

The *Leiognathus splendens* complex (Perciformes: Leiognathidae) with the description of a new species, *Leiognathus kupanensis*

Kimura and Peristiwady

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Abstract Taxonomic analysis of a group of morphologically similar ponyfishes (Perciformes: Leiognathidae) establishes the *Leiognathus splendens* complex comprising four valid species: *L. jonesi* James, 1971, widely distributed in the Indo-West Pacific, from Mauritius to Papua New Guinea, north to Hainan I. (China), and south to Brisbane, Australia; *L. kupanensis* sp. nov., currently known only from Kupang, Timor, Indonesia; *L. rapsoni* Munro, 1964, currently known only from India, Indonesia, and Papua New Guinea, and *L. splendens* Cuvier, 1829, widely distributed in the eastern Indian and western Pacific oceans, from India to Papua New Guinea, and from southern Japan to northern Australia. The *L. splendens* complex can be defined by the following combination of characters: body depth 42–60% of standard length; mouth protruding downward; slender, minute teeth uniserially on jaws; lower margin of orbit above the horizontal through the gape when mouth closed; breast almost completely scaled; lateral line complete, and a dark blotch on top of spinous dorsal fin. Diagnostic characters of the members are as follows: *L. jonesi*—anterior dorsolateral body surface with a semicircular naked area on nape, and a paler dark blotch on spinous dorsal fin; *L. kupanensis*—anterior dorsolateral body surface widely naked; *L. rapsoni*—cheek scaled; *L. splendens*—anterior dorsolateral body surface completely scaled and a jet black blotch on spinous dorsal fin.

Key words Leiognathidae · *Leiognathus jonesi* · *Leiognathus kupanensis* sp. nov. · *Leiognathus rapsoni* · *Leiognathus splendens*

The Indo-Pacific leiognathid fishes belonging to the genus *Leiognathus*, characterized by a forward- or downward-protruding mouth and small or minute teeth on jaws, have long been confused taxonomically because of their similar body shape, almost entirely silvery body coloration, and overlapping meristics. Our recent revisional study of the *Leiognathus aureus* complex (Kimura et al., 2003a), however, has resulted in the redescription of *Leiognathus aureus* Abe and Haneda, 1972, and *Leiognathus hataii* Abe and Haneda, 1972, and the description of *Leiognathus panayensis* Kimura and Dunlap in Kimura et al., 2003a. Here we examine and resolve the taxonomic status of another group of morphologically very similar leiognathids, referred to as the “*Leiognathus splendens* complex,” which is composed of *Leiognathus*

splendens (Cuvier, 1829), *Leiognathus rapsoni* Munro, 1964, *Leiognathus jonesi* James, 1971, and a new species. These fishes share the following combination of characters: a dark blotch on top of spinous dorsal fin, breast almost fully scaled, and lower margin of orbit above the horizontal through the gape when mouth closed.

In this species complex, the oldest nominal species is *L. splendens*, which was named by Cuvier (1829) as *Equula splendens* in a footnote in “Règne Animal,” based on a description and drawing given by Russell (1803). Valenciennes in Cuvier and Valenciennes (1835) described *Equula gomorah* based on the specimens collected from India and Red Sea, but Day (1876) synonymized the species under *E. splendens*. Subsequently, *Equula ovalis* De Vis, 1884 and *Equula simplex* De Vis, 1884, from northern

Australia, *Leiognathus philippinus* Fowler, 1918, from the Philippines, and *L. rapsoni* Munro, 1964, from Papua New Guinea were described. James (1971) described *L. jonesi* on the basis of the specimens from India; subsequently, in his revisory work on the family Leiognathidae (James, 1978), he recognized *L. splendens* and *L. jonesi* as valid species, synonymizing *E. gomorah* and *L. philippinus* under *L. splendens*. Fowler (1904) described *Leiognathus spilotos*, based on the specimen collected from Sumatra, Indonesia. This species had once been suggested to be a junior synonym of *Leiognathus blochii* (Valenciennes in Cuvier and Valenciennes, 1835) by Weber and de Beaufort (1931). Although *Leiognathus indicus* Singh and Talwar, 1978, was described from specimens collected from the Bay of Bengal (India), the validity of this species has not been discussed; no other specimens have been reported and the literature contains no further reference to this species. Subsequently, Jones (1985) carried out a revision of Australian leiognathids and treated *E. ovalis*, *E. simplex*, and *L. jonesi* as junior synonyms of *L. splendens*. Jones (1985) also recognized *L. rapsoni* as a valid species, despite its absence from Australian waters, but did not refer *L. indicus*. Therefore, in accordance with Jones (1985), the *Leiognathus splendens* complex has been thought to contain only two valid species, *L. splendens* and *L. rapsoni*.

In the present account, we have revised the *L. splendens* complex based on the examination of many specimens collected from a variety of locations throughout Indo-West Pacific. We recognize four species in this complex: *L. jonesi*, *L. rapsoni*, and *L. splendens*, which are redescribed here, and a newly described species, *Leiognathus kupanensis*.

Materials and Methods

Counts and measurements generally followed Hubbs and Lagler (1947) and Kimura et al. (2003a). Additional measurements include widths of second spines of dorsal and anal fins, which were measured bilaterally as horizontal widths at the level of the tip of the first spines when fins were extended so that spines were perpendicular to fin bases. All measurements were made with a digital caliper to the nearest 0.01 mm. Cyanine blue was used to examine and count scales. Osteological observation was made from soft X-ray photos and from cleared and stained specimens. Standard and head lengths are abbreviated as SL and HL, respectively. Institutional codes follow Leviton et al. (1985) with additional abbreviations as follows: MUFS, Division of Fisheries Sciences, Faculty of Agriculture, Miyazaki University, Miyazaki, Japan; SFU, Shanghai Fisheries University, Shanghai, China; ZRC, Raffles Museum of Biodiversity Research, Department of Biological Sciences, National University of Singapore.

The *Leiognathus splendens* Complex

Diagnosis. A species group of the genus *Leiognathus* as defined by the following combination of characters: body

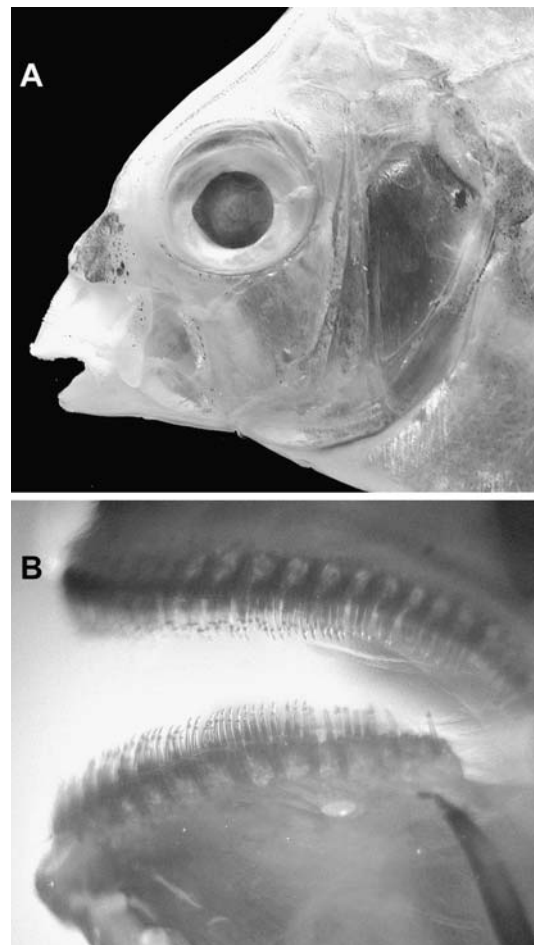


Fig. 1. **A** Head of *Leiognathus splendens*, MUFS 16917, 62 mm SL. **B** Jaw teeth of *L. jonesi*, FRLM 30062, 70 mm SL

deep, body depth 42–60% SL; mouth protruding downward (Fig. 1A); jaw teeth slender, minute (Fig. 1B); lower margin of orbit above the horizontal through the gape when mouth closed; breast almost completely scaled; lateral line complete; dark blotch on top of spinous dorsal fin.

Description. Characters given in the diagnosis are not repeated. Body strongly compressed, dorsal profile convex, similar to or somewhat more strongly so than ventral; mouth subterminal, gape almost horizontal; snout blunt, anteroventral profile of lower jaw almost straight or weakly concave; vomer and palatines toothless; lateral ethmoid bearing a small forked spine on dorsal end, just anterior to supraorbital ridge; tip of posterior limb of maxilla exceeding beyond the vertical through anterior margin of eye; lower edge of preopercle serrated; corner of preopercle rounded; gill rakers 5–7 + 18–24; two small papillae on rear edge of gill cavity supported by cleithrum; scales small covering most of body; lateral line complete, with 46–66 scales; a single dorsal fin with usually VIII, 16, anal fin usually III, 14, the second spines of both fins longest; third and fourth dorsal and third anal fin spines serrated proximally along anterior margin; anal fin spines more slender than those of dorsal fin; pelvic fins I, 5; with paired axillary scalelike process; caudal fin forked; vertebrae 10 + 14 = 24; tip of neural and hemal

spines of fifth preural centrum pointed, but those of fourth preural centrum expanded, flattened; first to fourth hypurals forming two plates (first + second and third + fourth); ribs 7, epipleurals 13; a single supraneural; middle pterygiophores of dorsal and anal fin soft rays with pair of exposed retrorse sharp spines on outer edge.

Light organ morphologically similar in all species of the complex; single, internal, circumesophageal, inflated or anteroventrally/posterodorsally compressed torus, flesh colored with black and black spot-embedded white sheath over ventral half; visible internally as a flattened surface at anterior end of gasbladder; lateral lobes not enlarged; sexually dimorphic in *Leiognathus splendens*, volume 1.6 to 3 times greater in males compared to similarly sized females (McFall-Ngai and Dunlap, 1984); light organ shape and pigmentation and gasbladder lining not dimorphic; external dimorphism (male-specific or male-enhanced external skin patches) not present; volume dimorphism of light organ probable in *L. rapsoni* (ca. 49 mm³ in UMMZ 243702-1, male, 81 mm SL; ca. 6.5 mm³ in UMMZ 243702-2, possible female, 65 mm SL), and likely in *L. jonesi* and *L. kupanensis* sp. nov. but present material insufficient for determination.

Key to the Species

- 1a. Cheek naked (Fig. 2A,B,D); interspace of pelvic keels naked (Fig. 3A,B,E) 2
- 1b. Cheek scaled (Fig. 2C); interspace of pelvic keels scaled (Fig. 3C,D) *Leiognathus rapsoni*
- 2a. Anterior dorsolateral surface of body widely naked (Fig. 2B) *Leiognathus kupanensis* sp. nov.
- 2b. Anterior dorsolateral surface of body almost entirely scaled (Fig. 2A,C,D) 3
- 3a. Dark blotch on dorsal fin paler, dark gray (Fig. 4A–C); nape with a semicircular naked area (Fig. 2A); second spines of dorsal and anal fins weak, slender (width of second spines of dorsal and anal fins 0.72–1.1% of SL and 0.60–0.95% of SL, respectively; Fig. 5) *Leiognathus jonesi*
- 3b. Dark blotch on dorsal fin jet black (Fig. 4D); nape without a semicircular naked area (Fig. 2D); second spines of dorsal and anal fins robust (width of second spines of dorsal and anal fins 0.87–1.6% of SL and 0.76–1.7% of SL, respectively; Fig. 5) *Leiognathus splendens*

***Leiognathus jonesi* James, 1971**

(New English name: Jones' pony fish)

(Fig. 6, Table 1)

Leiognathus jonesi James, 1971; 316–319 (type locality: Palk Bay, Tamil Nadu, India); James, 1978: 149–151 (Palk Bay, Tamil Nadu, India); Iwatsuki et al., 2000: 100 (listed only, Makassar, Sulawesi, Indonesia). *Leiognathus splendens* (not of Cuvier); Zheng, 1962: 446–447 (Hainan I., China); Kühlmorgen-Hille, 1974: LEIOG Leiog 10 (in part, Eastern Indian Ocean and Western Central Pacific); Gloerfelt-Tarp and Kailola, 1984: 171 (Java, Indonesia); Mohsin and Ambak, 1996: 349–350, fig. 256 (Malaysia); Mansor et al., 1998: 158, fig. 157 (South China

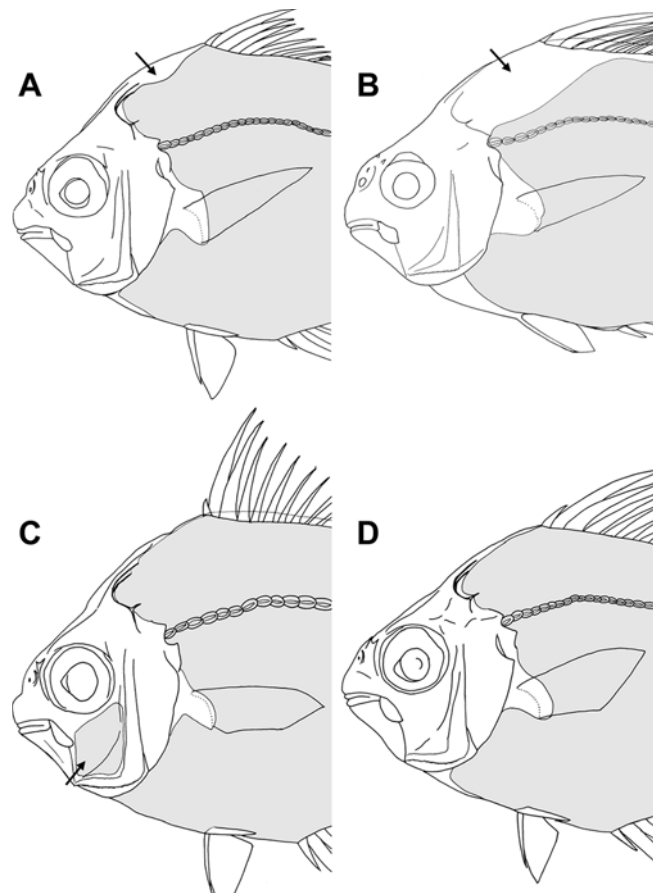


Fig. 2. Cheek and anterior part of body; scaled area shaded. **A** *Leiognathus jonesi*, FRLM 28686, 73 mm SL. Arrow indicates a semicircular naked area on nape. **B** *Leiognathus kupanensis*, holotype, NSMT-P 69427, 80 mm SL. Arrow indicates a wide naked area on anterior dorsolateral surface of body. **C** *Leiognathus rapsoni*, FRLM 16699, 64 mm SL. Arrow indicates a scaled area on cheek. **D** *Leiognathus splendens*, MUFS 16920, 61 mm SL

Sea); Woodland et al., 2001: 2815 (in part, Western Central Pacific); Fish Team of the Trang Project, 2002: 14, fig. 59 (Trang, Thailand).

Non-type materials. 99 specimens, 33–139 mm SL. CAS SU 69867, 50 mm SL, Vizagapatam, Chennai, India; CAS SU 37222, 72 mm SL, Mergui Archipelago, Myanmar; CAS SU 69868 (2 specimens), 43–47 mm SL, Calicut, Kerala, India; FAKU 103832, 68 mm SL, Port Luis, Mauritius; FAKU 110585, 103 mm SL, Bay of Thailand, FRLM 16700, 78 mm SL, Kuta, Lombok, Indonesia; FRLM 16993–16996, 17008, 17009, 20392, 20404, 9 specimens, 84–109 mm SL, Tanjung Luar, Lombok, Indonesia; FRLM 21493, 21495, 21498, 21628, 4 specimens, 80–101 mm SL, Passo, Ambon, Indonesia; FRLM 28682, 28683, 28685–28695, 11 specimens, 73–88 mm SL, Phuket, Thailand; MUFS 9344, 9345, 2 specimens, 72–75 mm SL, Iloilo, Panay, Philippines; MUFS 14468, 14506–14518, 14 specimens, Hat Yai, Thailand; MUFS 22485–22489, 5 specimens, 52–67 mm SL, Makassar, Sulawesi, Indonesia; NSMT-P 54716 (4), 55138, 60719, 60721–60723, 60733, 10 specimens, 61–94 mm SL, Sanya Bay, Hainan, China; SFU 3855, 90 mm SL, Hainan, China; UMMZ 213558, 74 mm SL, Phuket, Thailand; UMMZ 219157 (4), 219520, 219600 (3), 219610, 219711 (2), 219740, 220067, 220288 (2), 226772, 227346 (3), 19 specimens, 33–114 mm SL, mouth of Mekong River, Vietnam; UMMZ 224912 (3), 73–83 mm SL, off Pattaya,

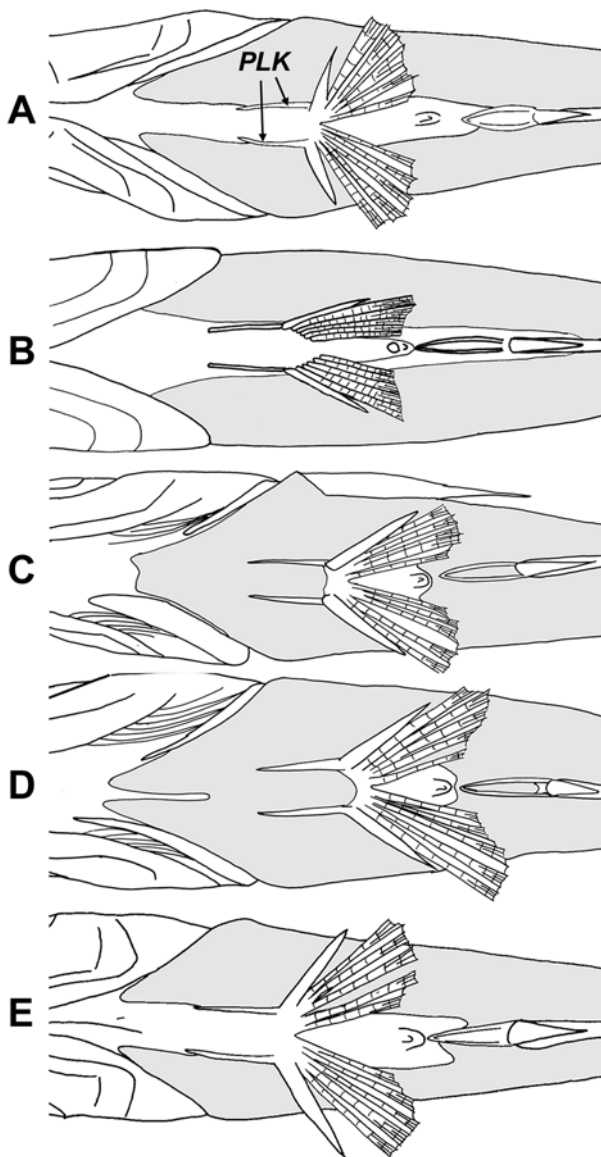


Fig. 3. Ventral surface of anterior body; scaled area shaded. **A** *Leiongnathus jonesi*, FRLM 28691, 75 mm SL. **B** *Leiongnathus kupanensis*, holotype, NSMT-P 69427, 80 mm SL. **C** *Leiongnathus rapsoni*, UMMZ 243702-2, 65 mm SL. **D** *Leiongnathus rapsoni*, FRLM 15720, 66 mm SL. **E** *Leiongnathus splendens*, MUFS 16917, 62 mm SL. *PLK*, pelvic keels

Thailand; UMMZ 226379 (2), 109–114 mm SL, Penang, Malaysia; UMMZ 235095 (2), 102–108 mm SL, Kota Kinabalu, Sabah, Borneo Malaysia; URM-P 9277, 27425, 27426, 3 specimens, 75–139, Phuket, Thailand; ZRC 1332 (2), 98–103 mm SL, off Sarawaku, Borneo, Malaysia; ZRC 2717 (3), 37–53 mm SL, Berih, Singapore.

Materials for distributional records. 139 specimens, 26–100 mm SL. FRLM 30062, 70 mm SL, Phuket, Thailand; FRLM 30474–30482, 9 specimens, 65–98 mm SL, Hua Hin, Thailand; FRLM 30483, 60 mm SL, Bang Phe, Thailand; FRLM 30493–30496, 4 specimens, 47–67 mm SL, Pran Buri, Thailand; FRLM 30771–30779, 8 specimens, 68–91 mm SL, Iloilo, Panay, Philippines; MUFS 15013, 15127–15129, 15274–15286, 17 specimens, 40–91 mm SL, Bangsapanoi, Thailand; NSMT-P 57234, 65 mm SL, Rayong, Thailand; NSMT-P 65883, 60 mm SL, Long Chau Bay, Vietnam; NSMT-P 65884, 67899 (6), 67901, 67910, 9 specimens, 61–89 mm SL, Cat Ba, Haiphong, Vietnam; NSMT-P 67896, 67905, 67906,

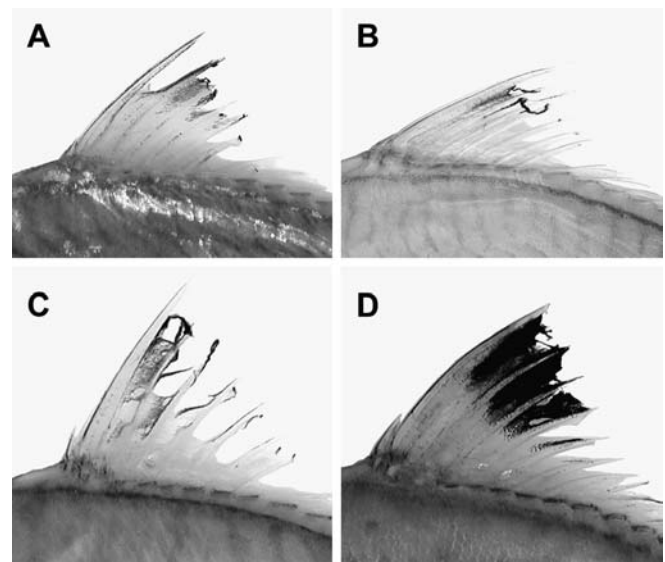


Fig. 4. Dark blotch on the tip of spinous dorsal fin. **A** *Leiongnathus jonesi*, MUFS 14518, 48 mm SL. **B** *Leiongnathus kupanensis*, holotype, NSMT-P 69427, 80 mm SL. **C** *Leiongnathus rapsoni*, FRLM 16699, 64 mm SL. **D** *Leiongnathus splendens*, MUFS 16916, 68 mm SL

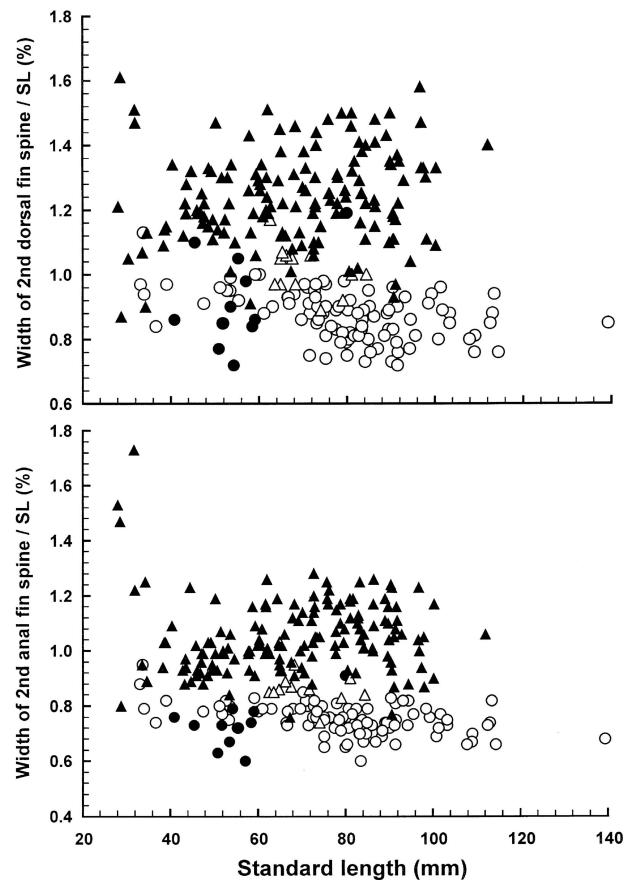


Fig. 5. Proportions of widths of second dorsal and anal fin spines in *Leiongnathus jonesi* (open circles), *L. kupanensis* sp. nov. (solid circles), *L. rapsoni* (open triangles), and *L. splendens* (solid triangles)

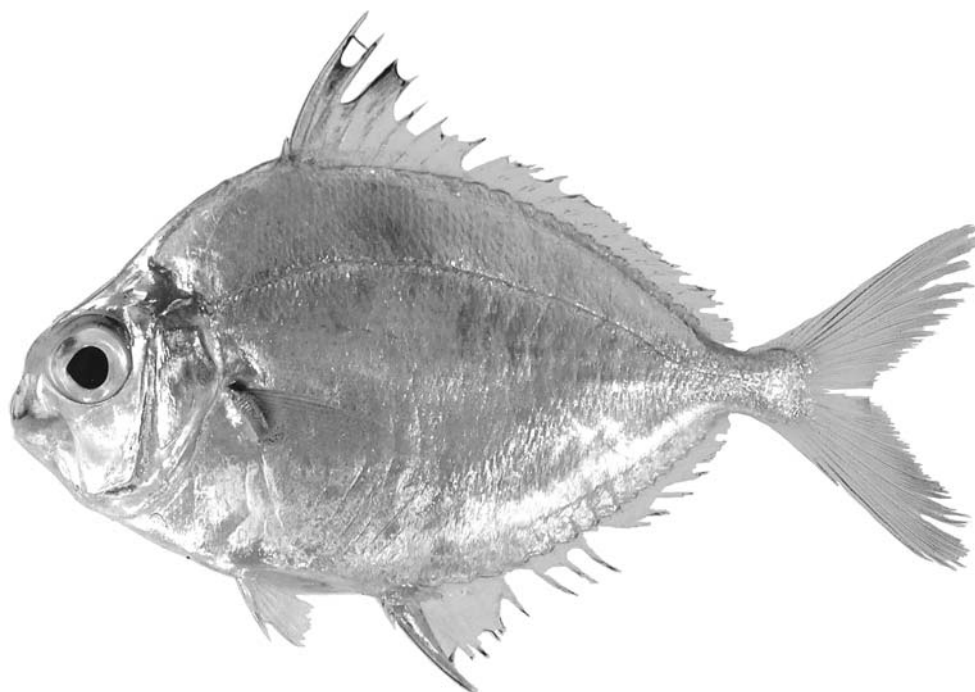


Fig. 6. Non-type material of *Leiognathus jonesi*, FRLM 20392, 89 mm SL, from Lombok, Indonesia

67909, 67916 (10), 14 specimens, 64–100 mm SL, Nha Trang, Vietnam; UMMZ 221933 (13), 74–84 mm SL, mouth of Mekong River, Vietnam; UMMZ 237293 (24), 26–47 mm SL, Songkhla, Thailand, URM-P 9130–9136, 7 specimens, 73–80 mm SL, Phuket, Thailand; URM-P 12538, 66 mm SL, Songkhla, Thailand; URM-P 14350, 66 mm SL, Ranong, Thailand; YCM-HLP 211, 671, 2 specimens, 67–92 mm SL, Jakarta, Indonesia; YCM-HLP 224 (5), 637 (2), 7 specimens, 68–93 mm SL, Maiwara, Madang, Papua New Guinea; YCM-HLP 434 (2), 77–78 mm SL, Cebu, Philippines; YCM-HLP 650 (2), 802, 803 (12), 15 specimens, 52–68 mm SL, Sandakan, Sabah, Borneo, Malaysia; YCM-HLP 804, 42 mm SL, Moreton Bay, Brisbane, Queensland.

Diagnosis. A species belonging to the *Leiognathus splendens* complex as defined by the following characters: cheek naked; anterior dorsolateral body surface almost entirely scaled with a semicircular naked area on nape (Fig. 2A); lower margin of inner preopercular ridge smooth; interspace of pelvic keels naked (Fig. 3A); second spines of dorsal and anal fins weak (width of second spines of dorsal and anal fins 0.72–1.1% SL and 0.60–0.95% SL, respectively; Fig. 5); a dark blotch on spinous dorsal fin rather pale, grayish (Fig. 4A).

Description. Counts and measurements of the type specimens after James (1971) and non-type materials are shown in Table 1. Characters given in description of the complex and the specific diagnosis are not repeated. Body rhomboidal, dorsal profile more strongly convex than ventral one; supraorbital ridge smooth or weakly rugged with series of minute spines; ventral surface of breast naked (Fig. 3A). Maximum recorded length 139 mm SL (URM-P 9277, from Phuket, Thailand).

Color of fresh specimens.—Head and body almost uniformly silvery-white; tip of snout dark; lateral line scales

prominent yellow but easily fade out; distal half of fin membranes between second and fifth spines of dorsal fin with a somewhat pale black blotch; fin membrane between second and third spines of anal fin white or pale yellow; spines and margin of soft portion of anal fin yellowish; posterior margin of caudal fin dark; pectoral axil dark; pectoral fin proximally with narrow dark band; pelvic fin pearl-white.

Color of preserved specimens.—Head and body almost uniformly light brown; tip of snout dark; ca. 20 wavy dark vertical lines dorsolaterally on body; distal half of fin membranes between second and fifth spines of dorsal fin with a pale black blotch; dorsal surfaces of middle pterygiophores of dorsal fin black; pectoral axil dark; pectoral fin proximally with narrow dark band.

Distribution. *Leiognathus jonesi* is known from Mauritius, India [Calicut, Palk Bay (type locality), and Chennai], Myanmar (Mergui), Thailand (Ranong, Phuket, Songkhla, Hat Yai, Bangsapnoi, Bang Phe, Pran Buri, Hua Hin, Pattaya, and Layong), Vietnam (mouth of Mekong River, Nha Trang, Haiphong, and Long Chau Bay), China [Hainan I. (Sanya)], Philippines [Panay (Iloilo) and Cebu], Malaysia [Penang, Sabah (Kota Kinabalu and Sandakan), and off Sarawaku], Singapore (Berih), Indonesia [Jawa (Jakarta), Lombok, Sulawesi (Makassar), and Ambon], Papua New Guinea (Madan), and Australia [Queensland (Brisbane)] (Fig. 7).

Remarks. *Leiognathus jonesi* was established by James (1971) based on the holotype (95 mm SL) and 49 paratypes (35–92.5 mm SL) collected from Palk Bay, Tamil Nadu, southeastern India. According to the original description, all type specimens were deposited in “Central Marine Fisheries Research Institute, Mandapam Regional Centre”; however, registration numbers were not assigned. We inquired

Table 1. Counts and measurements of *Leiognathus jonesi*

	Holotype and paratypes ^a	Other specimens
Standard length (mm)	35–95	33–139 (78.8, 99)
Counts		
Dorsal fin rays	VIII, 16	VIII, 16 (99)
Anal fin rays	III, 14	III, 14–15 (14.0, 99)
Pectoral fin rays	No data	16–19 (18.0, 99)
Lateral line scales	40–53	50–61 (54.3, 99)
Scales above lateral line	11–13	9–14 (11.6, 71)
Scales below lateral line	22–26	22–28 (24.8, 71)
Gill rakers on upper arch	5–7	5–7 (5.8, 99)
Gill rakers on lower arch	21–24	19–24 (20.9, 99)
Measurements		
As % of standard length		
Head length	25–34	29–34 (31.4, 98)
Predorsal length	No data	46–51 (48.5, 99)
Length of dorsal fin base	No data	54–60 (57.7, 99)
Length of anal fin base	No data	44–51 (46.4, 99)
Snout to pectoral fin insertion	No data	51–59 (54.7, 99)
Snout to pelvic fin insertion	No data	30–35 (32.5, 99)
Snout to anal fin origin	No data	35–41 (37.9, 99)
Pectoral fin insertion to pelvic fin insertion	No data	23–26 (24.5, 99)
Pelvic fin insertion to anal fin origin	No data	14–21 (17.8, 96)
Caudal peduncle length	No data	9.1–14 (11.3, 99)
Body depth	51–56	51–58 (54.5, 99)
Caudal peduncle depth	No data	6.6–8.7 (7.59, 99)
As % of head length		
Snout length	No data	26–36 (31.6, 98)
Eye diameter	33–44	30–40 (34.8, 98)
Upper jaw length	No data	32–44 (36.1, 98)
Interorbital width	No data	22–32 (26.2, 98)
Length of 1st dorsal fin spine	No data	8.1–14 (10.9, 88)
Length of 2nd dorsal fin spine	No data	65–80 (71.9, 31)
Length of 3rd dorsal fin spine	No data	56–71 (65.1, 15)
Length of 1st anal fin spine	No data	7.5–16 (12.0, 94)
Length of 2nd anal fin spine	No data	50–68 (59.7, 53)
Length of 3rd anal fin spine	No data	39–59 (49.5, 46)
Length of pectoral fin	No data	74–91 (83.5, 83)
Length of pelvic fin spine	No data	30–39 (34.9, 87)

Figures in parentheses indicate mean values and sample size

^aData from James (1971)

Fig. 7. Distributional records of *Leiognathus jonesi* (circles), *L. kupanensis* sp. nov. (star), *L. rapsoni* (triangles), and *L. splendens* (squares)

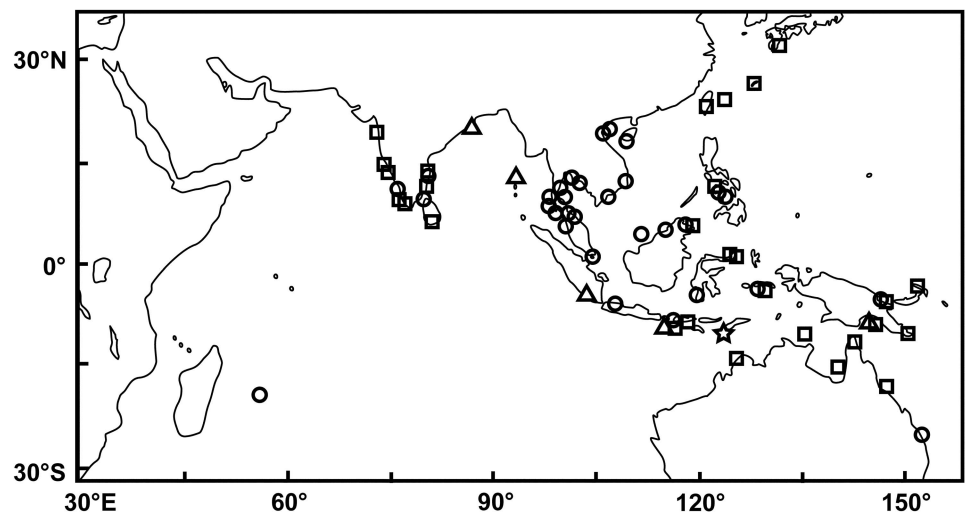




Fig. 8. Holotype of *Leiognathus kupanensis*, NSMT-P 69427, 80 mm SL, from Kupang, Timor, Indonesia

several times whether the types exist and are available for examination, but no reply was received. Accordingly, we asked Rohan Pethiyagoda, Wildlife Heritage Trust of Sri Lanka, to investigate the existence of the types at the “Mandapam Regional Centre” during his field research in Tamil Nadu. In early November 2003, he visited the “Mandapam Regional Centre” and tried to locate the types. However, his attempt resulted in failure; the specimens deposited there were in much confusion, no labels were in or on the specimen bottles, and there were no curatorial staff. He concluded that it would not be possible to locate and examine specific specimens. Therefore, identification of this species must be based on the original description and drawing.

According to the original description, the diagnostic characters of the species in comparison with *L. splendens* were as follows: a dark blotch on spinous dorsal fin gray (vs. jet black in *L. splendens*), spines of dorsal and anal fins weak (vs. strong), first dorsal fin spine large (second spine/first spine 4.6–7.0 vs. 3.3–8.0), and first anal fin spine large (second spine/first spine 3.1–6.0 vs. 2.5–4.5) (however, the descriptions of first spines of dorsal and anal fins are probably erroneous; the spines are somewhat smaller than those of *L. splendens* based on his data). Subsequently, Jones (1985) treated *L. jonesi* as a junior synonym of *L. splendens*, basing this decision on the density of a dark blotch on the dorsal fin, the lesser objectiveness of strengths of fin spines, and the wide overlap of proportions of first and second spines of the dorsal and anal fins. However, the specimens of *L. jonesi* examined here clearly have a more pale dark blotch on the spinous dorsal fin (Fig. 4A) and narrower second spines of dorsal and anal fins than specimens of *L. splendens* (Fig. 5). Additionally, *L. jonesi* has a small semicircular naked area on nape that is not present in *L. splendens* (Fig. 2). Therefore, we recognize *L. jonesi* here as a valid species. The first spines of dorsal and anal fins are relatively shorter than those of *L. splendens* in mean values, but the ranges widely overlap (Table 1; see also Table 4).

The fish described as “*L. splendens*” from Hainan I., southern China, by Zheng (1962: fig. 368) can be identified as *L. jonesi* on the basis of its somewhat paler dark marking on the dorsal fin.

Comparisons. *Leiognathus jonesi* is easily distinguished from *L. splendens* in having a paler dark blotch on dorsal fin (vs. jet black blotch in the latter; Fig. 4), prominent yellow lateral line scales if fresh (vs. dull pale to dark yellow), a semicircular naked area on nape (vs. anterior dorsolateral surface almost entirely scaled with no semicircular naked area on nape; see Fig. 2), and weak dorsal and anal fin spines (width of second spines of dorsal and anal fins 0.72–1.1% of SL and 0.60–0.95% of SL, respectively vs. 0.87–1.6% of SL and 0.76–1.7% of SL, respectively; Fig. 5), and is distinguished from *L. rapsoni* in lacking scales on cheek and interspace of pelvic keels (vs. scales present on cheek and interspace of pelvic keels in the latter; Figs. 2, 3). *Leiognathus jonesi* most closely resembles *L. kupanensis* sp. nov. in general body appearance and counts. However, it is distinguishable from the latter in having an almost entirely scaled anterior dorsolateral body surface with a semicircular naked area on nape (vs. widely naked anterior dorsolateral body surface; Fig. 2).

Leiognathus kupanensis Kimura and Peristiwady, sp. nov.

(New English name: Kupang pony fish)
(Fig. 8, Table 2)

Holotype. NSMT-P 69427, 80 mm SL, Kupang, Timor, Indonesia, 18 Oct. 1999, collected by T. Peristiwady.

Paratypes. 10 specimens, 41–59 mm SL. AMS I.43380-001, 58 mm SL, same data as the holotype; BMNH 2004.10.26.1, 55 mm SL, same data as the holotype; CAS 220612, 54 mm SL, Kupang, Timor, Indonesia, 6 Jan. 2002, collected by T. Peristiwady; FRLM 30464, 30469, 2 specimens, 41–59 mm SL, same data as the holotype; FRLM 30470, 30473, 2 specimens, 45–52 mm SL, same data as CAS 220612; MNHN 2004-1856, 51 mm SL, same data as CAS 220612; UMMZ 243701, 57 mm

Table 2. Counts and measurements of *Leiognathus kupanensis* sp. nov.

	Holotype NSMT-P 69427	Paratypes
Standard length (mm)	80	41–59 (52.7, 10)
Counts		
Dorsal fin rays	VIII, 16	VIII, 16 (10)
Anal fin rays	III, 14	III, 14 (10)
Pectoral fin rays	18	17–18 (17.8, 10)
Lateral line scales	56	52–56 (54.0, 9)
Scales below lateral line	25	22–26 (23.6, 8)
Gill rakers on upper arch	5	5–6 (5.7, 9)
Gill rakers on lower arch	22	22–26 (23.9, 9)
Measurement		
As % of standard length		
Head length	31	30–33 (31.5, 10)
Predorsal length	50	48–51 (48.8, 10)
Length of dorsal fin base	58	55–59 (57.2, 10)
Length of anal fin base	48	45–49 (47.1, 10)
Snout to pectoral fin insertion	56	54–57 (55.0, 10)
Snout to pelvic fin insertion	32	32–35 (33.6, 10)
Snout to anal fin origin	39	38–42 (39.9, 10)
Pectoral fin insertion to pelvic fin insertion	25	23–26 (24.6, 10)
Pelvic fin insertion to anal fin origin	18	16–19 (17.1, 10)
Caudal peduncle length	10	8.5–13 (11.0, 10)
Body depth	55	52–57 (54.8, 10)
Caudal peduncle depth	7.5	6.3–7.5 (6.76, 10)
As % of head length		
Snout length	33	29–33 (30.6, 10)
Eye diameter	35	33–40 (37.2, 10)
Upper jaw length	35	31–41 (36.1, 10)
Interorbital width	35	27–36 (32.8, 10)
Length of 1st dorsal fin spine	9.8	9.2–16 (11.1, 10)
Length of 2nd dorsal fin spine	70	62–74 (68.9, 8)
Length of 3rd dorsal fin spine	62	53–65 (59.8, 5)
Length of 1st anal fin spine	14	13–19 (16.0, 10)
Length of 2nd anal fin spine	65	50–64 (58.0, 9)
Length of 3rd anal fin spine	53	48–53 (49.7, 6)
Length of pectoral fin	83	79–89 (84.7, 10)
Length of pelvic fin spine	38	31–39 (34.3, 10)

Figures in parentheses indicate mean values and sample size

SL, same data as the holotype; USNM 380182, 54 mm SL, same data as the holotype.

Diagnosis. A species belonging to the *Leiognathus splendens* complex as defined by the following characters: cheek naked (Fig. 2B); anterior dorsolateral body surface widely naked (Fig. 2B); lower margin of inner preopercular ridge smooth; interspace of pelvic keels naked (Fig. 3B); second spines of dorsal and anal fins weak (widths of dorsal and anal spines 0.72–1.2% SL and 0.60–0.91% SL, respectively; Fig. 5); dark blotch on dorsal fin rather pale, grayish (Fig. 4B).

Description. Counts and measurements of the holotype and paratypes are shown in Table 2. Characters given in description of the complex and the specific diagnosis are not

repeated. Body rhomboidal, dorsal profile similar to or more strongly convex (including the holotype) than ventral one; supraorbital ridge weakly rugged with series of minute spines; ventral surface of breast naked (Fig. 3B). Maximum recorded length 80 mm SL (holotype).

Color of preserved specimens.—Head and body almost uniformly light brown; tip of snout dark; ca. 20 wavy dark vertical lines dorsolaterally on body; distal half of fin membranes between second and fifth spines of dorsal fin with a pale black blotch; dorsal surfaces of middle pterygiophores of dorsal fin black; pectoral axil dark; pectoral fin proximally with narrow dark band.

Distribution. *Leiognathus kupanensis* sp. nov. is known only from the area of Kupang, Timor, Indonesia (Fig. 7).

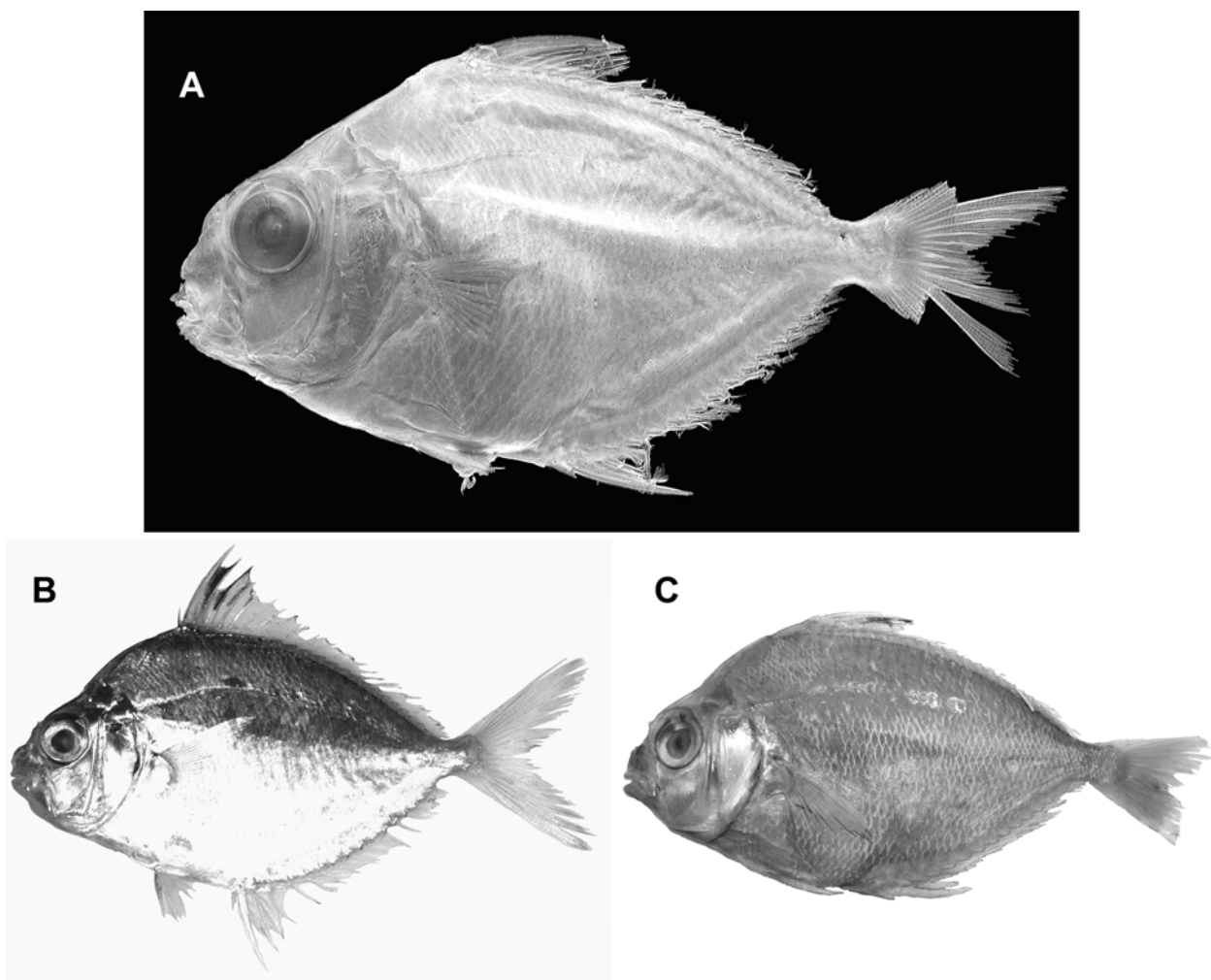


Fig. 9. *Leiognathus rapsoni*. **A** Holotype, CSIRO A 2137, 68 mm SL, from Papua New Guinea. **B** Non-type material, FRLM 15669, 79 mm SL, from Lombok, Indonesia. **C** Holotype of *Leiognathus indicus*, 84 mm SL, from Puri, Orissa, India

Etymology. The specific name “kupanensis” derived from the name of the type locality of the species.

Comparisons. *Leiognathus kupanensis* sp. nov. is easily distinguished from the other species of the *L. splendens* complex in having a widely naked anterior dorsolateral body surface (vs. almost entirely scaled in the latter; Fig. 2).

***Leiognathus rapsoni* Munro, 1964**

(English name: Papuan pony fish)

(Fig. 9, Table 3)

Leiognathus rapsoni Munro, 1964: 170–171 (type locality: Redscar Bay, Gulf of Papua, Papua New Guinea); Gloerfelt-Tarp and Kailola, 1984: 171 (off Bali, Indonesia); Kimura and Peristiwady, 2000: 225 (Lombok, Indonesia); Woodland et al., 2001: 2814 (Papua New Guinea).

Leiognathus indicus Singh and Talwar, 1978: 275–277 (Puri, Orissa, India).

Holotype. CSIRO A 2137, 68 mm SL, off Redscar Bay, Gulf of Papua, Papua New Guinea, 26 Mar. 1955.

Paratypes. CSIRO A 3087–3089, 3 specimens, 63–68 mm SL, same data as holotype.

Non-type materials. 10 specimens, 64–84 mm SL. CAS SU 8026, 65 mm SL, Sumatra, Indonesia; FRLM 14647, 15669, 15720, 16694, 16699, 5 specimens, 64–84 mm SL, Kuta, Lombok, Indonesia; FRLM 16999, 74 mm SL, Tanjung Luar, Lombok, Indonesia; UMMZ 243702 (2), 65–81 mm SL, Kuta, Lombok, Indonesia; ZSIF 7363/2 (holotype of *L. indicus*), 84 mm SL, Puri, Orissa, India, 21 Jan. 1977.

Diagnosis. A species belonging to the *Leiognathus splendens* complex as defined by the following characters: cheek scaled (Fig. 2C); anterior dorsolateral body surface almost completely scaled (Fig. 2C); lower margin of inner preopercular ridge serrated; interspace of pelvic keels scaled (Fig. 3C, D); dark blotch on dorsal fin rather pale, grayish (Fig. 4C).

Description. Counts and measurements of the holotype, paratypes, and other specimens are shown in Table 3. Characters given in description of the complex and the specific diagnosis are not repeated. Body ovoid, dorsal and ventral profiles of body similarly convex; supraorbital ridge rugged with series of many minute granules; ventral surface of breast

Table 3. Counts and measurements of *Leiognathus rapsoni*

	Holotype CSIRO A 2137	Paratypes CSIRO A 3087– 3089	Holotype of <i>L. indicus</i> ZSI F7363/2	Other specimens
Standard length (mm)	68	63–68 (65.1, 3)	88	64–84 (72.3, 9)
Counts				
Dorsal fin rays	VIII, 16	VIII, 16 (3)	VIII, 16	VIII, 16 (9)
Anal fin rays	III, 14	III, 14 (3)	III, 14	III, 14 (9)
Pectoral fin rays	17	17–18 (17.7, 3)	17	17 (9)
Lateral line scales	51	49–53 (51.0, 3)	52	46–51 (47.9, 9)
Scales above lateral line	10	8–10 (9.0, 3)	10	8–9 (8.4, 9)
Scales below lateral line	18	18–19 (18.3, 3)	20	18–21 (19.3, 9)
Gill rakers on upper arch	5	4–6 (5.0, 3)	4	5–6 (5.4, 9)
Gill rakers on lower arch	19	21–22 (21.3, 3)	22	18–20 (19.1, 9)
Measurements				
As % of standard length				
Head length	33	31–32 (31.7, 3)	33	29–32 (30.8, 9)
Predorsal length	49	45–47 (45.7, 3)	No data	44–49 (46.7, 9)
Length of dorsal fin base	57	55–57 (56.3, 3)	No data	57–61 (58.8, 9)
Length of anal fin base	47	45–48 (46.8, 3)	No data	47–50 (48.6, 9)
Snout to pectoral fin insertion	58	56–57 (56.3, 3)	No data	53–57 (54.6, 9)
Snout to pelvic fin insertion	33	35–36 (35.7, 3)	No data	30–34 (32.2, 9)
Snout to anal fin origin	39	42–43 (42.7, 3)	No data	36–43 (39.0, 8)
Pectoral fin insertion to pelvic fin insertion	23	22–31 (26.0, 3)	No data	24–25 (24.6, 8)
Pelvic fin insertion to anal fin origin	18	14–16 (15.3, 3)	No data	15–19 (16.9, 8)
Caudal peduncle length	10	11–12 (11.3, 3)	No data	9.4–11 (10.1, 9)
Body depth	52	50–52 (51.0, 3)	54	53–57 (24.7, 9)
Caudal peduncle depth	7.6	5.7–6.6 (6.23, 3)	No data	6.8–8.3 (7.60, 9)
As % of head length				
Snout length	28	26–30 (28.0, 3)	30	29–35 (31.4, 9)
Eye diameter	36	34–39 (37.0, 3)	No data	33–36 (34.6, 9)
Upper jaw length	Damaged	31 (1)	No data	29–37 (33.6, 8)
Interorbital width	28	32–37 (34.0, 3)	No data	24–28 (26.8, 9)
Length of 1st dorsal fin spine	12	12–13 (12.3, 3)	No data	10–16 (12.8, 8)
Length of 2nd dorsal fin spine	68	59–69 (60.7, 3)	No data	68–74 (70.5, 6)
Length of 3rd dorsal fin spine	53	48 (2)	No data	56–63 (59.5, 2)
Length of 1st anal fin spine	12	16–18 (17.0, 3)	No data	13–19 (15.9, 8)
Length of 2nd anal fin spine	58	56–62 (58.0, 3)	61	62–65 (63.6, 5)
Length of 3rd anal fin spine	Damaged	36 (1)	No data	52–58 (54.8, 4)
Length of pectoral fin	74	74 (1)	No data	70–79 (74.7, 9)
Length of pelvic fin spine	Damaged	33–38 (36.0, 3)	No data	37–43 (40.1, 7)

Figures in parentheses indicate mean values and sample size

completely scaled (holotype) or very narrow naked area anteriorly (Fig. 3C,D). Maximum recorded length 84 mm SL [FRLM 14647 from Lombok, Indonesia, and ZSIF 7363/2 (holotype of *Leiognathus indicus*) from Puri, Orissa, India].

Color of fresh specimens.—Head and body almost uniformly silvery-white, somewhat bluish dorsally; tip of snout dark; lateral line scales yellowish; dorsal fin membrane between second and fifth spines with a somewhat pale black blotch; anal fin membrane between second and third spines, caudal fin, and pectoral fin proximally yellow; dorsal, anal, and caudal fin margins dark; pectoral axil blackish.

Color of preserved specimens.—Head and body almost uniformly light brown; tip of snout dark; ca. 20 wavy dark vertical lines dorsolaterally on body; dorsal fin membrane between second and fifth spines with a pale black blotch;

dorsal surfaces of middle pterygiophores of dorsal fin black; pectoral axil dark; pectoral fin proximally with narrow dark band.

Distribution. *Leiognathus rapsoni* is known only from India [Puri, Orissa (type locality of *L. indicus*) and North Andaman I.], Indonesia (Sumatra and Lombok), and Papua New Guinea [Gulf of Papua (type locality)] (Fig. 7).

Remarks: Munro (1964) established *Leiognathus rapsoni* based on the holotype (CSIRO A 2137; Fig. 9A) and three paratypes (CSIRO A 3087–3089) from Red Scar Bay, Gulf of Papua, Papua New Guinea. He stated in the original description that *L. rapsoni* differs from the closest species, *L. splendens*, in having scales on cheek, shallower body (SL/body depth = 1.9–2.1 vs. 1.75–1.8 in *L. splendens*), fewer lateral line scale count (51–55 vs. 55–60), and more numer-

ous dark streaks dorsolaterally on body (20 vs. 12). From our observation and measurements, the scaled cheek is the best diagnostic character of the species, whereas proportion of body depth (50–57% SL vs. 42–60% in *L. splendens*) and number of dark streaks on body (ca. 20 in both species) are unusable for discriminating between the two species. Although *L. rapsoni* has a somewhat lower scale count than the other species belonging to the *L. splendens* complex, the ranges overlap (46–53 in the former vs. 50–66 in the latter).

Leiognathus indicus was described by Singh and Talwer (1978) based on the holotype (ZSI 7363/2; Fig. 9C) and eight paratypes [ZSI 7364/2 (7 specimens) and 7365/2 (1 specimen)] from Puri, Orissa and North Andaman I., India as a new *Leiognathus* species characterized by possession of cheek scales, deep body, and conspicuous black blotch on spinous dorsal fin. Comparing the original description of *L. rapsoni*, they stated that *L. indicus* differed from the latter species in having fewer gill rakers (18–19 vs. 21–23 in the latter) and a short second spine of anal fin (2.1–2.5 in body depth vs. 2.7–2.9). However, the gill raker counts of the holotype of *L. indicus* and the type series of *L. rapsoni* in the original descriptions (4 + 18 and 3 + 5 + 21–23, respectively) are erroneous; the correct counts are 4 + 22 and 4–6 + 19–22 (Table 3). Furthermore, the proportion of second spine of anal fin in the holotype of *L. indicus* (2.6 in body depth) agrees with that in the type series of *L. rapsoni* (2.6–2.9). Therefore, we conclude that *L. indicus* is a junior synonym of *L. rapsoni*.

Comparisons. *Leiognathus rapsoni* is easily distinguished from the other species of the *L. splendens* complex in having scales on cheek and interspace between pelvic keels (vs. cheek and interspace between pelvic keels completely naked; Figs. 2, 3).

Leiognathus splendens (Cuvier, 1829)

(English name: Splendid pony fish)

(Japanese name: Taiwan-hiiragi)

(Figs. 10, 11, Table 4)

Equula splendens Cuvier 1829: 212 (type locality: Chennai, India); Day, 1876: 239–240, pl. 55, fig. 3 (? in part, Red Sea, sea of India to the Malay Archipelago).

Equula gomorah Valenciennes in Cuvier and Valenciennes, 1835: 80–82 (type locality: Pondicherry, India).

Equula ovalis De Vis, 1884: 543 (type locality: Cape York, Queensland, Australia).

Equula simplex De Vis, 1884: 544 (type locality: Cape York, Queensland, Australia).

Leiognathus spilolus Fowler, 1904: 516–517 (type locality: Padang, Sumatra, Indonesia).

Leiognathus philippinus Fowler, 1918: 15–17 (type locality: Philippines).

Leiognathus splendens Weber and de Beaufort, 1931: 324–326 [in part, Sea of Penang, Singapore, Banka, Sumatra, Java, Madura, Bawean, Bali, Lombok, Sumbawa, Borneo (Kalimantan), Sulawesi, Batjan, Ternate, Ambon, Buru, Seram, Obi major, Aru Is., Timor, Red Sea, Madagascar, Mauritius, British India, Sri Lanka, Andamans, Thailand, China (Including Taiwan), Philippines, Queensland, Fiji Is.];

Kühlmorgan-Hille, 1974: LEIOG Leiog 10 (in part, Eastern Indian Ocean and Western Central Pacific); James, 1978: 148–149 [? in part, India (Gulf of Mannar, Arabian Sea, Bay of Bengal)]; Uyeno and Yabumoto, 1984: 159 (Okinawa, Japan); Gloerfelt-Tarp and Kailola, 1984: 171 (off Bali); James, 1984: LEIOG Leiog 10 (? in part, Mauritius, Madagascar, Red Sea, India, Sri Lanka, eastern Indian Ocean, Western Central Pacific); Jones, 1985: (northern Australia); Shen and Lin, 1985: 125–138 (Taiwan); Shen, 1993: 345 (Taiwan); Kimura and Peristiwady, 2000: 227 (Lombok, Indonesia); Woodland et al., 2001: 2815 (in part, Mauritius, Madagascar, Red Sea, India to island of western Central Pacific as far as Fiji, north to Okinawa, south to northern part of Australia); Senou, 2002: 811 (Ryukyu Is, Japan, Indo-West Pacific); Kimura et al., 2003b: 84 (Bitung, Sulawesi, Indonesia).

Leiognathus daura (not of Cuvier); Mohsin and Ambak, 1996: 346, fig. 251 (Malaysia).

Neotype. RMNH 1441, 98 mm SL, Chennai, India.

Non-type materials. 164 specimens, 25–125 mm SL. AMS I. 15557-126, 90 mm SL, Gulf of Carpentaria, Australia; AMS I. 20402-045 (3), 58–80 mm SL, Bonaparte Archipelago, Western Australia; AMS I. 20826-019 (5), 80–97 mm SL, Palm I., Queensland, Australia, AMS I. 21841-004 (6), 78–84 mm SL, Arafura Sea, Australia; AMS IA. 4900, 30 mm SL, Bonaparte Archipelago, Western Australia (paralectotype of *E. ovalis*); ANSP 27529, 25 mm SL, Padang, Sumatra, Indonesia, date unknown (holotype of *L. spilolus*); ANSP 47486, 53 mm SL, Philippines, Nov. 1917 (holotype of *L. philippinus*); ANSP 47487–47490, 4 specimens, 49–53 mm SL, Philippines, Nov. 1917 (paratypes of *L. philippinus*); ASIZP 57566 (4), 57611 (7), 11 specimens, 44–584 mm SL, Tzengwen River, Taiwan; ASIZP 57614, 70 mm SL, Shuanghsi River, Taiwan; ASIZP 57685 (2), 60–83 mm SL, Erhjen River, Taiwan; ASIZP 57689, 43 mm SL, Tungshiao, Taiwan; ASIZP 58819, 86 mm SL, Nanliao, Taiwan; BMNH 1889.2.1.3262, 78 mm SL, Chennai, India; CAS SU 30512, 86 mm SL, Vizagapatam, Chennai, India, CAS SU 41642 (3), 40–48 mm SL, Kerala, India; CSIRO A 41, A 43, 2 specimens, 58–77 mm SL, Salamaua, Morobe, Papua New Guinea; CSIRO A 2176–2179, A 2348, A 2349, A 3995, A 3996, C 3424, C 3425, CA2690, H 3610 (4), 15 specimens, 73–10 mm SL, Gulf of Carpentaria, Australia; CSIRO A 3034, 54 mm SL, Kerema Bay, Gulf of Papua, Papua New Guinea; CSIRO B 2215 (7), 83–112 mm SL, Arafura Sea, Australia; CSIRO C 1784, 84 mm SL, Manus Island, Bismarck Archipelago, Papua New Guinea; FRLM 14788, 14789, 16997, 16998, 17000, 20047, 20385, 7 specimens, 60–91 mm SL, Tanjung Luar, Lombok, Indonesia; FRLM 15724, 16695, 17267, 17268, 20248, 5 specimens, 38–71 mm SL, Kuta, Lombok, Indonesia; FRLM 17126, 17272, 2 specimens, 40–45 mm SL, Gerupuk, Lombok, Indonesia; FRLM 21492, 21497, 21501, 23514, 23775, 5 specimens, 55–98 mm SL, Passo, Ambon, Indonesia; FRLM 21518, 65 mm SL, Guru Guru, Ambon, Indonesia; FRLM 25568–25570, 25795–25797, 26464, 26465, 8 specimens, 61–90 mm SL, Pintukota, Lembah I., North Sulawesi, Indonesia; FRLM 30790, 92 mm SL, Iloilo, Panay I., Philippine; MNHN A-6724, 50 mm SL, Pondicherry, India, date unknown (lectotype of *E. gomorah*); MNHN A-6726, 89 mm SL, Malabar, India, date unknown (paralectotype of *E. gomorah*); MNHN A-6727 (2), 94–100 mm SL, Ambon, Indonesia; MUFS 9346, 82 mm SL, Iloilo, Panay I., Philippines; MUFS 12909, 125 mm SL, Meitsu, Nango, Miyazaki, Japan; MUFS 13095–13098, 4 specimens, 73–91 mm SL, Ambon, Indonesia; MUFS 16915–16919, 17022–17024, 9 specimens, 61–79 mm SL, Mangalore, India; MUFS 16970–16973, 4 specimens, 81–84 mm SL, Malpe, India; NSMT-P 35323 (2), 70–81 mm SL, Tainan, Taiwan; QM I.1702, 35 mm SL, Cape York, Australia, date unknown (lectotype of *E. simplex*); QM I.1703, 34 mm SL, Cape York, Australia, date unknown (lectotype of *E. ovalis*); QM I.9810 (6 of 8), 28–34 mm SL, Cape York, Australia, date unknown (paralectotypes of *E. ovalis*); QM I.9811 (1 of 2), 35 mm SL, Cape York,

Table 4. Counts and measurements of *Leiognathus splendens*

	Neotype RMNH 1441	Lectotype of <i>E. gomorah</i> MNHN 6724	Paralectotype of <i>E. gomorah</i> MNHN 6726	Lectotype of <i>E. ovalis</i> QM I. 1703	Paralectotypes of <i>E. ovalis</i> AMS IA. 4900, QM I. 9810
Standard length (mm)	68	50	89	34	28–34 (30.6, 7)
Counts					
Dorsal fin rays	VIII, 16	VIII, 16	VIII, 16	VIII, 16	VIII, 16 (7)
Anal fin rays	III, 14	III, 14	III, 14	III, 14	III, 14 (7)
Pectoral fin rays	17	18	17	18	17–19 (17.7, 3)
Lateral line scales	51	52	55	Damaged	56–61 (57.8, 6)
Scales above lateral line	10	13	14	Damaged	12–14 (13.0, 3)
Scales below lateral line	18	30	29	Damaged	28–30 (29.0, 2)
Gill rakers on upper arch	5	6	6	5	5 (5)
Gill rakers on lower arch	19	21	21	20	19–22 (20.4, 5)
Measurements					
As % of standard length					
Head length	33	32	31	33	29–34 (32.0, 7)
Predorsal length	49	45	46	43	38–48 (42.9, 7)
Length of dorsal fin base	57	58	58	55	52–58 (55.3, 7)
Length of anal fin base	47	47	46	45	39–46 (42.9, 7)
Snout to pectoral fin insertion	58	55	58	55	50–59 (54.4, 7)
Snout to pelvic fin insertion	33	34	34	34	32–54 (37.6, 7)
Snout to anal fin origin	39	38	41	40	36–43 (39.3, 7)
Pectoral fin insertion to pelvic fin insertion	23	22	24	22	20–26 (21.6, 7)
Pelvic fin insertion to anal fin origin	18	17	19	Damaged	13–20 (16.3, 6)
Caudal peduncle length	10	11	11	13	9.2–12 (11.0, 7)
Body depth	52	53	55	45	42–48 (45.6, 7)
Caudal peduncle depth	7.6	7.4	7.5	6.7	5.9–7.0 (6.5, 7)
As % of head length					
Snout length	28	29	28	25	20–40 (27.6, 7)
Eye diameter	36	39	38	35	34–44 (39.6, 7)
Upper jaw length	39	31	33	32	27–38 (33.3, 4)
Interorbital width	28	29	28	29	28–35 (31.0, 7)
Length of 1st dorsal fin spine	12	14	Damaged	12	12–16 (13.8, 4)
Length of 2nd dorsal fin spine	68	Damaged	Damaged	Damaged	61–71 (66.8, 4)
Length of 3rd dorsal fin spine	53	Damaged	Damaged	Damaged	48–51 (49.7, 3)
Length of 1st anal fin spine	12	19	22	Damaged	18–25 (21.0, 5)
Length of 2nd anal fin spine	58	58	Damaged	Damaged	55–62 (59.0, 6)
Length of 3rd anal fin spine	Damaged	45	Damaged	Damaged	40 (1)
Length of pectoral fin	74	83	77	Damaged	78 (1)
Length of pelvic fin spine	45	39	43	Damaged	34–41 (38.0, 2)

Figures in parentheses indicate mean values and sample size

Australia, date unknown (paralectotype of *E. simplex*); UMMZ 243703 (10), 59–73 mm SL, Tigbauan, Iloilo, Panay I., Philippines; URM-P 928, 37983, 37984, 3 specimens, 66–78 mm SL, Haneji-naikai, Okinawa, Japan; URM-P 6348, 117 mm SL, Zamami I., Kerama I., Okinawa, Japan; URM-P 11733, 31209, 32176, 32177, 32196–32199, 34227, 9 specimens, 39–52 mm SL, Iriomote I., Okinawa, Japan; URM-P 20854–20855, 2 specimens, 59–72 mm SL, Kavieng, New Ireland, Papua New Guinea; URM-P 33227, 33228, 2 specimens, 44–45 mm SL, Jilong, Taiwan; YCM-HLP 184, 68 mm SL, Sandakan, Sabah, Borneo, Malaysia; YCM-HLP 648 (3), 59–65 mm SL, Sandakan, Sabah, Borneo, Malaysia; ZRC 3771, 84 mm SL, Sabah, Borneo, Malaysia.

Materials for distributional records. 29 specimens, 27–82 mm SL. BMNH 1871.7.20.128, 75 mm SL, Manado, Sulawesi, Indonesia; BMNH 1884.5.15.8–9 (2), 44 mm SL, southern Taiwan; BMNH 1983.10.19.28, 52 mm SL, Sri Lanka; CSIRO A 124, 125, 2 specimens, 46–52 mm SL, Kapa Kapa, Papua New Guinea; CSIRO A 44, A 49, A 50, 3 specimens, 41–53 mm SL, Salamaua, Papua New Guinea; CSIRO A 182, 27 mm SL, Madang, Papua New Guinea; CSIRO A 206, 34 mm SL, Oro Bay, Papua New Guinea; FRLM 30948, 30949, 2 specimens, 78–79 mm SL, Roxas, Panay, Philippines; MUFS 19416, 19419, 19421, 19423–19428, 12 specimens, 58–82 mm SL, Mangalore, India; MUFS 19521, 64 mm SL, Trivandram, India; NSMT-P 547070, 2 specimens, 60–63 mm SL, Kuta,

Lectotype of <i>E. simplex</i> QM I. 1702	Paralectotype of <i>E. simplex</i> QM I. 9811	Holotype of <i>E. spilotus</i> ANSP 27529	Holotype of <i>L. philippinus</i> ANSP 47486	Paratypes of <i>L. philippinus</i> ANSP 47487–47490	Other specimens
35	35	25	53	49–53 (50.8, 4)	38–125 (71.5, 146)
VIII, 16	VIII, 16	VIII, 16	VIII, 16	VIII, 16 (4)	VIII–IX, 15–17 (III, 16.0, 146)
III, 14	III, 14	III, 14	III, 14	III, 14 (4)	III, 13–15 (III, 14.0, 146)
18	Damaged	Damaged	18	17–18 (17.5, 4)	16–19 (17.3, 146)
64	58	Damaged	55	57–61 (58.5, 4)	50–66 (56.7, 142)
13	12	Damaged	13	12–13 (12.5, 4)	9–26 (13.1, 142)
29	28	Damaged	24	26–29 (27.0, 4)	12–33 (27.1, 141)
6	6	Damaged	6	5–6 (5.5, 4)	4–7 (5.7, 145)
20	19	Damaged	19	19 (4)	18–24 (20.6, 145)
34	32	30	32	31–33 (32.0, 4)	29–35 (31.9, 145)
45	45	43	45	44–47 (45.3, 4)	42–51 (46.4, 142)
55	57	59	57	55–58 (56.0, 4)	53–61 (57.6, 146)
45	43	Damaged	45	44–45 (44.3, 4)	42–50 (45.3, 146)
53	54	Damaged	54	52–54 (53.0, 4)	50–61 (55.3, 146)
34	33	Damaged	34	32–34 (33.3, 4)	30–36 (33.1, 146)
39	40	Damaged	38	36–37 (36.5, 4)	34–42 (37.9, 146)
22	20	Damaged	21	21–22 (21.8, 4)	19–26 (22.6, 145)
Damaged	16	Damaged	Damaged	Damaged	15–22 (18.6, 135)
13	12	10	11	12–13 (12.3, 4)	9.0–13 (10.9, 146)
46	47	45	46	47–48 (47.3, 4)	42–60 (50.5, 146)
7.2	6.7	7.3	6.3	6.6–7.0 (6.78, 4)	5.8–9.3 (7.28, 146)
24	29		26	26–29 (27.5, 4)	24–37 (28.9, 145)
33	36	43	37	36–38 (37.0, 4)	31–40 (35.5, 145)
35	32	34	35	33–35 (33.8, 4)	23–38 (33.9, 104)
30	31	Damaged	28	27–29 (28.0, 4)	25–36 (28.2, 145)
13	Damaged	12	12	12 (3)	7.0–15.5 (14.6, 140)
65	47	75	69	61–68 (65.7, 3)	59–80 (68.3, 108)
Damaged		Damaged	Damaged	62 (1)	44–73 (58.1, 77)
17	11	20	18	17–20 (18.3, 4)	12–22 (17.3, 139)
Damaged	43	Damaged	Damaged	52–55 (53.3, 3)	46–71 (56.8, 117)
Damaged	Damaged	Damaged	Damaged	44–51 (47.5, 2)	32–57 (46.9, 103)
81	Damaged	Damaged	81	77–87 (81.8, 4)	66–87 (78.4, 140)
Damaged	36	Damaged	Damaged	Damaged	32–47 (38.2, 129)

Lombok, Indonesia; SMF 4311, 58mm SL, Belang I., Sumbawa, Indonesia; YCM-HLP 801, 60mm SL, Mumbai, India.

Diagnosis. A species belonging to the *Leiognathus splendens* complex as defined by the following characters: cheek naked (Fig. 2D); anterior dorsolateral body surface almost completely scaled without a semicircular naked area on nape (Fig. 2D); lower margin of inner preopercular ridge smooth or weakly serrated (including the neotype); interspace of pelvic keels naked (Fig. 3E); second spines of

dorsal and anal fins robust (width of second spines of dorsal and anal fins 0.87–1.6% of SL and 0.76–1.7% of SL, respectively; Fig. 5); a jet black blotch on spinous dorsal fin (Fig. 4D).

Description. Counts and measurements of the neotype and other specimens are shown in Table 4. Characters given in description of the complex and the specific diagnosis are not repeated. Body rhomboidal to somewhat oblong, dorsal profile similar to or somewhat more strongly convex (including the neotype) than ventral one; supraorbital ridge

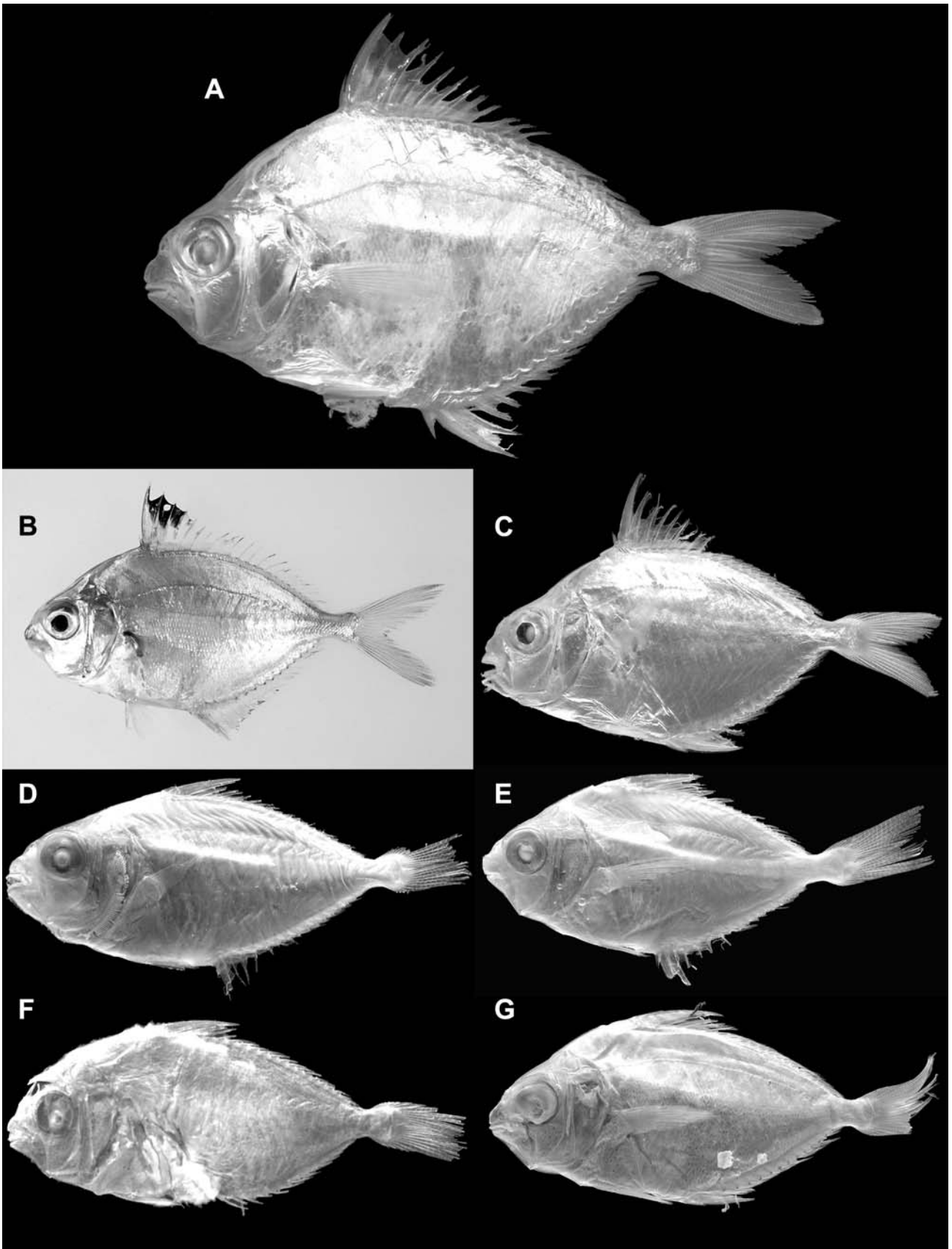


Fig. 10. *Leiognathus splendens*. **A** Neotype, RMNH 1441, 98 mm SL, from Chennai, India. **B** Non-type material, FRLM 20385, 60 mm SL, from Lombok, Indonesia. **C** Lectotype of *Equula gomorah*, MNHN A6724, 50 mm SL, from Pondicherry, India. **D** Lectotype of *E. ovalis*, QM I. 1703, 34 mm SL, from Cape York, Australia. **E** Lectotype of *E. simplex*, QM I. 1702, 35 mm SL, from Cape York, Australia. **F** Holotype of *L. spilottus*, ANSP 27529, 25 mm SL, from Padan, Sumatra, Indonesia. **G** Holotype of *L. philippinus*, ANSP 47486, 53 mm SL, from Philippines

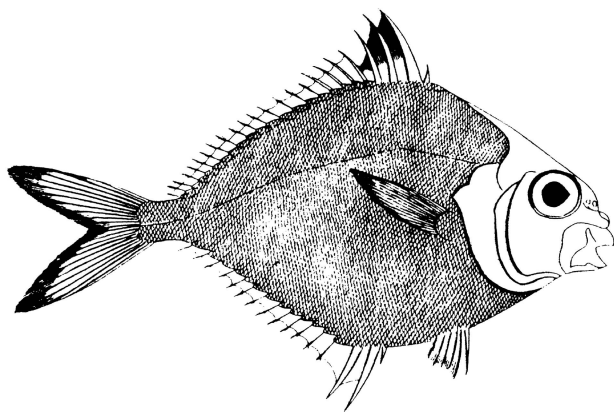


Fig. 11. A drawing of “Goomorah Karah” after Russell (1803)

smooth or weakly rugged with series of minute spines (including the neotype); ventral surface of breast naked (Fig. 3E). Maximum recorded length 125 mm SL (MUFS 12909, from Miyazaki, Japan).

Color of fresh specimens.—Head and body almost uniformly silvery-white; tip of snout dark; lateral line scales pale yellow; distal half of fin membranes between second and sixth spines of dorsal fin with a jet black blotch; margins of soft dorsal, soft anal, and caudal fins pale yellow, spinous anal and pectoral fins pale yellow; caudal fin and sometimes soft dorsal fin additionally fringed with pale black; pelvic fin pearl white; pectoral axil dark.

Color of preserved specimens.—Head and body almost uniformly light brown or light brown dorsally and silvery-white ventrally; tip of snout dark; wavy dark vertical lines dorsolaterally on body; distal half of fin membranes between second and fifth spines of dorsal fin with a jet black blotch; dorsal surfaces of middle pterygiophores of dorsal fin black; pectoral axil dark; pectoral fin proximally with narrow dark band.

Distribution. *Leiognathus splendens* is known from India [Mumbai, Malpe, Mangalore, Kerala State, Malabar, Trivandrum, Pondicherry, Chennai (type locality)], Sri Lanka, Japan (Miyazaki, Okinawa I., Iriomote I.), Taiwan, Philippines, Malaysia (Sabah), Indonesia [Sulawesi (Manado, Bitung), Lombok, Sumbawa, Ambon], Papua New Guinea (Madan, Kapa kappa, Salamaua, Gulf of Papua, Admiralty Is., Kavieng), and Australia [Palm I. (Queensland), Cape York, Gulf of Carpentaria, Arafura Sea, Admiralty Gulf (Western Australia)] (Fig. 7).

Remarks. *Leiognathus splendens* was originally described by Cuvier (1829) as *Equula splendens* based on Russell’s (1803) description and drawing of “Goomorah karah” from Vizagapatam, Chennai, India (Fig. 11). Russell’s fish undoubtedly belongs to the *L. splendens* complex because of the orbit above the horizontal through the gape and presence of a black blotch on top of spinous dorsal fin. Russell (1803) stated that the fish had no scales on head, and consequently it was not *L. rapsoni*. However, it is impossible to identify accurately the fish as *L. splendens* or the sympatric species, *L. jonesi*, because he did not describe density of a dark blotch on spinous dorsal fin, thickness of

second spines of dorsal and anal fins, or squamation on anterodorsal surface of body. On the other hand, the name “*Leiognathus splendens*” is the most widespread among the complex, and James (1971) regarded “*L. splendens*” as the species having a denser marking on dorsal fin and more robust second spines of dorsal and anal fins in comparison with *L. jonesi*. Therefore, we consider *L. splendens* to be valid and define it as the species having no cheek scales, no naked area on nape, robust dorsal and anal fin spines, and a jet black marking on dorsal fin. To clarify the taxonomic status of this species and avoid future confusion, we designate here the specimen collected from Chennai (RMNH 1441) as the neotype.

Equula gomorah was established by Valenciennes in Cuvier and Valenciennes (1835) based on four syntypes collected from Malabar Coast, Pondicherry, India, and the Red Sea. The lectotype (MNHN A 6724, 50 mm SL, from Pondicherry, India; here designated; Fig. 10C) and paralectotype (MNHN A 6726, 89 mm SL, from the Malabar Coast, India) were examined here and are considered to be conspecific with *L. splendens* based on the jet black marking on dorsal fin, robust second spine of anal fin, fine weak serration on lower margin of inner preopercular ridge, and no naked area on anterodorsal surface of body. Therefore, *E. gomorah* is regarded as a junior synonym of *L. splendens*.

Both *E. ovalis* (Fig. 10D) and *E. simplex* (Fig. 10E) were originally described by De Vis (1884) based on several specimens from Cape York, Queensland, Australia. Although some differences in morphology between these two species can be found in the original descriptions, e.g., scales large in *E. ovalis* (vs. short in *E. simplex*), lower margin of preopercle distinctly serrated in *E. ovalis* (vs. serrated in *E. simplex*), angle formed by lower jaw 40° in *E. ovalis* (vs. 45° in *E. simplex*), Whitely (1932) designated the lectotypes of both species and stated that he found no characters to maintain the two as distinct species. Therefore, Whitely (1932) regarded *E. ovalis* as a senior synonym of *E. simplex*, being distinct from the Indian *L. splendens*, based on the differences in position of mouth, body depth, pattern of lateral line, and head profile. Subsequently, Munro (1960) and Jones (1985) synonymized *E. ovalis* and *E. simplex* under *L. splendens*. From the present examination of the types of *E. ovalis* and *E. simplex*, we conclude that the two species are junior synonyms of *L. splendens* as stated by Munro (1960) and Jones (1985), because they have a relatively lower body depth (42–48% SL in *E. ovalis*; 46–47% SL in *E. simplex*), serrated inner ridge of preopercle, and robust second spine of dorsal fin (width: 0.87–1.6% of SL in *E. ovalis*; 1.1% of SL in *E. simplex*), although the black markings on dorsal fin were obscure for all specimens.

Leiognathus spilotus was originally described by Fowler (1904) based on a single juvenile (25 mm SL) collected from Padang, Sumatra, Indonesia (Fig. 10F). Because the holotype has the lower margin of orbit located above the horizontal through the gape when mouth closed and a dark blotch on top of spinous dorsal fin, the species undoubtedly belongs to the *L. splendens* complex. Furthermore, the holotype can be regarded as conspecific with *L. splendens* because it has a black blotch on the upper spinous dorsal

fin (nearly indistinct) and serrated inner edge of preopercle.

Leiognathus philippinus (Fig. 10G) was established by Fowler (1918) based on the holotype and four paratypes collected from Philippines, being distinct from *L. splendens* in body color. After that, James (1978) synonymized *L. philippinus* under *L. splendens* without explanation. The present examination of the holotype and paratypes of *L. philippinus* confirmed that the species is a junior synonym of *L. splendens*, based on a jet black blotch on spinous dorsal fin, robust second spine of dorsal fin (width: 1.1–1.3% of SL), no naked area on nape, and relatively lower body depth (46–48% SL). Additionally, it should be noted that Fowler (1918) regarded *L. jonesi* as *L. splendens*.

Comparisons. *Leiognathus splendens* is easily distinguished from *L. jonesi* in having a jet black blotch on dorsal fin (vs. paler dark blotch in the latter; Fig. 4), dull pale to dark yellow lateral line scales if fresh (vs. prominent yellow), anterior dorsolateral surface almost completely scaled (vs. a semicircular naked area on nape; see Fig. 2), and robust dorsal and anal fin spines (width of second spines of dorsal and anal fins 0.87–1.6% of SL and 0.76–1.7% of SL, respectively, vs. 0.72–1.1% of SL and 0.60–0.95% of SL, respectively; Fig. 5), and is distinguished from *L. rapsoni* in lacking scales on cheek and interspace of pelvic keels (vs. scales present on cheek and interspace of pelvic keels in the latter; Figs. 2, 3). *Leiognathus splendens* is also distinguished from *L. kupanensis* sp. nov. in having almost completely scaled anterior dorsolateral body surface (vs. widely naked anterior dorsolateral body surface; Fig. 2).

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