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Redescription of *Paragaleus tengi* (Chen, 1963) (Carcharhiniformes: Hemigaleidae) and first record of *Paragaleus randalli* Compagno, Krupp & Carpenter, 1996 from the western North Pacific

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Abstract

Paragaleus tengi was previously considered to be the only member of this genus occurring in the Western Pacific, with *Paragaleus randalli* occurring in the Indian Ocean and allopatric in distribution. Recent molecular and morphological studies showed that *P. randalli* also occurs in the Western Pacific with records from Thailand, Malaysia and Indonesia previously mostly incorrectly attributed to *P. tengi*. This paper provides a redescription of *P. tengi* and confirms the presence of *P. randalli* from off Taiwan in the western North Pacific. These two species are morphologically very similar in appearance but differ in meristics, dentition, some coloration attributes and minor morphological characters. The conservation status of these two species needs to be reassessed based on this new information.

Key words: *Paragaleus tengi*, Hemigaleidae, redescription, Taiwan, *Paragaleus randalli,* new record

Introduction

The genus *Paragaleus* Budker, 1935, proposed for *Paragaleus pectoralis* (Garman, 1906), consists of four species: *P. leucolomatus* Compagno & Smale, 1985, *P. pectoralis*, *P. randalli* Compagno, Krupp & Carpenter, 1996, and *P. tengi* (Chen, 1963). *Paragaleus pectoralis* was described based on a specimen from the "Aquarial Gardens", a marine aquarium, from which Garman (1906) stated that their collections were made off the coasts of Massachusetts and Rhode Island. Interestingly, this species is common in the Eastern Atlantic, but the only record in the Western Atlantic is the holotype. Compagno (1984) suggested that this holotype may have been based on a specimen that crossed the Atlantic on the North Equatorial Current and rode the Gulf Stream up to off New England. He also suggested the possibility that the locality data for the type specimen was erroneous and could have actually come from West Africa. However, it seems unlikely that a shark specimen was transported alive across the Atlantic at that time due to limited aquarial technology.

Chen (1963) described *Negogaleus tengi* based on three specimens collected from Taichung fish market in Taiwan. The genus *Negogaleus* was proposed by Whitley (1931) for *Hemigaleus microstoma* Bleeker, 1852, but is considered an unneeded replacement name for *Hemigaleus* Bleeker, 1852. Compagno (1979) placed *N. tengi* into the genus *Paragaleus* based on its dentition, which he considered to be intermediate between *Paragaleus* and *Hemigaleus*, and redefined the genus to accommodate this species. Compagno (1979) included *Negogaleus longicaudatus* Bessednov, 1966, from the South China Sea, as a probable junior synonym of *P. tengi*. Unfortunately, the three types of *P. tengi* (THUP 1802–4) are believed to be lost (Ho & Shao, 2011). *Paragaleus tengi* is known from the Gulf of Thailand, Vietnam, southern Japan, Taiwan and off Hong Kong (Compagno *et al.*, 2005). Although also recorded from off Indonesia and Borneo (White *et al.*, 2006; Last *et al.*, 2010), these were recently confirmed as misidentifications of *P. randalli* (Naylor *et al.*, 2012), originally considered to be restricted to the Western Indian Ocean. Weigmann (2012) recorded *P. randalli* off eastern Thailand, representing the most easterly records of this species and extensively widening the known distribution.

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During a recent visit to the museum collections of Taiwan, two specimens at the Taiwan Fisheries Research Institute in Keelung identified as *Paragaleus tengi* were examined. While these two specimens are clearly a species of *Paragaleus*, they were found to not be conspecific with *P. tengi*. The identity of this second *Paragaleus* species is discussed. During examination of the carcharhinid material at the fish collection at the National Museum of Marine Biology and Aquarium in Pingtung, a specimen previously identified as *Carcharhinus dussumieri* was re-identified as *P. tengi*. This specimen was collected from Wu-chi (Taichong), the same location as the lost type series. Thus, this specimen was considered a suitable specimen to be designated as the neotype of this species. *Paragaleus tengi* is herein redescribed and a key to the hemigaleid species found in Taiwanese waters is provided.

Methods

The neotype herein designated (NMMB-P6452) and two other specimens (GVF-83 and GVF-87) of *P. tengi* were measured in full. The two *Paragaleus* sp. from TFRI (FRIP 03574) were also measured. For comparison, the holotype (BPBM 21196), two paratypes (BPBM 19923, SU 67145) and 6 other specimens (AB 4B-260 A [2 specimens], FAO/DAN uncatalogued, SV uncatalogued [2 specimens] and TRR 70–14) of *P. randalli*; and two specimens of *P. pectoralis* (AMNH 44120 and AMNH 97267) were also measured. In the redescription, morphometric and meristic values for the neotype of *P. tengi* are given first followed in parantheses by the ranges of the two other specimens. Morphometrics methodology follows Compagno (2001). Meristics were taken from radiographs of the neotype of *P. tengi*, the two *Paragaleus* sp. from TFRI, and 3 specimens of *P. randalli* (CSIRO H 7409–01, CSIRO H 7409–02 and CSIRO H 7410–01). Ranges for the vertebral counts of the 3 non-type *P. tengi* specimens were taken from Compagno (1984). Additional meristic information was taken from Compagno & Smale (1985) and Compagno *et al.* (1996). Vertebral counts were obtained separately for trunk (monospondylous centra), precaudal (monospondylous + diplospondylous centra to origin of upper lobe of the caudal fin) and caudal (centra of the caudal fin) regions. Tooth counts were obtained *in situ* from the neotype and three additional jaw specimens (PMH 197–01, PMH 197–02 and PMH 197–03). Additional tooth counts were taken from Chen (1963). Specimens, including types, are referred to by the following prefixes for their catalog, registration and field numbers: AB—RV "Anton Bruun" station numbers, in SAM; AMNH—American Natural History Museum, New York, USA; BPBM—Bernice P. Bishop Museum, Honolulu, Hawaii; CAS—California Academy of Sciences fish collection, San Francisco, California, USA; collection; CSIRO—Commonwealth Scientific and Industrial Research Organisation, Hobart, Tasmania, Australia; FAO/DAN—FAO/DANIDA Lemuru station 1-14, in SAM collection; FRIP—Taiwan Fisheries Research Institute, Keelung, Taiwan; GVF—George Vanderbilt Foundation, in CAS collection; NMMB-P—National Museum of Marine Biology, Pingtung, Taiwan; PMH, Mark Harris personal collection (jaws only); SU—Stanford University, in CAS collection; SV—Smith-Vaniz field number for FAO collections, Arabian (Persian) Gulf, in SAM collection; TRR—Tyson R. Roberts field number for southern Indian specimen in CAS collection. Note that the holotype and two paratypes registered as BPBM and SU specimens are currently located in the SAM collection.

Paragaleus tengi **(**Chen, 1963)
(Figures 1– 3, Table 1)

Negogaleus tengi Chen, 1963: 77, fig. 24 (Taiwan); Chen & Yu, 1986: 140 (Taiwan); Yu, 1988: 8 (Taiwan).
Negogaleus longicaudatus Bessednov, 1966: 302, figs 1 and 2 (South China Sea).
Paragaleus tengi (Chen, 1963): Compagno, 1984: 444, fig.; Compagno & Smale, 1985: 2; Compagno, 1988: 259, fig. 18.1, pls 20K, 21K; Compagno *et al.*, 1996: 392; Compagno, 1998: 1311, fig.; Shen *et al.*, 1993: 60; Chu, 1994: 132; Nakabo, 2002: 136, fig.; Compagno *et al.*, 2005:287, fig., pl. 49; Shao *et al*., 2008: 236; Ho & Shao, 2011: 18; Shen, 2011: fig.

Neotype. NMMB-P6452 (formerly THUP 1807), adult male 745 mm TL, Taichong, Taiwan, 20 Apr 1962, collected by M.-J. Yu. Herein designated.

Other material examined in this study. GVF HK-83, adult male 862 mm TL, south of Hong Kong, South China Sea; GVF HK-87, adult male 876 mm TL, about 100 miles southwest of Hong Kong, South China Sea; PMH 197–01, female 930 mm TL, PMH 197–02, female 925 mm TL, PMH 197–03, male 810 mm TL, Penang, Malaysia.

Other material examined by Compagno (1988). UMMZ 177114, adult male 784 mm TL, East China Sea, from Nagasaki, Japan.

Diagnosis. A medium-sized hemigaleid shark with the following combination of characters: snout narrowly parabolic in dorsoventral view, narrowly pointed in lateral view, preoral snout about 1.1 times mouth width; dorsal fins moderately tall and not falcate; mouth long, symphysis extending well anterior to upper labial furrows; upper labial furrows relatively short, 1.4–1.8% TL; pectoral fins broad and slightly falcate; claspers of adults moderately long, outer length 5.7–6.6% TL; teeth in upper and lower jaws dimorphic; upper teeth compressed and distally oblique with smooth mesial edges and five or six large distal cusplets; lower teeth narrow, triangular and essentially perpendicular to distally angular with basal lobes on mesial/distal shoulders of crown feet in anteriors and distal cusplets in posteriors; teeth in 26–30/25–32 rows; total vertebral centra 127–135; grey dorsally, whitish ventrally; no prominent fin markings; no dark markings on underside of prenarial snout; no horizontal yellow lines on sides of body.

Description. Proportions as percentages of total length for the neotype and two other specimens are presented in Table 1.

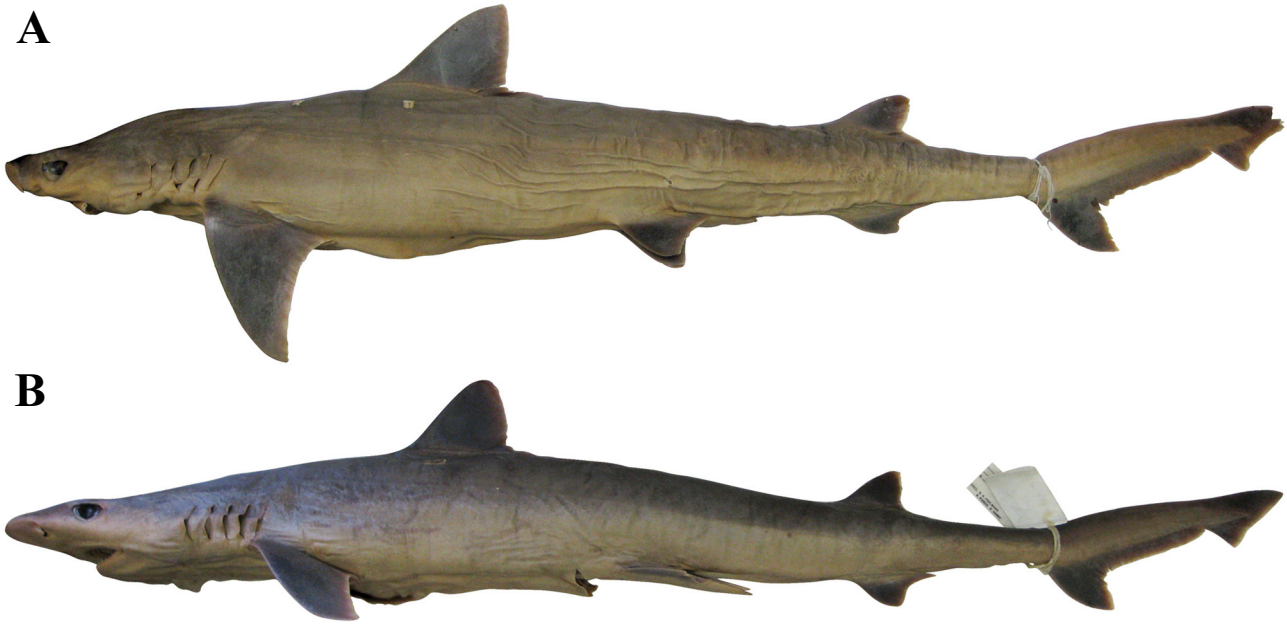

FIGURE 1. Lateral view of *Paragaleus tengi*. A. neotype NMMBP 6452 (adult male 745 mm TL); B. GVF HK-87 (adult male 876 mm TL).

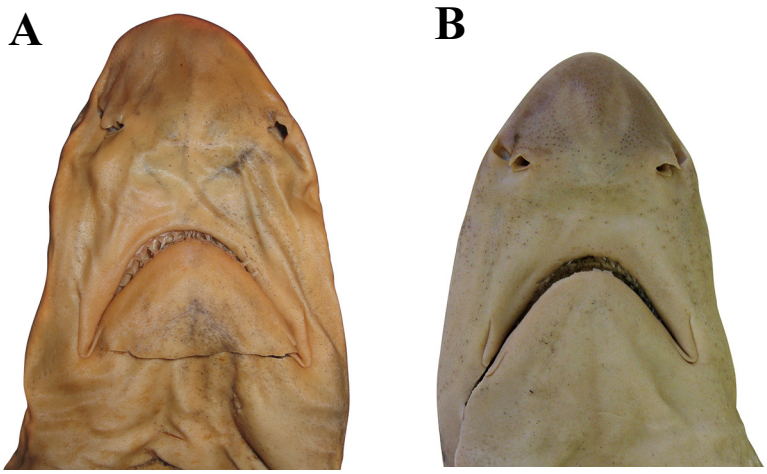

FIGURE 2. Ventral view of head of *Paragaleus tengi*. A. neotype NMMBP 6452 (adult male 745 mm TL); B. GVF HK-87 (adult male 876 mm TL).

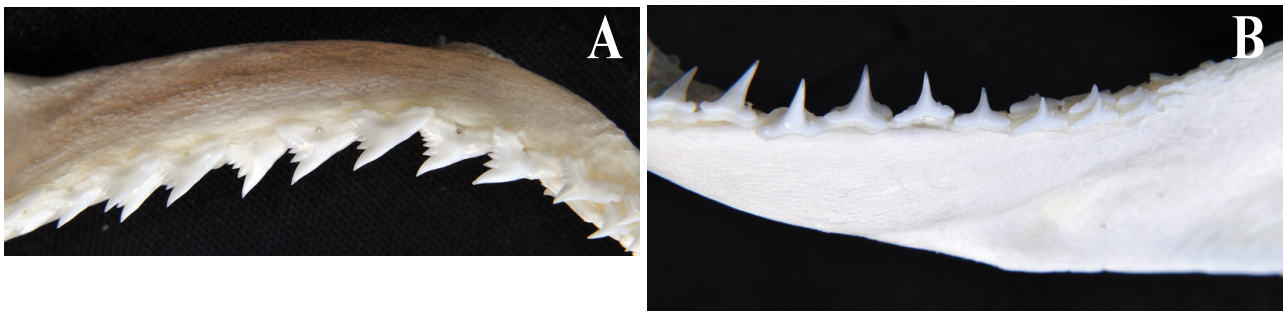

FIGURE 3. Upper (A) and lower teeth (B) series of *Paragaleus tengi* (PMH 197–01, female 930 mm TL).

Body elongate, trunk weakly compressed, somewhat pear-shaped in cross-section at first dorsal-fin base; length of trunk from fifth gill openings to vent 1.42 in the neotype (1.38–1.42 in two other specimens) times head length; second dorsal-fin origin to anal-fin origin 7.25 (7.23–12.95) in second dorsal-fin origin to pelvic-fin midpoint; anal-caudal space 6.94 (6.33–6.44) in preanal length; predorsal ridge absent; interdorsal ridge present, stronger anteriorly; postdorsal ridge absent; lateral line distinct with a pronounced dip under second dorsal-fin base, forming a very weak ridge laterally. Caudal peduncle slender, weakly hexagonal in cross section with dorsal and ventral surface flattened, tapering; without lateral keels; height 1.11 (0.98–1.21) in width at upper caudal-fin origin, 3.45 (3.51–3.92) in dorsal-caudal space. Precaudal pits present and crescentic; lower pit weak.

Head moderate-sized, length 0.82 (0.89) in pectoral-pelvic space; relatively narrow, moderately depressed, roughly trapezoidal in cross-section at eyes; outline of prespiracular head in lateral view nearly straight dorsally, becoming convex above gills; post-oral head slightly convex; narrowly parabolic in dorsoventral view; preoral snout moderate, 1.06 (1.09–1.12) in mouth width. Snout narrowly pointed in lateral view, slightly convex above and below; tip narrowly parabolic in dorsoventral view, with no indentations but a slight angle change adjacent to nostrils.

Eyes large and slightly oval to subcircular in shape, eye length 7.28 (8.37–8.71) in head length; slightly dorsolateral on head; lower edges in line with lateral margin of head in dorsal view; subocular ridges strong; external opening with prominent posterior notch, no anterior notch; nictitating lower eyelids external; subocular pouches narrow but deep, entirely scaled with secondary lower eyelids. Spiracles minute, their length much shorter than eye to spiracle distance, located dorsally to median level of eye. Gill slits subequal in length, height of fifth 1.06 (1.00–1.05) of first; height of first 6.85 (6.86–7.64) in head and 1.06 (1.14–1.22) of eye length. Anterior margin of gill slits slightly convex; slightly elevated on dorsolateral surface of head, upper margins about level with upper margin of eye; gill filaments not visible from outside.

Nostrils with large oval incurrent apertures lacking posterolateral keels; well in front of mouth; width 2.39 (2.65–2.79) in internarial space, 1.66 (1.70–1.71) in eye length, and 1.76 (1.94–2.09) in first gill-slit opening; excurrent apertures small, oval. Anterior nasal flaps subtriangular and moderately long, low mesonarial flaps, and small posterior nasal flaps. Anterior nasal aperture broadly rounded anteriorly, forming a gradual depression.

Mouth moderately rounded to broadly arched in shape and moderately large; width 3.28 (3.37–3.48) in head length; length 1.91 (2.05–2.20) in width; tongue large, flat, broadly rounded, filling floor of mouth, with a weakly notched bilobate tip; buccal papillae absent; labial furrows long, upper 1.62 (1.28–1.43) times lower furrows; anterior ends of uppers extending ahead of posterior corners of eyes.

Dentition groups include medials, symphysials, anteriors, laterals and posteriors in both jaws with some variations in lateral and posterior counts; not sexually dimorphic; dignathic heterodonty very strongly evident in all but extreme posteriors; monognathic heterodonty noted below; bilateral symmetry present in all quadrants with exception to lower posteriors which vary in placement; in 29/25 in neotype (26–30/27–32 in 4 other specimens) rows; functional tooth series 1–2 / 2–3; dental formula, 13 + 4 + 12 in upper jaw, 12 + 1 + 12 in lower jaw in neotype (12–14 + 2 + 12–14 in upper jaw, 12–15 + 3 + 12–15 in lower jaw in 4 other specimens).

TABLE 1. Morphometric data for the neotype of *Paragaleus tengi*, with ranges provided for the two other specimens; the holotype of *P. randalli,* with ranges for eight other specimens; and ranges for two specimens of *P.pectoralis*. Measurements expressed as percentage of total length.

	P. tengi			*P. randalli*			*P. pectoralis*	
	Neotype	Others; n = 2		Holotype	Others; n=8		n=2	
		Min.	Max.		Min.	Max.	Min.	Max.
Total length (mm)	745	862	876	719	587	722	590	890
Pre-second dorsal length	60.5	60.3	61.4	58.4	57.4	59.9	56.9	59.7
Pre-first dorsal length	28.3	27.6	28.8	26.8	26.3	28.0	27.6	28.0
Head length	19.6	19.8	19.8	20.5	19.8	22.3	20.2	20.9
Pre-branchial length	15.4	14.9	15.2	15.7	15.2	17.2	–	–
Pre-spiracular length	10.1	9.6	9.7	10.4	9.6	11.3	10.4	11.5
Pre-orbital length (direct)	6.5	6.4	6.5	7.1	6.3	7.3	7.2	7.7
Pre-pectoral length	18.6	19.0	19.4	18.6	18.5	20.3	19.7	20.3
Pre-pelvic length	45.6	44.8	46.1	43.0	40.9	45.7	43.4	44.4
Snout-vent distance	47.4	47.2	48.0	43.8	43.4	47.0	45.4	46.6
Pre-anal length	61.3	61.4	61.5	59.8	59.3	61.5	58.0	60.4
Interdorsal distance	21.6	24.3	25.1	21.9	20.5	24.0	21.3	22.3
Dorsal-caudal distance	9.9	10.7	11.1	10.5	9.6	11.3	9.8	11.0
Pectoral-pelvic distance	24.0	22.2	22.4	19.2	18.6	23.0	18.9	21.8
Pelvic-anal distance	10.7	10.9	11.3	12.6	11.6	14.5	8.9	10.5
Anal-caudal distance	8.8	9.6	9.7	8.5	8.3	9.2	8.1	8.4
Pelvic caudal distance	26.0	26.3	27.3	27.5	26.5	29.0	23.9	25.7
Pre-narial length	4.5	4.2	4.5	4.7	4.4	5.1	4.5	4.8
Pre-oral length	6.3	6.4	6.4	6.7	6.3	7.1	7.2	7.7
Eye length	2.7	2.3	2.4	2.4	2.5	2.9	2.2	2.5
Eye height	1.4	1.4	1.6	1.8	1.2	1.6	1.5	1.6
First gill slit height	2.9	2.6	2.9	2.8	2.2	3.1	2.3	2.5
Fifth gill slit height	3.0	2.7	2.9	2.6	2.0	2.6	2.2	2.7
Pectoral fin - anterior margin length	13.9	12.1	13.3	13.9	13.1	15.4	15.1	15.5
Pectoral fin - base length	4.9	4.2	4.5	4.6	3.9	4.3	4.1	4.3
Pectoral fin - posterior margin length	10.3	9.2	9.9	10.4	9.0	12.7	9.9	9.9
Pectoral fin - inner margin length	5.6	4.8	4.9	4.9	5.1	5.6	6.1	6.2
Caudal fin - dorsal margin length	21.5	20.8	21.3	23.1	22.2	23.7	23.2	25.6
Caudal fin - preventral margin length	9.3	8.4	8.5	8.3	8.3	9.2	9.8	10.0
Caudal fin - upper postventral margin length	9.8	9.6	10.0	10.1	9.4	10.9	10.3	12.7
Caudal fin - lower postventral margin length	3.4	3.3	3.3	3.0	2.3	3.0	3.0	3.4
Caudal fin - fork width	5.5	4.9	5.0	5.1	4.8	5.5	5.4	5.6
Caudal fin - fork length	6.7	6.3	6.7	6.4	5.9	7.2	7.3	7.4
Caudal fin - subterminal margin length	3.6	3.3	3.4	3.1	3.2	3.6	3.6	3.7
Caudal fin - subterminal margin width	2.6	2.3	2.4	2.4	2.3	2.7	2.0	2.3
Caudal fin - terminal margin length	–	6.2	6.3	6.7	5.9	7.4	5.8	6.5
Caudal fin - terminal lobe length	–	7.2	7.4	8.3	7.5	8.6	7.7	8.5
First dorsal fin - length	13.2	12.2	12.7	–	13.0	14.6	13.2	13.3
First dorsal fin - anterior margin length	12.2	11.2	11.6	12.7	11.7	14.0	13.0	13.3
First dorsal fin - base length	10.3	9.3	10.8	10.6	10.0	11.3	9.9	10.0
First dorsal fin - height	7.9	6.9	7.6	7.9	7.7	8.1	8.9	9.2
First dorsal fin - inner margin length	3.3	2.5	3.7	–	3.0	3.6	3.4	3.6

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TABLE 1 (continued)

	P. tengi			*P. randalli*			*P. pectoralis*	
	Neotype	Others; n = 2		Holotype	Others; n=8		n=2	
		Min.	Max.		Min.	Max.	Min.	Max.
First dorsal fin - posterior margin length	8.3	7.9	7.9	–	7.6	8.5	9.0	9.8
Second dorsal fin - length	10.0	9.8	9.8	10.3	10.0	11.1	9.8	10.4
Second dorsal fin - anterior margin length	8.7	7.5	7.7	8.8	8.0	9.4	8.6	8.7
Second dorsal fin - base length	8.0	7.6	8.0	8.2	6.9	8.2	7.5	7.6
Second dorsal fin - height	4.5	4.4	4.7	5.4	4.5	5.3	5.0	5.5
Second dorsal fin - inner margin length	2.3	2.2	2.6	2.4	2.4	3.0	2.9	3.2
Second dorsal fin - posterior margin length	4.8	5.1	6.0	6.0	4.9	6.1	5.8	6.7
Pelvic fin - length	8.5	7.3	7.8	8.0	7.8	8.5	7.9	8.6
Pelvic fin - anterior margin length	7.6	5.9	6.5	6.4	6.3	7.2	7.1	8.1
Pelvic fin - height	5.9	5.2	5.5	4.9	4.6	6.1	5.0	5.3
Pelvic fin - inner margin length	3.0	2.8	3.4	3.1	2.8	3.6	3.1	3.6
Pelvic fin - posterior margin length	4.9	4.6	5.1	4.6	4.1	5.3	4.6	5.1
Anal fin - length	9.0	8.5	8.8	8.8	8.2	9.6	9.2	9.8
Anal fin - anterior margin length	7.3	6.3	6.6	6.5	6.2	7.4	7.6	8.1
Anal fin - base length	6.4	6.5	6.6	6.3	6.0	7.1	6.8	7.0
Anal fin - height	3.5	3.4	3.5	3.1	3.1	3.6	3.8	3.9
Anal fin - inner margin length	2.5	2.2	2.4	2.6	2.0	2.7	2.8	3.1
Anal fin - posterior margin length	4.4	4.3	4.4	3.3	3.4	4.1	3.9	4.8
Head height	9.3	8.3	9.0	7.9	7.3	9.7	9.3	9.5
Trunk height	10.1	9.1	9.7	9.1	8.5	10.3	9.7	10.0
Abdomen height	10.2	9.5	9.6	11.1	8.9	10.5	9.5	10.2
Tail height	6.8	7.1	7.4	7.0	6.4	7.6	7.2	7.6
Caudal peduncle height	2.9	2.7	3.2	2.5	2.8	3.1	3.0	3.0
Pelvic midpoint-first dorsal insertion	9.8	10.8	11.0	9.1	8.5	10.3	9.1	11.0
Pelvic midpoint-second dorsal origin	11.3	11.9	12.1	12.5	11.2	14.8	10.6	11.1
Second dorsal origin-anal origin	1.6	0.9	1.7	1.5	0.6	2.9	1.0	1.2
Second dorsal insertion-anal insertion	0.3	0.5	0.6	0.9	0.4	1.1	0.8	1.0
Mouth length	3.1	2.6	2.9	2.4	2.4	2.8	2.1	2.3
Mouth width	6.0	5.7	5.9	5.7	5.0	5.8	6.1	6.8
Upper labial furrow length	1.8	1.4	1.5	1.7	1.7	2.2	2.2	2.3
Lower labial furrow length	1.1	1.0	1.1	1.2	1.1	1.4	1.5	1.5
Nostril width	1.6	1.3	1.4	1.5	1.5	1.7	1.6	1.9
Anterior nasal flap length	0.6	0.6	0.6	0.8	0.6	1.0	0.8	0.9
Internarial space	3.9	3.7	3.7	3.3	3.1	3.7	3.2	3.3
Clasper inner length	6.6	5.7	6.1	7.1	3.8	7.0	–	–
Clasper base width	1.4	1.3	1.3	1.3	0.8	1.4	–	–
Interorbital space	7.4	6.9	6.9	6.4	5.9	7.1	6.6	6.8
Head width	9.0	8.5	8.7	9.5	7.5	9.8	8.3	9.2
Trunk width	8.5	8.3	8.5	9.2	6.9	8.9	7.6	8.5
Abdomen width	7.3	7.6	7.7	–	6.1	7.9	6.4	7.5
Tail width	5.6	5.9	6.5	5.2	5.2	6.1	5.2	5.7
Caudal peduncle width	2.6	2.6	2.8	2.3	2.2	2.6	2.7	2.8

Upper jaw with monognathic heterodonty graduated but evident in series; both alternate and imbricate overlapping of basal lobes noticeable; usually two rows (files) of well-developed medial teeth adjacent to one symphysial and one anterior tooth per quadrant; anterolateral and lateral teeth proceeded by only three to five posteriors, usually one half of which are molariform with apical surface reduced to a low, carinate crown. Upper teeth compressed and expanded laterally with high crowns and distal angularity; distal side of cusp usually with 5–6 disproportionately long distal cusplets graduating basal-apically to a very heavily cleaved primary cusp subterminally; apical section nearly bilobate with lower primary cusp distally angled and apex slightly re-curved mesially; mesial side of cusp only slightly convex basal-apically above the lower crown area and concave apically, again with mesial curvature to the apex; both distal and mesial cutting edges smooth including surfaces of distal cusplets; mesial cusplets only present on two symphysials; root moderately wide, somewhat shallow and concave with a deep transverse notch on surface; asymmetrical with distal lobe noticeably shorter than mesial lobe; basal groove deep; basal ledge short distally and mesially, wider centrally.

Lower jaw with monognathic heterodonty present in series, most notably with posterolaterals; only slight alternate overlapping of basal lobes present without imbricate positioning; usually one small medial tooth adjacent to one symphysial and one anterior tooth per quadrant; anterolateral and lateral teeth followed by approximately 5–7 posterior teeth, two to four of which are molariform with apical surface reduced to a low, carinate crown. Lower teeth with four diagnostic structural changes occurring within post-symphysial teeth in series; first two rows of lower teeth perpendicular to very slightly angular and subsequently developing a slight distal angularity anterolaterally; laterals again become perpendicular before a gradient change to distally angular but low-crowned posteriors; apical sections of laterals to posterolaterals variably re-curved mesially. Pre-posterior teeth compressed apically but heavier labial-lingually at basal margins and roots; expanded laterally with high crowns and wide mesial and distal shoulders; basal area of crown wide, graduating to conically shaped cusps; straight edged distally and slightly convex mesially, tapering gradually to a thinly pointed apex. Extreme ends of mesial and distal shoulders of anterior through anterolateral teeth with fairly well-developed, knob-like basal cusplets, one per side. Crown surface of cusplets form round to slightly angular protrusions, tapering off postero-laterally where distal blade cusplets form. Roots moderately wide; weekly concave basally with a heavy lingual structure and shallow transverse notch; root lobes slightly asymmetrical with distal lobe shorter; basal groove deep and basal ledge very pronounced.

Lateral trunk denticles below first dorsal fin small, closely imbricated; broad and multicuspidate with about five longitudinal ridges extending entire length of crown; crown length slightly shorter or equal to its width. Denticles absent near insertion of the pectoral and pelvic fins.

First dorsal fin moderately tall, not falcate; anterior margin slightly convex, moderately rounded apically; posterior margin convex distally becoming broadly concave near free tip; free rear tip acutely pointed; inner margin nearly straight; fin origin slightly posterior to free rear tips of pectoral fins; midpoint of base 1.15 (1.09–1.12) times closer to pectoral-fin insertions than pelvic-fin origins; free tip well anterior to pelvic-fin origins; posterior margin slanting slightly posteroventrally from apex; insertion posterior to level of fin apex; first dorsal-fin base 2.11 (2.25–2.69) in interdorsal space, 2.10 (1.92–2.29) in dorsal caudal-fin margin; fin height 1.29 (1.22–1.57) in base length; inner margin 2.43 (2.06–2.71) in height, 3.15 (2.52–4.27) in base length.

Second dorsal fin moderately tall, apically narrow, not falcate; much smaller than first dorsal fin, height 0.56 (0.62–0.64) of first dorsal-fin height, base length 0.78 (0.73–0.81) of first dorsal-fin base length; anterior margin weakly convex; apex narrowly rounded; posterior margin moderately convex distally and strongly concave near free tip; inner margin straight or slightly concave; free rear tip acutely pointed, terminating about level with anal-fin free rear tip and well in front of upper caudal-fin origin; origin separated from pelvic-fin midpoint by a space about 1.41 (1.52–1.58) times second dorsal-fin base; posterior margin almost upright to slanting slightly anteroventrally from apex; insertion posterior to fin apex; second dorsal-fin base 1.24 (1.34–1.47) in dorsal-caudal space; fin height 1.78 (1.60–1.79) in base length; inner margin 1.95 (1.85–1.98) in height, 3.47 (2.95–3.55) in base length.

Anal fin moderately tall, apically narrow, semi-falcate, smaller than second dorsal fin; height 0.77 (0.73–0.79) in second dorsal-fin height, base length 0.80 (0.83–0.86) times second dorsal-fin base length; anterior margin moderately convex; apex somewhat angular; posterior margin broadly concave, almost upright distally then slanting strongly posterodorsally near free tip; free rear tip acutely pointed, well in front of lower caudal-fin origin; inner margin nearly straight; base expanded anteriorly as short preanal ridges less than half length of rest of base;

origin slightly behind second dorsal-fin origin, by 0.19 (0.12–0.22) of second dorsal-fin base; insertion slightly posterior to apex, almost level with second-dorsal fin insertion; anal-fin base length 1.38 (1.46–1.47) in anal–caudal space; fin height 1.85 (1.88–1.89) in base length; inner margin 1.39 (1.41–1.58) in height, 2.58 (2.66–2.97) in base length.

Pectoral fins narrow and falcate; anterior margins broadly convex, length 1.35 (1.31–1.35) times posterior margin; bases narrow; apices narrowly pointed, posterior margins moderately concave; free rear tips somewhat angular, inner margins strongly convex; origin under space between fourth and fifth gill openings; slightly larger in area than first dorsal fin. Apex of pectoral fin well posterior to its free rear tip when fin is elevated and adpressed to body.

Pelvic fins triangular and weakly falcate; area slightly greater than anal-fin area, length 0.55 (0.49) length of pectoral-fin anterior margins; anterior margin very slightly convex; apex narrowly pointed; posterior margins shallowly concave; free rear tips pointed, inner margins nearly straight to slightly concave. Claspers of adult males relatively long and basally stout; slightly convex for most of outer margin length, tapering near tip; extending well behind pelvic-fin free rear tips and well short of anal-fin origin; glans moderately long, length almost half length of outer margin of clasper; blunt distally with a narrow apex; covered laterally and ventrally with small clasper denticles; dorsomedial surfaces of glans (including rhipidion) and lateral strip adjacent to clasper groove naked.

Caudal fin narrow-lobed and asymmetrical, with a short terminal lobe and a prominent ventral lobe prominent; dorsal caudal margin moderately long, 3.64 (3.70–3.85) in precaudal length, slightly convex to nearly straight, without lateral undulations; preventral margin convex, length 2.31 (2.44–2.53) in dorsal caudal margin; tip of ventral lobe narrowly angular; lower postventral margin nearly straight; upper postventral margin mostly straight and slightly convex near terminal lobe; subterminal notch a narrow, shallow slot; subterminal margin nearly straight, terminal margin nearly straight to slightly concave, fin tip angular; subterminal margin (1.83–1.92) in terminal margin; caudal tip pointed, terminal lobe length (2.82–2.97) in dorsal caudal margin.

Vertebral counts and ratios of the neotype and the two other specimens are summarised as follows: total (TC) centra 127 (131–135), precaudal (PC) centra 74, monospondylous precaudal (MP) centra 46, diplospondylous precaudal (DP) centra 28, caudal centra 53 (55 or 56). Transition between MP and DP posterior to pelvic girdle. Last few MP centra before MP–DP moderately enlarged, not forming 'stutter zone' of alternating long and short centra.

Coloration. Light grey dorsally, whitish ventrally; no prominent markings on fins or underside of snout.

Size. The four specimens of *P. tengi* currently housed in collections were all adult males ranging from 745 to 876 mm TL. The three male types of Chen (1963) ranged from 750 to 810 mm TL. The three jaws collected from Penang (Malaysia) consisted of two females, 925 and 930 mm TL and a male of 810 mm TL. Thus, females and males of this species attain at least 930 and 876 mm TL, respectively.

Distribution. Specimens examined were from southern Japan, Taiwan and Hong Kong. In addition, three jaws from Penang in Malaysia examined by one of us (MH) also agree with this species. *Paragaleus tengi* has also been recorded from China, Vietnam and Thailand (Compagno, 1988, 1998).

Discussion

Ho & Shao (2011) confirmed that the type series of *Paragaleus tengi* was lost. The information available on this species to date is based on only three adult male specimens, two from off Hong Kong and one from off Japan (Compagno, 1988; Compagno *et al.*, 1996). In this study, a neotype is designated which was collected from the same location as the original type series, and *P. tengi* is redescribed based on this specimen and the two from off Hong Kong. Whole female and juvenile specimens of this species are not present in any collections to date. Three *P. tengi* jaws collected from Penang (Malaysia) were also examined by one of us (MH). It appears as though no specimens of *P. tengi* have been recorded from Taiwan in the last few decades. This species has possibly been extirpated from Taiwanese waters and although the *IUCN Red List of Threatened Animals* currently lists it as Data Deficient, this should be reinvestigated to determine whether it should be listed as a highly threatened species.

It has previously been thought that *P. tengi* is the only member of this genus occurring in Taiwan waters. However, examination of two specimens in the fish collection of the Taiwan Fisheries Research Institute in Keelung (FRIP 03574) revealed a second *Paragaleus* species (Figures 4 and 5). Vertebral counts of these two

specimens were far higher (159 and 161 total centra) than that of *P. tengi* (127–135), and close to that of *P. randalli* (164–187). Also, these two specimens possessed a pair of longitudinal dark lines on the underside of the prenarial snout which is a characteristic of *P. randalli*, and is absent in *P. tengi* (Compagno *et al.*, 1996). *Paragaleus* species are very similar morphologically and it is difficult to obtain good characters to distinguish them apart. The few morphometric characters which could be used to distinguish *P. tengi* from *P. randalli* (excluding the two TFRI specimens) based on the specimens measured in this study are: pelvic–anal space (10.7–11.3 vs. 11.6–14.5% TL); dorsal caudal margin (20.8–21.5 vs. 22.2–23.7% TL); prebranchial length (14.9–15.4 vs. 15.2–17.2% TL); lower postventral caudal margin (3.3–3.4 vs. 2.3–3.0% TL), first dorsal-fin length (12.2–13.2 vs. 13.0–14.6), upper labial furrow length (1.4–1.8 vs. 1.7–2.2% TL) and pre-second dorsal-fin length (60.3–61.4 vs. 57.4–59.9% TL). When measurements of the two TFRI specimens (FRIP 03574) were compared with those of *P. tengi* and *P. randalli*, they clearly aligned with those of *P. randalli*.

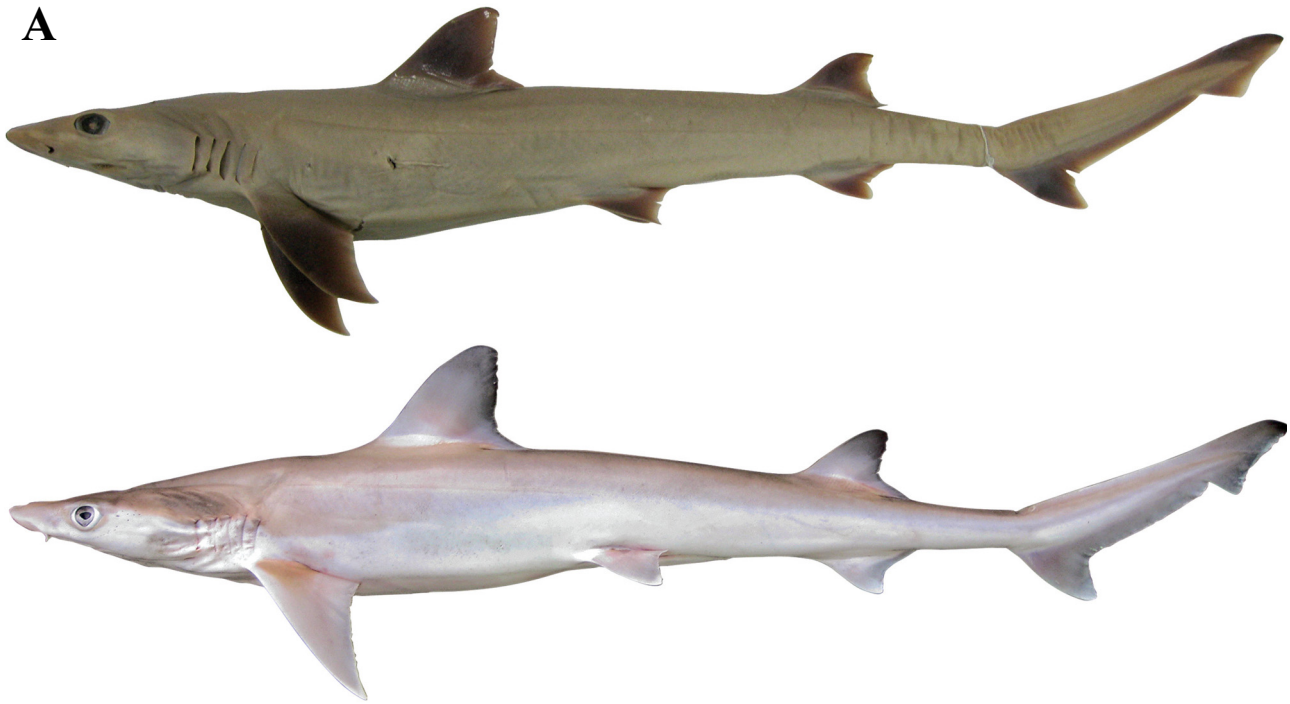

FIGURE 4. Lateral view of *Paragaleus randalli*. A. FRIP 03574 (female 488 mm TL); B. CSIRO H 7414–02, adult male 646 mm TL.

FIGURE 5. Ventral view of head of *Paragaleus randalli*, FRIP 03574 (female 488 mm TL).

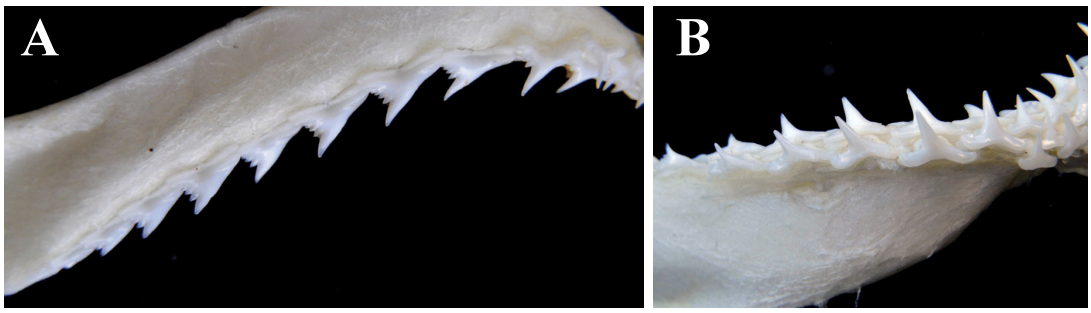

FIGURE 6. Upper (A) and lower teeth (B) series of *Paragaleus randalli* (PMH 129–02, female 807 mm TL).

In most Carcharhiniformes, the upper teeth are chiefly diagnostic as to the species or genus if at all distinguishable. Specifically, this applies to most species that possess dignathic heterodonty as with all members of Hemigaleidae. However, *Paragaleus* is the exception to this in that it possesses a reverse heterodonty, therefore having more diagnostic features of the tooth morphology in the lower jaw than in the upper jaw. These characters may in fact aid in the separation of all four species within the genus known as of this publication. Some of these diagnostic characters are noted in Table 2 in conjunction with other morphological features of the dentition that may further aid in separating *P. tengi* from *P. randalli*.

TABLE 2. Comparative morphological features of the dentition between *Paragaleus tengi* and *Paragaleus randalli* (see Figures 3 and 6).

Paragaleus tengi	*Paragaleus randalli*
Upper lateral teeth usually with 5 or 6 large distal cusplets located somewhat apically and with a small primary cusp	Upper lateral teeth usually with 3 or 4 modestly sized distal cusplets located centrally and with a long primary cusp
Lower anteriors mostly perpendicular to very slightly angular, and only slightly angled distally in anterolaterals	Lower anteriors angular, becoming distally oblique in anterolaterals
Lower laterals perpendicular	Lower laterals oblique distally
Mesial and distal shoulders of lower anteriors to anterolaterals with fairly well-developed, round to slightly angular, knob-like basal cusplets; one per side	Lower anteriors to anterolaterals without mesial and distal basal cusplets
Distal cusplet development in lower teeth usually beginning in posterolaterals but not well developed until posteriors	Distal cusplet development in lower teeth usually beginning in laterals, well developed by posterolaterals (see below for sexual dimorphism comments)
Sexual dimorphism not evident in adults	Sexual dimorphism evident. Adult males with more oblique cusps, particularly in lower jaw, and weakly developed distal cusplets
Transverse notch in upper teeth deep and strongly developed	Transverse notch in upper teeth shallow and weakly developed
Lower posteriors usually with only 2–4 rows of carinate, molariform teeth	Lower posteriors usually with 5–7 rows of carinate, molariform teeth
In upper jaw cartilage, the otic flange of the palatoquadrate fairly evenly expanded and not noticeably flared out just above maxillary articulation	Otic flange of the palatoquadrate noticeably flared out to a rounded protrusion followed by a deep concavity in the quadrate ridge

Two jaws of *P. randalli* examined by one of us (MH) were collected from off Kaohsiung in Taiwan. These are the first records of *P. randalli* from Taiwanese waters and the most northerly record of this species in the western North Pacific.

Paragaleus tengi can be readily distinguished from *Paragaleus leucolomatus* from eastern South Africa in having: much lower number of vertebrae (total 127–135 vs. 180); no dusky markings on underside of snout (vs.

present); and fins without white margins (vs. with conspicuous white margins) (Compagno & Smale, 1985). *Paragaleus tengi* can also be readily distinguished from *Paragaleus pectoralis* from the Eastern Atlantic in having: plain grey dorsal coloration (vs. with horizontal yellow stripes); shorter snout (preoral length 6.3–6.4 vs. 7.2–7.7% TL; preorbital length 6.4–6.5 vs. 7.2–7.7% TL); shorter pectoral anterior margin (12.1–13.9 vs. 15.1–15.5% TL); shorter upper labial furrows (1.4–1.8 vs. 2.2–2.3% TL); shorter first dorsal fin (height 6.9–7.9 vs. 8.9–9.2% TL); shorter caudal fin (dorsal caudal margin 20.8–21.5 vs. 23.2–25.6% TL); and 2 or 3 rows of lower anterolateral teeth with distal cusplets (vs. 5 or more rows).

Compagno (1988) tentatively synonymised *Negogaleus longicaudatus* Bessednov, 1966 from the Gulf of Tonkin with *P. tengi*, based on comparison of Bessednov's description with Chen's description plus three specimens of *P. tengi*. Given that there are few distinct morphological differences between most *Paragaleus* species and there is no information on vertebral counts and little information on dentition in Bessednov's description, it appears that this decision was based mainly on the fact that *P. tengi* was the only species previously considered to occur in the western North Pacific. Some of the characters described in Bessednov (1966) give some indication that perhaps this species actually refers to *P. randalli* rather than *P. tengi*. Firstly, dorsal caudal margin for the two *N. longicaudatus* types was ~24% TL, which is closer to the range for *P. randalli* (22.2–23.7% TL) than *P. tengi* (20.8–21.5% TL). Furthermore, the dorsal fins of *N. longicaudatus* have black anterior margins that more closely resembles *P. randalli* (apices of dorsal fins sometimes blackish based on fresh specimens examined) than *P. tengi*. An important point to mention here is that the two types of *N. longicaudatus* are smaller specimens (380 and 375 mm TL) than what has been examined for *P. tengi*, thus these differences may only represent ontogenetic differences. Vertebral counts and detailed information on the dentition of the *N. longicaudatus* types are required to accurately determine the identity of these specimens. If found to be conspecific with *P. randalli*, which there is some indication they might be, then *N. longicaudatus* would be a senior synonym of this species. If this situation did arise then, according to the International Code of Zoological Nomenclature (ICZN), this species would need to be referred to as *P. longicaudatus* with *P. randalli* as a junior synonym. It could be argued that *P. randalli* has been used as a valid name in at least 25 works by at least 10 authors in the preceding 50 years and encompassing a span of not less than 10 years (Article 23.9.1.2). However, since *N. longicaudatus* was described in 1966, it does not meet Article 23.9.1.1 that "the senior synonym or homonym has not been used as a valid name after 1899", thus reversal of precedence cannot be enforced in this case. Until the types of *N. longicaudatus* can be examined, it should be considered as a tentative synonym of *P. tengi*.

Key to the species of Hemigaleidae from the western North Pacific (adapted from Compagno, 1998)

1. Lower teeth near symphysis with long, strongly hooked cusps that prominently protrude from mouth when closed; gill slits large, usually more than twice eye length 2
- Lower teeth near symphysis with short, straight or weakly hooked cusps that are mostly concealed when mouth is closed; gill slits small, less than twice eye length 3

2. Snout obtusely wedge-shaped in ventral view; fins not falcate, with posterior margins of paired fins straight to slightly concave; teeth present at symphysis of lower jaw . . . . . *Chaenogaleus macrostoma* (Indo–West Pacific)
- Snout bluntly rounded in ventral view; fins strongly falcate, with posterior margins of paired fins deeply concave; teeth absent at symphysis of lower jaw. . . . . *Hemipristis elongata* (Indo–West Pacific)

3. Lower teeth near symphysis with erect cusps and highly arched roots giving them an inverted Y-shape; no cusplets on lower teeth; mouth very short and broadly arched; pelvic, both dorsal and lower caudal fins strongly falcate . . . . . *Hemigaleus microstoma* (Indo–West Pacific)
- Lower teeth near symphysis with mostly erect cusps and slightly arched roots giving them an inverted T-shape; cusplets present on lower teeth; mouth longer and narrowly arched; pelvic, dorsal and caudal fins not falcate 4

4. 5 or more rows of lower anterolateral teeth with distal cusplets; lower anterior teeth mostly with oblique cusps; a pair of longitudinal black lines on underside of prenarial snout; total vertebrae 164–187. . . . . *Paragaleus randalli* (Indo–West Pacific)
- 2 or 3 rows of lower anterolateral teeth with distal cusplets; lower anterior teeth mostly with erect cusps; no black lines on underside of prenarial snout; total vertebrae 127–135 . . . . . *Paragaleus tengi* (western North Pacific)

Comparative material

Paragaleus pectoralis—AMNH 44120, female 890 mm TL, Congo River mouth near Malela, Democratic Republic of the Congo, 1909, collected by H. Lang & J.P. Chapin; AMNH 97267, female 590 mm TL, Angola or Namibia, collected by H. Lang & R. Boulton.

Paragaleus randalli—BPBM 21196 (holotype), adult male 719 mm TL, Bahrain, Arabian (Persian) Gulf. BPBM 19923 (paratype), adolescent male 594 mm TL, Oman; SU 67145 (paratype), adolescent male 621 mm TL, Vizagapatam fish market, Andhra Pradesh State, India, 28 Dec 1940; AB 4B-260 A (2 specimens), adult male 702 mm TL, adult male 688 mm TL, Ras Musandam, Oman, 26°15' N, 56°46' E; CSIRO H 7409–01, juvenile male 520 mm TL, CSIRO H 7409–02, female 540 mm TL, Manggar, East Kalimantan, Indonesia, 01°12'54" S, 116°58'24" E, 21 Nov 2006; CSIRO H 7410–01, adult male 810 mm TL, Manggar, East Kalimantan, Indonesia, 01°12'54" S, 116°58'24" E, 22 Nov 2006; CSIRO H 7414–02, adult male 646 mm TL, Deira fish market, United Arab Emirates, 11 Oct 2012; FAO/DAN, juvenile 587 mm TL, Bahrain, Arabian (Persian) Gulf, 26°31.5– 28.6' N, 51°05– 03.4' E, 16– 18 m depth; FRIP 03574 (2 specimens), subadult male 526 mm TL, female 488 mm TL, Taiwan; SV uncatalog. (2 specimens), female 703 mm TL, adult male 618 mm TL, Bahrain, Arabian (Persian Gulf); PMH 129–02, female 807 mm TL, PMH 129–03, female 650 mm TL, Kaohsiung, Taiwan; PMH 237–01, male 760 mm TL, PMH 237–02, female 740 mm TL, PMH 237–03, male 640 mm TL, PMH 237–04, female 610 mm TL, Musandam, Oman; PMH 237–05, male 833 mm TL, PMH 237–06, male 825 mm TL, Cebu, Philippines; PMH 237–07, female 625 mm TL, Palawan, Philippines; TRR 70–14, adult male 733 mm TL, Wedge Banks, Gulf of Mannar, Sri Lanka, 27–28 Mar 1970.

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