorsal-fin spine length, thirteenth dorsal-fin spine length, dorsal-fin soft ray length, all anal-fin ray lengths, pelvic-fin soft ray length and caudal-fin length.

The supraocular tentacle tends to become shorter (reduced in size) with growth in *P. paucispinula* and *P. mombasae* (Fig. 9), as in *P. antennata* (see Matsunuma and Motomura 2011) and *P. brevipectoralis* (see Matsunuma and Motomura 2013b). The smallest examined specimen of *P. paucispinula* (BSKU 100149, 22.7 mm SL) had a long supraocular tentacle (length more than twice orbit diameter), possessing six pairs of lateral branches and five black bands, whereas a large specimen (URM-P 4264, 134.7 mm SL) had a low skin flap (ca. one-fifth orbit diameter) on the supraocular without branches or bands.

The number of spinules on the head and body ctenoid scales increases with growth in both *P. paucispinula* and *P. mombasae* (Fig. 10), as do the numbers of spots on the median fins and blotches on the pectoral fin.

Species comparisons. Smith (1957) regarded *Pteropterus* as a valid genus, distinguishing it from *Pterois* on the basis of several external characters, including: dorsolateral body covered with ctenoid scales (vs. all scales cycloid in *Pterois*); fewer than 65 longitudinal series scale rows (vs. more than 65); suborbital ridge close to orbit (vs. widely separated); and pectoral-fin rays more than 15 (vs. less than 15). According to Smith (1957) and Mandrytsa (2001, 2002), the following five nominal species of *Pterois*, currently regarded as valid, can be assigned to *Pteropterus*, being distinguished from other congeners by the above-mentioned characters: *P. antennata*, *P. brevipectoralis*, *P. mombasae*, *Pterois radiata* (Cuvier *in* Cuvier and Valenciennes 1829) and *Pterois sphex* Jordan and Evermann 1903. The new species clearly also belongs to *Pteropterus* sensu Smith(1957). Examination of the available type specimens or original descriptions of all nominal species belonging to *Pteropterus* sensu Smith(1957) indicates that *P. paucispinula* is readily distinguishable from the others, except for *P. mombasae*, by the combination of the following characters: dorsal-fin rays usually XIII, 10; pectoral-fin rays usually more than 18; numerous blotches on pectoral-fin membrane; and several bands posteriorly on the pectoral-fin rays (not associated with fin membrane). However, *P. paucispinula* differed from *P. mombasae* in having usually one fewer pectoral-fin rays, 17–19 (modally 18) [vs. 18–20 (19) in *P. mombasae*, except for the Sri Lankan population, 18 or 19 (18) rays]; usually one more scale below the lateral line 11–15 (13) [vs. 11–14 (12)]; slightly shallower body depth at the anal-fin origin 26.0–32.8 (mean 30.2) % SL [vs. 27.4–35.2 (32.2) % SL], head width 12.6–15.6 (14.4) % SL [vs. 14.2–16.4 (15.2) % SL] and caudal-peduncle depth 9.9–11.9 (11.0) % SL [vs. 11.0–13.0 (11.9) % SL]; and slightly shorter postorbital length 15.4–20.0 (18.1) % SL [vs. 17.7–21.3 (19.6) % SL] (Fig. 7a–c, f). *Pterois paucispinula* tended to have relatively longer dorsal-fin spines compared with *P. mombasae*, except for the Sri Lankan population, e.g., fifth dorsal-fin spine 34.4–48.2 (mean 42.2) % SL in *P. paucispinula* [vs. 38.6–46.0 (42.2) % SL in the Sri Lankan population; 30.7–38.3 (34.3) % SL in remaining *P. mombasae*]; sixth dorsal-fin spine 37.9–54.1 (45.5) % SL [vs. 35.1–49.0 (43.1) % SL; 32.0–42.1 (37.4) % SL]; seventh dorsal-fin spine 39.2–53.8 (46.5) % SL [vs. 37.1–51.1 (44.6) % SL; 33.8–45.0 (39.4) % SL]; eighth dorsal-fin spine 41.6–51.5 (46.8) % SL [vs. 37.5–50.6 (45.1) % SL; 35.1–44.2 (39.5) % SL]; ninth dorsal-fin spine 39.0–51.7 (45.7) % SL

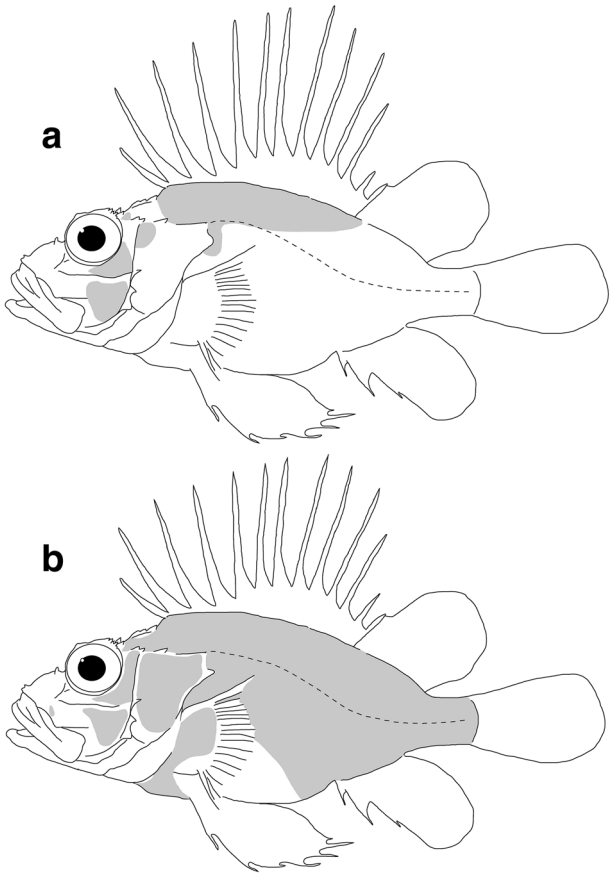

Fig. 11 Areas of ctenoid scales (shaded) in **a** *Pterois paucispinula* sp. nov. and **b** *P. mombasae*. Based on **a** BSKU 61062, 90.2 mm SL, holotype, Japan and **b** SMF 12797, 82.4 mm SL, Tanzania

[vs. 41.9–50.0 (45.9) % SL; 33.5–44.0 (33.5) % SL]; and longest dorsal-fin spine 42.9–51.7 (47.8) % SL [vs. 37.5–51.1 (45.1) % SL; 35.1–44.8 (39.8) % SL] (Figs. 6, 7d–e). The result of PCA conducted for 10 measurements of the two species showed only a slight overlap of the *P. paucispinula* and *P. mombasae* groups (Fig. 8), despite the limited number of specimens available for the analysis.

Furthermore, *P. paucispinula* tended to have small areas of the head and body covered with ctenoid scales, in contrast with *P. mombasae* including the Sri Lankan population. Counts of ctenoid scale spinules on the head and body showed significant differences between the two species (Fig. 10), notwithstanding a 108.2 mm SL specimen of *P. mombasae* (SMF 10055) from Sri Lanka having undeveloped ctenoid scales entirely covering the head and body, whereas an 84.5 mm SL specimen from the same lot had an irregularly low number of spinules on the dorsolateral scales (Fig. 10). These two examples are regarded herein as abnormal and are therefore excluded from the following discussion. *Pterois paucispinula* is distinguished from *P. mombasae* by having relatively fewer spinules on the pectoral-fin base scales 0–2.0 (mean 0.3) [vs. 0–14.8 (6.1) in *P. mombasae*], ventrolateral scales 0–11.7 (0.8) [vs. 2.8–42.0 (23.8)] and caudal-peduncle scales 0–4.5 (1.1) [vs. 11.8–47.7 (25.1)] (Fig. 11d–f). Furthermore, *P. paucispinula* lacks ctenoid scales on those areas until ca. 80 mm SL, with a small number of ctenoid scales in some larger adults. Both species have ctenoid scales on the cheek and preopercle area, although *P. paucispinula* tends to have fewer spinules on the scales compared with *P. mombasae*, viz., number of cheek scale spinules 0–8.8 (mean 2.8) in *P. paucispinula* vs. 2.3–15.3 (8.2) in *P. mombasae*; preopercle scale spinules 0–6.7 (1.7) vs. 1.1–12.9 (5.6) (Fig. 10b–c). In contrast, no significant difference between the species was apparent in spinule numbers on the dorsolateral scales (Fig. 10a). Areas on the head and body covered by ctenoid scales at ca. 90 mm SL in the two species are shown in Fig. 11. At this stage (Fig. 11a), *P. paucispinula* has large ctenoid scale areas on the cheek and preopercle, with smaller patches overlaying the suprapostorbital and anterodorsal part of the opercle. Additionally, ctenoid scales occur dorsolaterally on the body (bordered by the nuchal and lower post-temporal spine bases, the lateral line and base of the spinous portion of the dorsal fin). At the same stage (Fig. 11b), *P. mombasae* has similarly large ctenoid scale areas on the cheek and preopercle, but with the opercle also entirely covered with ctenoid scales. Furthermore, the ctenoid scale area on the body extends anteriorly to the suprapostorbital region. In addition, *P. mombasae* has ctenoid scales over almost all of the body, including the pectoral-fin base, chest and caudal peduncle, but excluding the abdomen. Ctenoid scale areas become more extensive with growth in both species, with large adult *P. paucispinula* having ctenoid scales on the ventrolateral portion of the body, caudal peduncle, pectoral-fin base, a large area over the opercle and the lacrimal. However, the development of ctenoid scales is clearly more rapid in *P. mombasae*.

Moreover, genetic analysis indicated a substantial degree of genetic divergence between *P. mombasae* and *P. paucispinula*. Comparisons on the basis of 333 bp of the mtDNA cytochrome *b* gene showed differences ranging from 2.5 % to 2.7 % between the two species; in contrast, the intraspecific sequence difference was 0.7 % in *P. mombasae*. The sequence data for *P. mombasae* (AJ429427–429428) was taken from Kochzius et al. (2003), who used material from Kenya.

Pterois paucispinula sp. nov. is also similar to *Pterois antennata* in having relatively narrow bands on the body and the pectoral fins with more than 17 rays. However *P. paucispinula* could be easily distinguished from *P. antennata* as follows: dorsal-fin rays usually XIII, 10 (rarely XIII, 11) [vs. usually XII, 11 (rarely XII, 10 or XII, 12) in *P. antennata*]; pectoral-fin rays usually more than 18 (rarely 17) [vs. usually less than 17 (rarely 18)]; and several bands on the posterior portion of the upper pectoral-fin rays (free from membrane) (vs. bands absent) (Matsunuma and Motomura 2011; this study). *Pterois sphex* and *P. brevipectoralis*, known from the Hawaiian Islands and southwestern Indian Ocean (Mascarene Islands and Saya de Malha Bank), respectively, are also similar to *P. paucispinula* in having dorsal-fin rays XIII, 10 and several bands posteriorly on the upper pectoral-fin rays. However, *P. paucispinula* can be clearly distinguished from *P. sphex* by having usually more than 18 pectoral-fin rays (vs. 15–16 in *P. sphex*), the body with approximately 18 relatively narrow vertical bands (vs. 4–5 broad vertical bands with narrow bands between) and several blotches, but without distinct vertical bands on the pectoral-fin membrane (vs. 3–13 vertical narrow bands without blotches) (Eschmeyer and Randall 1975; Matsunuma and Motomura 2013b; this study). It can be distinguished from *P. brevipectoralis* by having more than 17 pectoral-fin rays (vs. less than 16 in *P. brevipectoralis*) and skin flaps on the lacrimal and posterior margin of the preopercle not becoming larger with growth (vs. becoming extremely large, length greater than orbit diameter in large adults) (Mandrytsa 2002; Matsunuma and Motomura 2013b; this study). *Pterois paucispinula* is also readily distinguished from *P. radiata* by pectoral-fin ray number (usually more than 18 vs. 16–17 in *P. radiata*) and the nature of the bands on the caudal peduncle (2–6 narrow transverse bands vs. a single broad horizontal band in *P. radiata*) (Smith 1957; this study).

Comparative materials examined. *Pterois antennata*: 80 specimens (14.0–153.9 mm SL): JAPAN: BSKU 6942, 109.8 mm SL; BSKU 51076, 58.5 mm SL; BSKU 79021,

102.2 mm SL; BSKU 86405, 86.1 mm SL; BSKU 100096, 38.0 mm SL; BSKU 103166, 111.1 mm SL; FAKU 99045, 77.0 mm SL; FAKU 99086, 84.5 mm SL; HUMZ 53491, 118.1 mm SL; KAUM–I. 6436, 133.6 mm SL; KAUM–I. 6438, 120.1 mm SL; KAUM–I. 6586, 132.9 mm SL; KAUM–I. 29634, 72.8 mm SL; KAUM–I. 29635, 73.5 mm SL; KAUM–I. 29745, 100.6 mm SL; KAUM–I. 29746, 153.9 mm SL; KPM-NR 21471, 93.3 mm SL; KPM-NR 22989, 23.5 mm SL; KPM-NR 26918, 36.1 mm SL; NSMT-P 30809, 58.5 mm SL; NSMT-P 80768, 72.8 mm SL; NSMT-P 90778, 70.0 mm SL; URM-P 1324, 104.8 mm SL; URM-P 18654, 116.4 mm SL; URM-P 36009, 77.3 mm SL. TAIWAN: ASIZP 57316, 95.3 mm SL; ASIZP 59074, 66.0 mm SL; ZMB 16148, 31.3 mm SL. PHILIPPINES: AMS I. 40144-010, five specimens, 14.0–73.2 mm SL; NSMT-P 34677, 112.3 mm SL; NTOU-P 20080414-101, 106.4 mm SL; NTOU-P 20080414-116, 68.1 mm SL; SMF 10025, 66.2 mm SL; USNM 99021, 112.8 mm SL. INDONESIA: KPM-NR 14031, 74.5 mm SL; NSMT-P 62052, 72.3 mm SL; NSMT-P 63740, 84.8 mm SL; NSMT-P 71523, 49.0 mm SL;NSMT-P 71676, 76.6 mm SL; NSMT-P 102043, 72.2 mm SL; NSMT-P 102044, 49.0 mm SL; SMF 4204, 89.9 mm SL; ZMB 796, lectotype of *Scorpaena antennata* Bloch 1787, 117.6 mm SL. MICRONESIA: USNM 223578, 77.6 mm SL. GUAM: AMS I. 39371-001, 87.5 mm SL. PAPUA NEW GUINEA: NMV A13698, 121.7 mm SL; OMNH 13808, 109.6 mm SL. SOLOMON ISLANDS: AMS I. 39040-045, 57.5 mm SL. VANUATU: USNM 356588, 53.4 mm SL. WALLIS AND FUTUNA: USNM 374803, 81.5 mm SL. TONGA: USNM 337077, three specimens, 78.1–106.9 mm SL. COOK ISLANDS: FMNH 16311, three specimens, 49.2–88.8 mm SL; FMNH 44140, 22.8 mm SL. FRENCH POLYNESIA: MNHN 1984-279, 87.3 mm SL. AUSTRALIA: AMS I. 4119, 51.6 mm SL; AMS I. 20441-005, 83.2 mm SL; AMS I. 20756-044, 96.1 mm SL; AMS I. 20965-025, 88.8 mm SL; AMS I. 23847-027, 83.1 mm SL; FAKU 113358, 69.0 mm SL. INDIA: SMF 28932, 122.9 mm SL. SRI LANKA: SMF 4327, 85.2 mm SL. RED SEA: SMF 12887, 77.1 mm SL. YEMEN: SMF 4625, 128.2 mm SL; SMF 4626, 105.1 mm SL. SOMALIA: FMNH 484, holotype of *Pterois ellioti* Meek 1899, 48.8 mm SL. KENYA: SMF 9100, 67.5 mm SL; SMF 9932, 74.3 mm SL. MALDIVES: SMF 5386, 78.9 mm SL; SMF 9770, 30.5 mm SL. MAURITIUS: USNM 349900, 88.1 mm SL.

Pterois brevipectoralis: 10 specimens (49.2–117.9 mm SL) listed in Matsunuma and Motomura (2013b).

Pterois radiata: 45 specimens (23.3–151.4 mm SL): JAPAN: BSKU 2712, 66.8 mm SL; BSKU 3239, 57.7 mm SL; BSKU 3317, 46.4 mm SL; BSKU 63779, 61.6 mm SL; BSKU 74108, 83.3 mm SL; BSKU 106150, 24.5 mm SL; FAKU 6113, 98.7 mm SL; FAKU 98972, 56.9 mm SL; KAUM–I. 41254, 93.9 mm SL; KPM-NR 16856, 103.0 mm SL; KPM-NR 22714, 56.3 mm SL; NSMT-P 31593, 23.3 mm SL; NSMT-P 55493, 109.0 mm SL; NSMT-P 104342, 52.3 mm SL. TAIWAN: ASIZP 55046, 80.5 mm SL; ASIZP 56910, 123.8 mm SL; NMMB 10536, 129.3 mm SL;NTOU-P 2007-04-07-002, 80.2 mm SL; NTOU-P 20070625-008, 67.2 mm SL; NTOU-P 20070710-201, 88.9 mm SL; NTOU-P 20071111-401, 105.5 mm SL; NTOU-P 20071111-701, 112.7 mm SL. INDONESIA: KPM-NR 14056, 57.8 mm SL; KPM-NR 14057, 59.1 mm SL; NCIP 2024, 91.5 mm SL. KIRIBATI: NSMT-P 23485, 49.2 mm SL; NSMT-P 23266, two specimens, 52.2–55.8 mm SL. SAMOA: NMV A5290, 126.9 mm SL. FRENCH POLYNESIA: FMNH 23176, 151.4 mm SL; LACM 54162.001, 142.0 mm SL; MNHN 1984-280, two specimens, 103.6–108.3 mm SL; MNHN 6625, holotype of *Pterois* (*Pseudomonopterus*) *vittata* Sauvage 1878, 58.4 mm SL. MALDIVES: FMNH 75832, three specimens, 65.4–120.2 mm SL. SEYCHELLES: SMF 12794, two specimens, 76.5–94.9 mm SL; SMF 12882, 64.7 mm SL. SAUDI ARABIA: SMF 349, holotype of *Pterois cincta* Rüppell 1838, 141.5 mm SL. TANZANIA: SMF 12882, 64.7 mm SL. COMOROS: SAIAB 30752, 88.5 mm SL. MADAGASCAR: AMS 28107-013, 90.8 mm SL. MAURITIUS: USNM 349900, 88.1 mm SL.

Pterois sphex: six specimens (40.6–111.7 mm SL), including holotype of *Pterois sphex* Jordan and Evermann 1903, listed in Matsunuma and Motomura (2013b).

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