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A New Species of Ponyfish (Teleostei: Leiognathidae: *Photoplagios*) from Madagascar, with a Phylogeny for *Photoplagios* and Comments on the Status of *Equula lineolata* Valenciennes

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ABSTRACT

A new species of ponyfish in the genus *Photoplagios* is described from material collected in coastal waters of northeastern Madagascar. *Photoplagios antongil*, new species, is distinguished from congeners by the presence of a broad midlateral stripe and two darkly pigmented flank patches located ventral to the lateral midline, which are presumably translucent in life but darkly pigmented in preservative due to a concentration of melanophores. The new species is further distinguished from *P. leuciscus*, the only externally similar species occurring in the region, by the absence of a large translucent triangular patch on the flanks, a much shorter second dorsal-fin spine, a straight predorsal profile, pigmentation pattern on the upper flanks, absence of black pigment in the pectoral-fin axil, and exposed conical oral dentition in two distinct rows. A phylogeny for *Photoplagios* is provided based on the simultaneous analysis of anatomical features of the light-organ system and nucleotide characters. The taxonomic status of *Equula lineolata* Valenciennes, in Cuvier and Valenciennes, 1835 is discussed, and the species is herein concluded to be a nomen dubium of uncertain placement beyond the family level.

INTRODUCTION

Photoplagios Sparks, Dunlap, and Smith, 2005 comprises eight species: *P. elongatus* (Günther, 1874), *P. klunzingeri* (Steindachner, 1898), *P. leuciscus* (Günther, 1860), *P. line-*

olatus (Valenciennes, in Cuvier and Valenciennes, 1835), *P. moretoniensis* (Ogilby, 1912), *P. rivulatus* (Temminck and Schlegel, 1845), *P. stercorarius* (Evermann and Seale, 1907), and a new species from the coastal waters of Madagascar described herein.

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Although *P. klunzingeri* and *P. moretoniensis* were not included in the family-level phylogenetic analysis of Sparks et al. (2005), they possess the following apomorphic features of the light-organ system (LOS) that diagnose the genus. Members of *Photoplagios* are strongly sexually dimorphic, and males are distinguished from all other members of Leiognathidae by the presence of an expansive translucent lateral flank patch or stripe, dorso-lateral lobes of the light organ that are hypertrophied and extend posteriorly into the gas bladder (extensively in *P. elongatus* and *P. rivulatus*, less so in the remaining congeners), and lateral clearing of the silvery lining of the gas bladder, which is directly correlated with species-specific transparent lateral flank patches or stripes (Sparks et al., 2005: figs. 3–5).

A comprehensive phylogenetic and taxonomic study of Leiognathidae is needed, including detailed comparisons of the LOS, to establish the generic limits of *Photoplagios* and the other genera. For example, based on remarks in the original description, which refer to an elongate body and possession of a midlateral stripe, *Equula berbis* Valenciennes, in Cuvier and Valenciennes, 1835 also is potentially a member of *Photoplagios*, although no types are known and the original description (and earlier comments relating to this taxon by Forsskål, 1775: 58) does not serve to diagnose this species on the basis of unique anatomical features or to distinguish it from congeners on the basis of a combination of unique attributes. Likewise, based on similar remarks in the original description and an external examination of the holotype, *Equula oblonga* Valenciennes, in Cuvier and Valenciennes, 1835 is likely also to be a member of *Photoplagios*; however, the holotype is in poor condition with regard to pigmentation pattern, and the LOS cannot be studied.

Members of *Photoplagios* are bioluminescent schooling fishes and are distributed in shallow coastal habitats from the east coast of Africa and the Red Sea (including a single species, *P. klunzingeri*, which has dispersed into the Mediterranean Sea via the Suez Canal) to Japan and Australia. Within *Photoplagios*, *P. leuciscus* and *P. lineolatus* are reported to have extensive ranges (but see

Discussion); each of their putative ranges is nearly as great as that of the genus in its entirety. As Gill and Kemp (2002) stressed, however, putatively wide distributional ranges for many Indo-Pacific shore-fishes may simply reflect poor taxonomic understanding. This claim is corroborated for ponyfishes in general by a recent study using nucleotide characters to resolve phylogenetic intrarelationships (Sparks et al., 2005); the study indicated that many putatively widespread ponyfish species (e.g., *Leiognathus equulus*, *L. fasciatus*, *Photoplagios leuciscus*, *Photopectoralis bindus*, and *Gazza minuta*) may actually comprise species assemblages.

Luminescence in leiognathids is produced by large numbers of the symbiotic luminous bacterium *Photobacterium leiognathi*, which are harbored in an internal circumesophageal light organ (Boisvert et al., 1967; Hastings and Mitchell, 1971; Bassot, 1975; Reichelt et al., 1977; Dunlap, 1984). Collectively with the light organ, the leiognathid LOS comprises reflectors and chromatophore-embedded light-organ shutters, reflective and translucent tissues of the gas bladder, and translucent bone, musculature, and skin (Sparks et al., 2005). These highly modified accessory LOS tissues function to regulate, direct, and diffuse the intense blue-green bacterial light over the ventrum (Harms, 1928; Ahrens, 1965; Bassot, 1975; McFall-Ngai, 1983; Dunlap and McFall-Ngai, 1987). Additionally, males of most species possess the ability to emit light in rapid flashes from translucent patches located either on the flanks, along the opercular margin, in the buccal cavity, or some combination of these regions (Haneda, 1940; Hastings, 1971; Herring and Morin, 1978; McFall-Ngai and Dunlap, 1983; McFall-Ngai, 1991; Woodland et al., 2002; Sasaki et al., 2003; Sparks et al., 2005). Ventral luminescence is hypothesized to provide camouflage illumination against bottom-dwelling piscivorous fishes, whereas lateral, buccal, and opercular flashing may function in prey attraction, other forms of predator avoidance, schooling behavior, and sex-specific signaling (Hastings, 1971; Herring and Morin, 1978; McFall-Ngai, 1983; McFall-Ngai and Dunlap, 1983, 1984; Dunlap and McFall-Ngai, 1987; McFall-Ngai and Morin, 1991; Woodland et

al., 2002; Sasaki et al., 2003; Sparks and Dunlap, 2004; Sparks et al., 2005). The degree of species-specific anatomical specialization and strong sexual dimorphism of the light organ and associated structures of the LOS observed throughout the family suggest a system of mate recognition based on male species-specific luminescent signaling (Sparks et al., 2005).

In the present study, a new species belonging to the recently described genus *Photoplagios* Sparks, Dunlap, and Smith, 2005 is described from material collected in northeastern Madagascar. A phylogeny for *Photoplagios* is presented based on a reanalysis of the morphological transformations and nucleotide characters (comprising both mitochondrial and nuclear genes) analyzed by Sparks et al. (2005), with the addition of two new taxa, *P. klunzingeri* and *P. moretoniensis*, and additional anatomical features of the LOS. In the context of this phylogeny, placement of the new species within *Photoplagios* is discussed with reference to homologous features of the LOS. In addition, the taxonomic status of *Equula lineolata* Valenciennes, in Cuvier and Valenciennes, 1835, an allegedly widespread taxon to which several distinct species seem to have been historically attributed, and presumably including the new species, is discussed in detail.

MATERIALS AND METHODS

MORPHOLOGY

Osteological features of the new species and related taxa were examined using radiographs, specimens cleared and stained for bone and cartilage (C&S) using a protocol based on Taylor and Van Dyke (1985), and dry skeletal preparations. Comparative materials are listed in appendix 1. Light organs were either isolated from each taxon (except those represented only by type specimens) or examined in situ for rare species, to permit detailed morphological comparisons of the LOS. Morphometric measurements were recorded to the nearest 0.1 mm using dial calipers. Standard length (SL) is used throughout. Vertebral counts exclude the ural centrum (= last half-centrum). Following Hubbs and Lagler (1949), the first caudal vertebra is here

defined as the first vertebra bearing a definite hemal spine. Vertebral and fin spine/ray counts were obtained from radiographs. The terminal dorsal-fin and anal-fin rays, which are branched to the base of the fin, are counted as a single element. Pored scales in the lateral line are counted in series from the dorsal margin of the gill opening to the caudal flexure. Scale counts should be interpreted as approximations, due to high intraspecific variability, irregular arrangement, the deciduous nature of ponyfish scales in preservation, and because small scale size and the degree to which scales are embedded make accurate counts problematic.

INSTITUTIONAL ABBREVIATIONS

Institutional abbreviations follow Leviton et al. (1985):

AMNH	American Museum of Natural History, New York
AMS	Australian Museum, Sydney
ANSP	Academy of Natural Sciences, Philadelphia
BMNH	Natural History Museum, London
CAS	California Academy of Sciences, San Francisco
LACM	Los Angeles County Museum of Natural History
MNHN	Museum National d'Histoire Naturelle, Paris
NMW	Naturhistorisches Museum, Wien
QM	Queensland Museum, South Bank, Australia
SIO	Scripps Institution of Oceanography, Marine Vertebrates Collection, La Jolla
UMMZ	University of Michigan, Museum of Zoology, Ann Arbor
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C.
ZMB	Universitat Humboldt, Museum fur Naturkunde, Berlin
ZMUC	Kobenhavns Universitet, Zoologisk Museum, Copenhagen

PHYLOGENY RECONSTRUCTION

For the phylogenetic analysis, 6160 equally weighted nucleotide characters (based on the implied alignment [Wheeler, 2003]) from the seven mitochondrial (*16S*, *COI*, *ND4*, *ND5*,

TABLE 1

Morphological Character Matrix of Internal and External Features of the Leiognathid Light-Organ System (LOS)

Clade designations refer to those recovered in Sparks et al. (2005). Character descriptions are listed in appendix 2. Inapplicable characters are designated by (-).

	Characters																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Outgroups	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Clade I: <i>Leiognathus fasciatus complex</i>	1	0	0	0	0	0	0	0	-	-	0	0	0	0	0	-	-
Clade J: <i>Leiognathus equulus complex</i>	1	0	0	0	0	0	0	0	-	-	0	0	0	0	0	-	-
Clade K: <i>Leiognathus</i> sp. "Sri Lanka"	1	?	0	0	0	0	0	0	-	-	0	0	0	0	0	-	-
Clade L: <i>Photoplagios elongatus</i>	1	1	1	0	0	1	0	1	0	-	0	0	0	0	0	0	-
Clade L: <i>Photoplagios rivulatus</i>	1	1	1	0	0	1	0	1	0	-	0	0	0	0	0	0	-
Clade L: <i>Photoplagios leuciscus</i>	1	1	1	0	0	1	0	1	0	-	0	0	0	0	0	1	-
Clade L: <i>Photoplagios klunzingeri</i>	1	1	1	0	0	1	0	1	0	-	0	0	0	0	0	1	-
Clade M: <i>Photoplagios stercorarius</i>	1	1	1	0	0	1	0	1	1	1	0	0	0	0	0	0	1
Clade M: <i>Photoplagios moretoniensis</i>	1	1	1	0	0	1	0	1	1	1	0	0	0	0	0	0	0
Clade M: <i>Photoplagios</i> sp. "Sri Lanka" ^a	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Clade M: <i>Photoplagios antongil</i> , n. sp. ^b	1	1	1	0	0	1	0	1	1	0	0	0	0	0	0	0	-
Clade E: <i>Photopectoralis</i>	1	1	0	1	1	0	1	0	-	-	0	0	1	1	0	-	-
Clade D: <i>Secutor</i>	1	1	0	0	1	0	0	0	-	-	1	0	1	1	1	-	-
Clade F: <i>Gazza</i>	1	1	0	0	1	0	0	0	-	-	0	1	1	1	0	-	-
Clade G: " <i>Leiognathus</i> "	1	1	0	0	0	0	0	0	-	-	0	0	0	0	0	-	-
Clade H: " <i>Leiognathus</i> "	1	1	0	0	0	0	0	0	-	-	0	0	0	0	0	-	-

^a Identified as *Photoplagios lineolatus* in the study of Sparks et al. (2005).

^b Referred to as *Photoplagios* sp. "Madagascar" in the study of Sparks et al. (2005).

tRNA-His, *tRNA-Ser*, *tRNA-Leu*) and two nuclear genes (*28S*, *histone H3*) used by Sparks et al. (2005), and 17 morphological features of the LOS (see table 1 and appendix 2), were simultaneously analyzed under the optimality criterion of parsimony with all transformations given equal weight. Two taxa not included in the analysis of Sparks et al. (2005), *Photoplagios klunzingeri* and *P. moretoniensis*, are included here on the basis of morphological features of the LOS only, as no tissue sample suitable for molecular studies could be acquired for either taxon. The parsimony analysis for 103 terminals was conducted using direct optimization (Wheeler, 1996) as implemented in the program POY (Wheeler et al., 2003). All methods for sequence acquisition and phylogeny reconstruction are presented in Sparks et al. (2005), as are GenBank accession numbers for included taxa. The length of the resulting implied alignment (Wheeler, 2003) was verified in NONA (Goloboff, 1998). Patterns of character evolution were examined using NONA in conjunction with WinClada

(Nixon, 2000). Only unambiguous morphological transformations common to all most-parsimonious dichotomized trees are used to diagnose clades (Goloboff, 1995).

RESULTS

PHYLOGENETIC ANALYSIS

Simultaneous analysis of the 17 morphological transformations corresponding to features of the LOS (table 1) and the nine gene fragments used by Sparks et al. (2005), comprising a total of 6177 characters (2660 parsimony informative), resulted in 120 equally most-parsimonious trees with lengths of 20,080 steps, a consistency index of 0.30, and a retention index of 0.55 (when uninformative characters are retained). Given that relationships outside of *Photoplagios* are identical to those presented by Sparks et al. (2005), a strict consensus topology of these optimal trees restricted to *Photoplagios* is presented (fig. 1). All unambiguously optimized anatomical features of the LOS are indicated on this topology

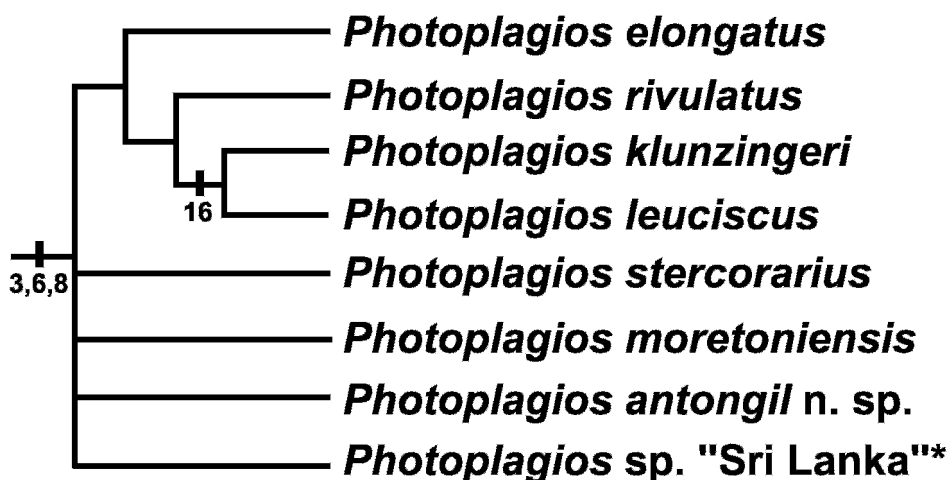


Fig. 1. Intrarelationships of *Photoplagios*, illustrating the placement of *Photoplagios antongil* and two additional congeners (*P. klunzingeri* and *P. moretoniensis*) that were not included in the phylogenetic study of Sparks et al. (2005). Unambiguously optimized anatomical features of the light-organ system (LOS) are indicated on the topology. *Photoplagios* is diagnosed by the presence in males of (character number is followed by state and indicated on the topology): (1) *Character 3:1*: Dorsolateral lobes of the light organ that are hypertrophied and extend posteriorly into the gas bladder (extensively in *P. elongatus* and *P. rivulatus*, less so in the remaining congeners). (2) *Character 6:1*: Lateral clearing of the silvery lining of the gas bladder, which is directly correlated with the species-specific transparent lateral flank patches or stripes (e.g., Sparks et al., 2005: figs. 4 and 5). (3) *Character 8:1*: Lateral luminescence via transparent flank patches or stripes in males. Within *Photoplagios*, the sister-group relationship between *P. klunzingeri* and *P. leuciscus* is supported by *Character 16:1*: The presence of a translucent triangular patch located ventral to the lateral midline and at mid-flank, which does not extend anteriorly to the pectoral-fin base (fig. 5). Additional putatively synapomorphic features supporting this sister-group relationship within *Photoplagios* include a highly speckled light organ, a unique pigmentation pattern (densely spotted and speckled with thin irregular lines) on the upper flanks, and a characteristically elongate second dorsal-fin spine. Although in the current analysis there is no synapomorphy supporting a sister-group relationship between *P. moretoniensis* and *P. stercorarius*, the shared possession of *Character 10:1*, a translucent flank stripe in males comprised of numerous, serially arranged, mid-lateral windows, which may be discrete or overlapping, is unique to these two species and may indicate a close relationship between them. Additional putatively synapomorphic features shared by *P. moretoniensis* and *P. stercorarius* include a unique pigmentation pattern on the upper flanks comprising large, sparse blotches and irregular lines, with a prominent black stripe just ventral to the dorsal fin, and lateral clearing of the silvery gas bladder lining in males that does not extend the length of the chamber. *Note: *Photoplagios* sp. "Sri Lanka" was identified as *P. lineolatus* in the phylogeny presented by Sparks et al. (2005: fig. 2) (see Discussion).

with numerations that match the character descriptions in table 1 and appendix 2.

In this reconstruction *Photoplagios* is monophyletic and is supported by three unambiguously optimized features of the LOS (figs. 1 and 2). Both *P. klunzingeri* and *P. moretoniensis*, included here on the basis of anatomical features of the LOS only, are recovered as members of *Photoplagios*. Members of *Photoplagios* that exhibit an expansive translucent triangular flank patch (*P. elongatus*, *P.*

rivulatus, *P. leuciscus*, and *P. klunzingeri*) are monophyletic, whereas the intrageneric relationships of *Photoplagios* with a translucent midlateral flank stripe (*P. stercorarius*, *P. moretoniensis*, and *P. antongil*, n. sp.) are unresolved. *Photoplagios klunzingeri* is recovered as the sister taxon to *P. leuciscus*, whereas the intrageneric placement of *P. moretoniensis* remains unresolved. The intrageneric placement of the new species is also unresolved in this reconstruction.

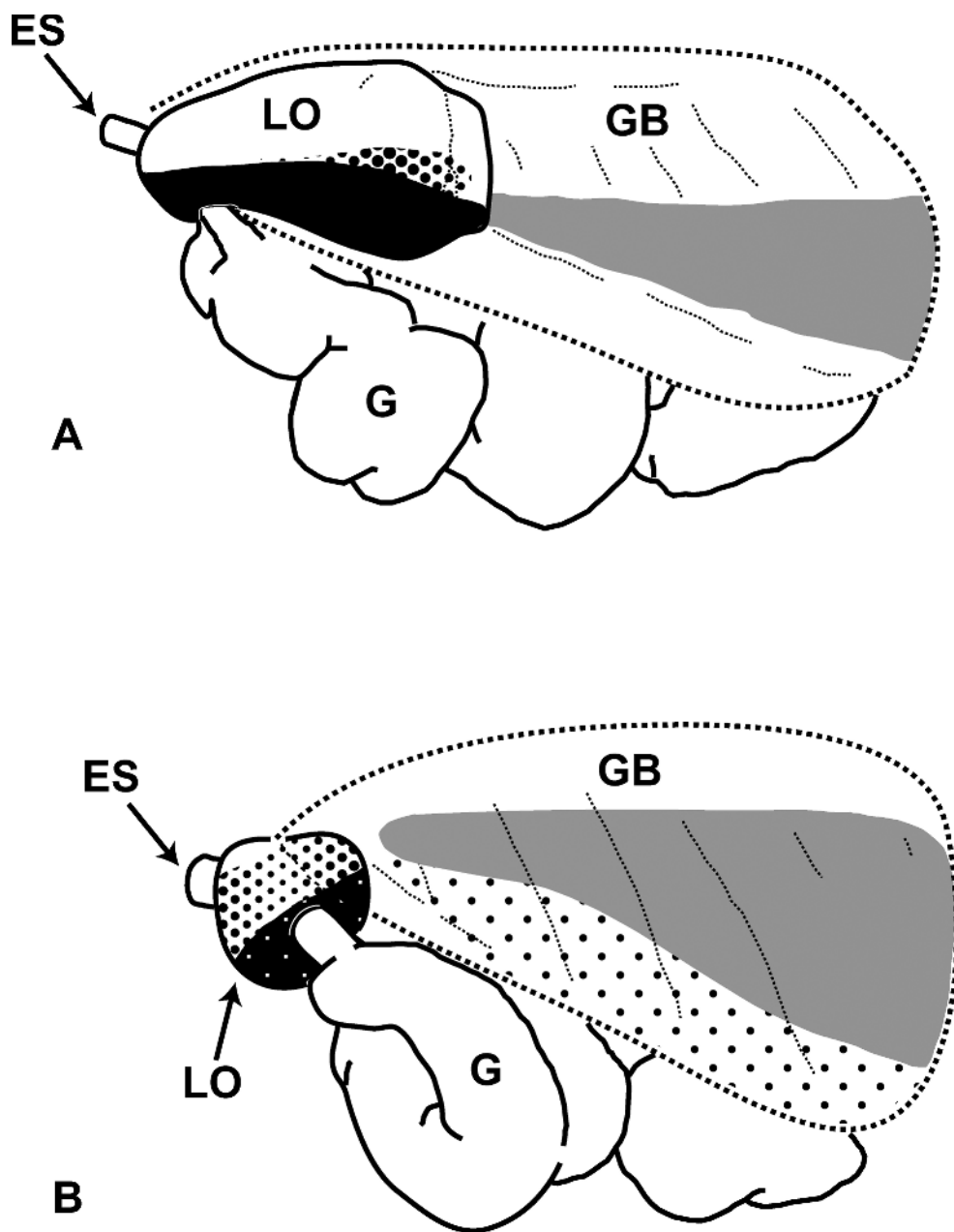


Fig. 2. Diagrammatic illustration of the light organ and associated internal features of the LOS in representative members of *Photoplagios*. (A) *Photoplagios elongatus* male, illustrating strongly sexually dimorphic internal features of the LOS. The dorsal lobes of the light organ are greatly enlarged in males and extend well into the gas bladder. (B) *Photoplagios antongil* male, illustrating sexually dimorphic internal features of the LOS. The dorsal lobes of the light organ are moderately enlarged in males and extend only slightly into the gas bladder chamber. Note variation in light organ pigmentation and the distribution of melanophores. Abbreviations: ES, esophagus; G, gut; GB, gas bladder; LO, light organ. Heavy dashed lines indicate the gas bladder, and gray shading indicates the extent of lateral clearing of the silvery, guanine-lined gas bladder chamber. Black spots indicate the distribution of melanophores on the light organ and gas bladder lining.



Fig. 3. *Photoplagios antongil*, holotype, AMNH 236544, adult male, 75.0 mm SL; Madagascar: Maroansetra market.

SYSTEMATIC ACCOUNT

Photoplagios antongil, new species

Figures 3, 4

Photoplagios n. sp. "Madagascar": Sparks et al. (2005).

HOLOTYPE: AMNH 236544, 75.0 mm SL, adult male; Northeastern Madagascar: Antongil Bay; Maroansetra market; J.S. Sparks, W.L. Smith, and K.L. Tang, Mad JSS 29-2003, Nov. 2003.

PARATYPES: AMNH 236545, 3 ex., 77.3–81.8 mm SL; data as for holotype. SIO 05-117, 1 ex., 76.0 mm SL; data as for holotype.

DIAGNOSIS: Males of *Photoplagios antongil* are distinguished from congeners by the presence of a broad and presumably translucent (in life) midlateral stripe, which is darkly pigmented in preservative due to a concentration of melanophores, and by the presence of two darkly pigmented flank patches (presumably also translucent in life) located ventral to the lateral midline, one anteroventral to the pectoral-fin base and another ventral to the lateral midline at about midbody. *Photoplagios antongil* is further distinguished from *P. leuciscus*, the only externally similar species occurring in the region, by the absence of a large translucent

triangular patch on the flanks (present in male *P. leuciscus*); upper flank pigmentation consisting of large, sparse spots and blotches (vs. highly speckled with fine lines and small spots); a much shorter, although elongate, second dorsal-fin spine; a straight predorsal profile (vs. weakly S-shaped); absence of black pigment in the pectoral-fin axil; and exposed conical oral dentition in two distinct rows (vs. multiple closely set and indistinct rows of unexposed villiform teeth).

DESCRIPTION: Selected proportional measurements and meristic data presented in table 2. A moderately shallow-bodied and elongate leiognathid. Body laterally compressed. Lateral snout outline mostly straight. Weak preorbital protuberance due to protrusion of both frontal and lateral ethmoid ossifications. Predorsal head profile mostly straight to mildly convex. Nuchal spine slightly protruding and distal tip exposed. Nuchal spine with distinct median keel. Two short and stout postnasal spines (= protuberances) present on lateral ethmoid, located posterior to nasal foramina and just rostrad of orbit. Postnasal spines followed posteriorly by well-developed supraorbital ridges that converge posteriorly. Dorsal and ventral body profiles moderately rounded. Dorsal-fin origin located slightly posterior to vertical through pelvic-fin origin. Anal-fin



Fig. 4. *Photoplagios antongil*, paratype, AMNH 236545, adult female, 81.8 mm SL; Madagascar: Maroansetra market.

TABLE 2
Morphometric and Meristic Data for *Photoplagios antongil*, New Species

Character	N	Holotype	Range	Mean	SD
Standard length (mm)	5	75.0	75.0–81.8	78.2	
Percentage of SL					
Head length	5	25.9	25.9–28.2	26.5	0.95
Body depth	5	42.9	41.1–44.1	42.7	1.11
Predorsal length	5	42.1	41.0–45.6	42.9	1.71
Preanal length	5	53.9	53.1–57.6	55.2	2.10
Prepelvic length	5	35.0	34.7–36.6	35.6	0.84
Head width (max.)	5	14.2	13.6–14.7	14.2	0.41
Caudal peduncle length	5	9.0	6.2–9.0	8.0	1.15
Caudal peduncle width	5	4.3	3.8–4.6	4.3	0.27
Caudal peduncle depth	5	6.3	6.3–6.7	6.5	0.18
Pectoral-fin length	5	17.4	17.1–17.5	17.3	0.15
Pelvic-fin length	5	12.2	12.0–14.7	13.2	1.20
Percentage of HL					
Snout length	5	32.9	32.8–38.2	34.1	2.33
Orbit diameter	5	31.9	30.9–31.9	31.5	0.36
Upper jaw length	5	19.4	15.0–21.4	17.3	2.90
Lower jaw length	5	49.8	47.9–54.2	51.8	2.80
Interorbital width	5	35.3	30.5–35.7	33.9	2.03
Caudal peduncle length/depth	5	1.4	0.9–1.4	1.2	0.20
Caudal peduncle length/width	5	2.1	1.6–2.1	1.9	0.18
Vertebrae (precaudal + caudal)	5	10 + 13 = 23			
Dorsal fin	5	VIII 16			
Anal fin	5	III 14			

origin located at about level of vertical through the last (= 8th) dorsal-fin spine or first dorsal-fin ray. Eye large. Caudal peduncle slender and shallow. Mouth small and terminal in position, directed slightly downward when protruded. Posterior margin of maxilla exposed, reaching to level of vertical through anterior margin of orbit. Anterior nasal pore small and round; posterior foramen much larger and crescent-shaped, partially encircling anterior pore. Preopercular margin weakly serrate along ventral and ventrocaudal margins. Vertebral count: 10 precaudal + 13 caudal = 23. Neural and hemal spines of vertebral centrum PU4 somewhat expanded and bladellike. Twelve or 13 elongate and triangular outer gill rakers arrayed along lower limb (= ceratobranchial one) of first gill arch.

Fins: Dorsal fin with VIII spines and 16 branched rays. First dorsal-fin spine greatly reduced in length and relatively robust. Second through fourth dorsal-fin spines elongate and robust; second spine longest. Second dorsal-fin spine moderately, but not exceedingly, elongate. Third and fourth dorsal-fin spines serrate along anterior margin and "lock" into groove on posterior margin of preceding spine when erect. Dorsal-fin spines five through eight feeble, shorter than second through fourth spines. Anal fin with III spines and 14 branched rays. First anal-fin spine very short. Second and third anal-fin spines robust and elongate; second spine longest, but not appreciably longer than third. Third anal-fin spine serrate along anterior margin and "locks" into groove on posterior margin of second spine when erect. Spinous dorsal and anal fins with asquamate basal sheath. Pelvic fins short, not reaching first anal-fin spine when adducted (i.e., an appreciable gap present). Eight upper and seven lower branched caudal-fin rays. Seventeen total pectoral-fin rays.

Dentition: Two distinct rows of closely set, elongate and recurved conical teeth present in both upper and lower jaws. Upper jaw teeth somewhat larger than those of lower jaw, particularly anteriorly. Lips not fleshy, and teeth exposed.

Squamation: Body scales cycloid, but not remarkably small. Head and opercular region asquamate. Chest fully scaled, except along

ventral midline. Scales conspicuous and extend anteriorly ventral to opercle to about anterior margin of chest. Lateral line arched and complete. Pored scales in lateral line number approximately 60 to 63. Scales difficult to count posteriorly due to high proportion missing. Pores well developed. Pelvic axillary scale well developed and elongate. All fins asquamate, except for caudal fin, which bears several rows of scales of reduced size, particularly centrally on fin.

PIGMENTATION IN PRESERVATIVE: Body ground coloration yellowish-olive above lateral midline and creamy pale yellow below. Iridescent silvery patches present to varying degree ventral to lateral midline (although much of guanine lost in preservation). Opercle, subopercle, and interopercle iridescent and silvery. Midlateral stripe present in males. Stripe broad and darker than flank regions above and below due to concentration of melanophores, and presumably translucent in life (compare figs. 3 and 4, illustrating an adult male and female, respectively). Stripe begins posterodorsal to pectoral-fin base and extends to about anterior margin of caudal peduncle. Two dark gray to charcoal, and also presumably translucent in life, patches present on flank in males, one anteroventral to pectoral-fin base in all specimens and another ventral to lateral midline at about midbody in only some specimens (compare figs. 3 and 4). Based on comparisons to the translucent flank patches in congeners (e.g., *P. leuciscus*, *P. klunzingeri*, *P. stercorarius*, and *P. moretoniensis*) in various states of preservation, in specimens in which the silvery guanine layer has faded in preservation, these flank patches are generally very obvious due to a concentration of melanophores causing them to appear blackish (see fig. 5). Thus, it is reasonable to conclude that the blackish midlateral stripe and two lower flank patches in the new species, in which the silvery guanine on the integument is mostly lost in preservation in all specimens, are also translucent in life.

Pigmentation pattern above lateral midline characteristically blotchy and mottled. Blotches large, variable in size, and sparsely arranged. Longitudinal series of blackish spots arrayed directly above midlateral stripe. Pores of lateral line scales edged dorsally and

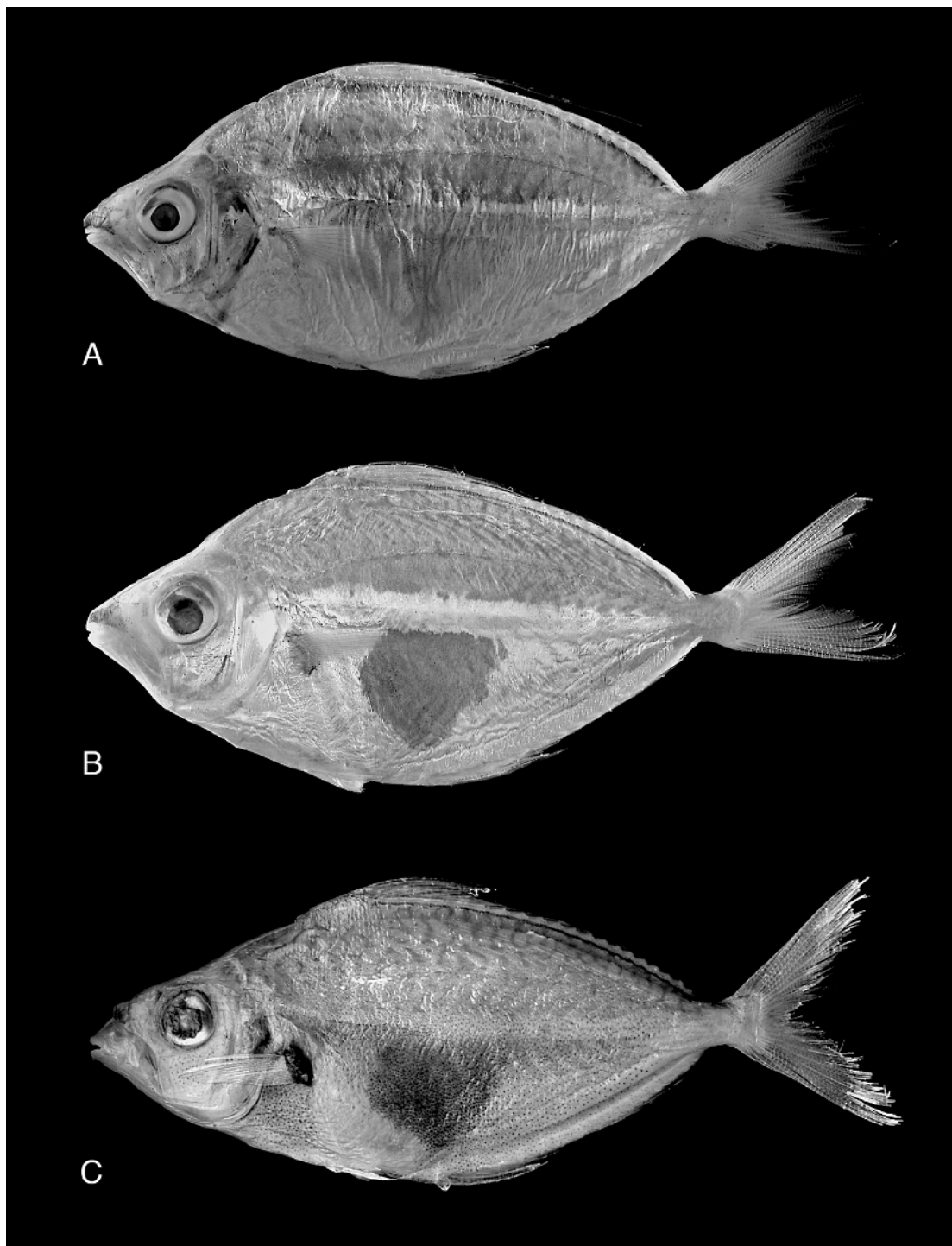


Fig. 5. *Photoplagios leuciscus*, illustrating expansive transparent triangular flank patch characteristic of males and how the patch may appear in different lots due to method of preservation and condition of material upon preservation. (A) AMNH 237149, adult male, 95.0 mm SL; northeastern Madagascar: Maroansetra

ventrally with melanophores; in combination with concentration of blackish blotches present along lateral line, melanophores create an arching and irregular stripe. Body ventral to lateral midline peppered with melanophores. Cheek and gular region pale yellow; some silvery iridescence on cheek. Head above orbit and nape grayish to grayish brown. Snout with large black patch above upper lip. Lips pale yellow. Two distinct black blotches present anterior to orbit; dorsal blotch covering postnasal spines. Line of black pigment ventral to eye. Chest and belly gray, silvery, or pale yellow; silvery along ventral midline. Caudal peduncle silvery with blackish saddle on dorsal margin. Base of caudal fin iridescent and silvery. Dorsal and anal fins hyaline to pale white, with a concentration of black pigment distally on dorsal-fin spines. Pectoral and pelvic fins pale yellow. Black stripe present on body ventral to dorsal-fin base; more prominent posteriorly. Caudal fin yellowish proximal to base, white distally. Membrane of caudal fin with concentration of black pigment, creating series of thin black radiating lines.

LIGHT-ORGAN SYSTEM (LOS): Sexual dimorphism of the light organ and associated internal structures is evident, but not striking as in some other members of the genus (e.g., *P. elongatus* and *P. rivulatus* [Dunlap and McFall-Ngai, 1984; Sparks et al., 2005]). The light organ of males in general is enlarged compared to similarly sized conspecific females. The dorsal lobes of the light organ in particular are enlarged in males, but not greatly, and extend into gas bladder only slightly at the light-organ window (fig. 2). The light organ itself is highly spotted, with prominent black melanophores on a yellow background, lending a leopard skin pattern to much of the light organ. Based on the limited material available, the light organ of females appears in general to be smaller and not as

densely spotted, but more solidly black. There is a broad lateral clearing of the gas bladder lining, extending almost the entire length of the gas bladder chamber, and the chamber is silvered laterally only at the anterior end near the light-organ window. The gas bladder is peppered with melanophores anteriorly near the light-organ window and also caudoventrally, but there are no melanophores present in the guanine-free (= clear) region of the gas bladder lining.

The material available is not ideally preserved for reliably sexing some of the specimens (i.e., the gonads are poorly preserved) or for interpreting the extent of flank pigmentation, translucence, or silvering in life. Therefore, until additional material becomes available, I am reluctant to comment further on external sexual dimorphism of the LOS apart from noting that in specimens of *Photoplagios* (and *Photopectoralis*) in which the silvery guanine is lost in preservative, as it is in the type series of *P. antongil*, regions that were translucent in life generally appear blackish due to a concentration of dispersed melanophores (fig. 5B and C). It would appear that these concentrated melanophores, which are generally aggregated and quite small in well-preserved specimens in which the guanine layer is intact (fig. 5A), can be rapidly dispersed to occlude the transparent flank patches and stripes so as to inhibit the emission of luminescence from the light organ.

DISTRIBUTION: Known only from market specimens purchased in northeastern Madagascar (Maroansetra market). The Malagasy fishermen who supply the market work locally in Antongil Bay, and it can safely be assumed that is where the type series was collected. Presumably the species is more widely distributed; however, it is not represented in collections made elsewhere in Madagascar that are available to the author. In their guide to the commercial fishes of Madagascar, Bauchot

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market. Specimen with silvery guanine intact. Flank patch difficult to discern unless specimen is examined obliquely. **(B)** AMS I.22978004, adult male, 95.8 mm SL; northern Australia. Specimen in which guanine is somewhat faded. Flank patch is easy to locate as darker triangular area surrounded by silvery integument. **(C)** USNM 373280, adult male, 79.8 mm SL; Iran. Specimen in which guanine is completely lost in preservative. Triangular flank patch appears black due to concentration of dispersed melanophores (see text for discussion).

and Bianchi (1984) list *Leiognathus lineolatus* as present in the region. The fish referred to as *L. lineolatus* may correspond to the new species; however, no specimens from the study of Bauchot and Bianchi (1984) appear to have been deposited at MNHN.

ETYMOLOGY: Named in reference to the type locality, Antongil Bay, in northeastern Madagascar. The specific epithet, *antongil*, is used as a noun in apposition.

DISCUSSION

COMPARISONS

When originally collected, specimens now assigned to the new species, *P. antongil*, were thought to represent rather uncharacteristic *P. leuciscus* females due to similarities in overall pigmentation pattern and body shape (fig. 5). The absence of an expansive triangular patch on the flanks in *P. antongil* males also led them to be confused initially with *P. leuciscus* females. Upon closer examination in the laboratory, however, it was obvious that two distinct species were represented in these collections. This hypothesis was corroborated by an analysis combining nucleotide characters from both mitochondrial and nuclear genes and anatomical features of the LOS, in which *P. leuciscus* was recovered as the sister taxon to *P. klunzingeri* and shown not to be conspecific with *P. antongil* (fig. 1).

Sparks et al. (2005: fig. 2) recovered *P. antongil* as the sister taxon to specimens collected in Sri Lanka that they referred to as *P. lineolatus* (here referred to as *Photoplagios* sp. “Sri Lanka”; see below). However, with the inclusion of two additional species of *Photoplagios* in the current analysis, the intrageneric relationships of *P. antongil* are unresolved (fig. 1). Unfortunately, Sparks et al. (2005) were able to obtain only a tissue sample of the Sri Lankan material (identified by Seishi Kimura, Mie University, Japan). Likewise, I have been unable to examine preserved specimens of the Sri Lankan material and cannot comment on morphological features that distinguish them from *P. antongil*. With regard to the molecular data set examined by Sparks et al. (2005) and reanalyzed herein, molecular divergence between *P. antongil* and the Sri Lankan specimens re-

ferred to as *P. lineolatus* is about 4% (uncorrected *p* distance) across the four genes sequenced, which is similar to divergences recovered between other species within the genus.

Of the other ponyfish species present in the Malagasy and Mascarene region, *P. antongil* is most similar to, and has likely been confused in the past with, *P. leuciscus*. The new species is easily distinguished from *P. leuciscus*, however, by the presence of a broad and presumably translucent midlateral stripe in males, which is darkly pigmented in preservative due to a concentration of melanophores; absence of a large translucent triangular patch on the flanks (present in *P. leuciscus* males; fig. 5); pigmentation pattern on the upper flanks (larger, sparse spotting and mottling vs. highly speckled and with thin lines in *P. leuciscus*; figs. 3–5); a much shorter, although still elongate, second dorsal-fin spine; a straight predorsal profile (vs. weakly S-shaped); absence of black pigment in the pectoral-fin axil; and exposed conical oral dentition in two distinct rows (vs. multiple indistinct rows of unexposed villiform teeth).

TAXONOMY OF *EQUULA LINEOLATA* VALENCIENNES

Although *Leiognathus lineolatus* (Valenciennes, in Cuvier and Valenciennes, 1835) is considered to be a common species distributed throughout the Indo-Pacific (references in Eschmeyer, 2005; Froese and Pauly, 2005), its taxonomic status is problematic and warrants discussion. In his systematic review of Leiognathidae, James (1975) considered *Leiognathus lineolatus* to be a valid species with a wide geographic distribution; however, he noted that the original description of Valenciennes “lacks many details of body proportions and colour”. He further commented that “the only important characters mentioned are the second dorsal spine is more than half [the] height of the body and the back with many small vertical lines and spots.” Both of these features, however, occur together in other leiognathid species (e.g., *P. leuciscus* and *P. klunzingeri*) and are, therefore, insufficient to distinguish *L. lineolatus*. James’s (1975: 163) reliance on these homoplasious features is exemplified by his admit-

tedly questionable synonymy of *Leiognathus vermiculatus* Fowler, 1904 with *L. lineolatus*. The holotype of *L. vermiculatus* (ANSP 27525), however, is clearly referable to *Photoplagios leuciscus*, due to the presence of an expansive triangular flank patch and other characteristic features, a synonymy that Jones (1985: 590–591) later proposed.

In a subsequent revision of Australian ponyfishes, Jones (1985) noted that based on an examination of the type series (or a portion thereof; see below) the name *Leiognathus lineolatus* (Valenciennes, in Cuvier and Valenciennes, 1835) seems traditionally to have been incorrectly used. Among the type specimens examined (those “collected by Quoy and Gaimard from Java”), Jones found a number of different species to be represented, none of which corresponded to the original description of Valenciennes (although this seems to have been overlooked by Jones as exemplified by the designation of lectotypes from among this material). According to Jones, “MNHN 6739 consists of one specimen of *L. elongatus* ..., two specimens of *Gazza minuta* ..., and one badly damaged specimen that could not be identified ...; MNHN 6738 consists of two specimens in fair condition, which represent *L. bindus*.” Without further explanation, Jones (1985: 575–576) then designated the “two specimens registered as MNHN 6738 as lectotypes of *E. lineolata* and regard[ed] this species then as a junior synonym of *L. bindus*.” Jones (1985) presented no justification as to why the specimens identified as *L. bindus* were designated lectotypes of *E. lineolata* (e.g., *Gazza minuta* [*Scomber minutus* Bloch, 1795] is an older name), not to mention that it was (and is) in violation of Article 74 of the International Code of Zoological Nomenclature (1961, 1999) to designate more than one lectotype. As discussed in detail below, it is clear from even a cursory reading of Valenciennes’s description of *E. lineolata* that he was describing a fish not easily confused with the deep-bodied *L. bindus* (fig. 6), which incidentally Valenciennes described earlier in that same publication, stating that “its proportions resemble much those of” *Equula ensifera* (= *Leiognathus equulus*), a conspicuously deep-bodied and disk-shaped leiognathid. As noted

by Eschmeyer (2005), Bauchot and Desoutter (1989: 21) subsequently restricted the lectotype designation to a single specimen (the larger specimen of 46 mm SL); therefore, they designated the lectotype.

According to Jones (1985: 575), however, only the type series of *Equula lineolata* “collected by Quoy and Gaimard from Java” was examined, whereas in the original description of *E. lineolata*, Valenciennes explicitly stated that specimens were “taken in Java by Mrs. Quoy and Gaimard, and in Antjer, in the strait of the Sonde, by Mr. Raynaud.” Eschmeyer (2005) stated that he was not able to locate the Antjer specimens. Likewise, in their type catalog of fishes in the MNHN, Bauchot and Desoutter (1989: 21) noted “the brought back specimens of Antjer (strait of the Sonde) were not found”. I have been unable to locate the Antjer specimens as well, and they are presumed lost. Jones (1985) apparently was unaware of the additional Antjer specimens, as no reference to this material was included. It is important to note that Valenciennes made no mention of the number of specimens he examined for the original description of *E. lineolata*, only the collection localities (thus, it is possible that the specimens subsequently assigned MNHN 6738 and 6739 were not part of the type series examined by Valenciennes [i.e., MNHN catalog numbers were not listed at that time], and represented other ponyfish species collected at those localities). It is also possible that the Antjer specimens would correspond to Valenciennes’s original description of *E. lineolata*. Unless they are located, however, this correspondence can never be established.

Regardless, it appears as though Jones (1985) did not formulate these taxonomic decisions regarding the status of *Equula lineolata* in consultation with the original description of that species; otherwise it would have been obvious that whatever taxon Valenciennes was describing, it was not *L. bindus*, a very deep-bodied and essentially disc-shaped ponyfish (fig. 6). In his opening comment to the description of *E. lineolata* (referring to the previously described taxon in that publication, *E. oblonga*), Valenciennes described *E. lineolata* as being similar in form and in the presence of a midlateral stripe to *E.*

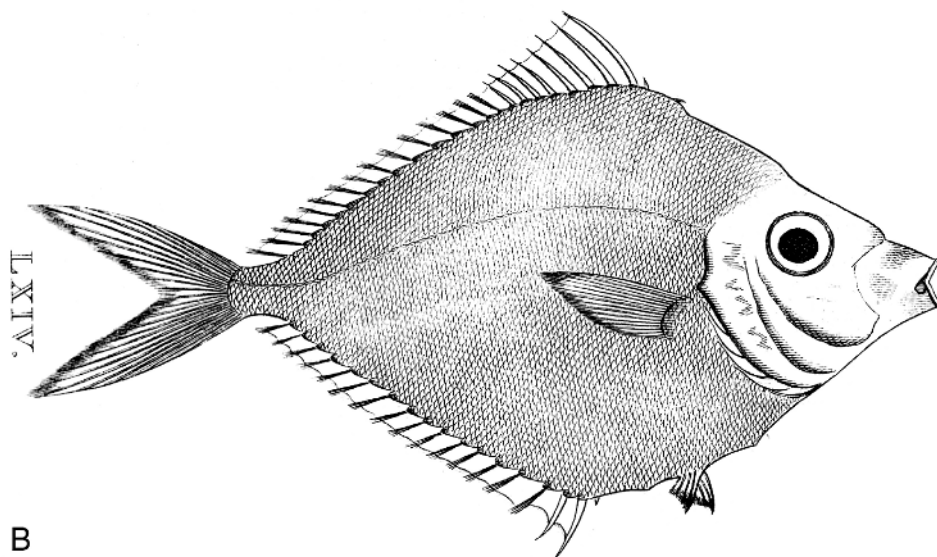
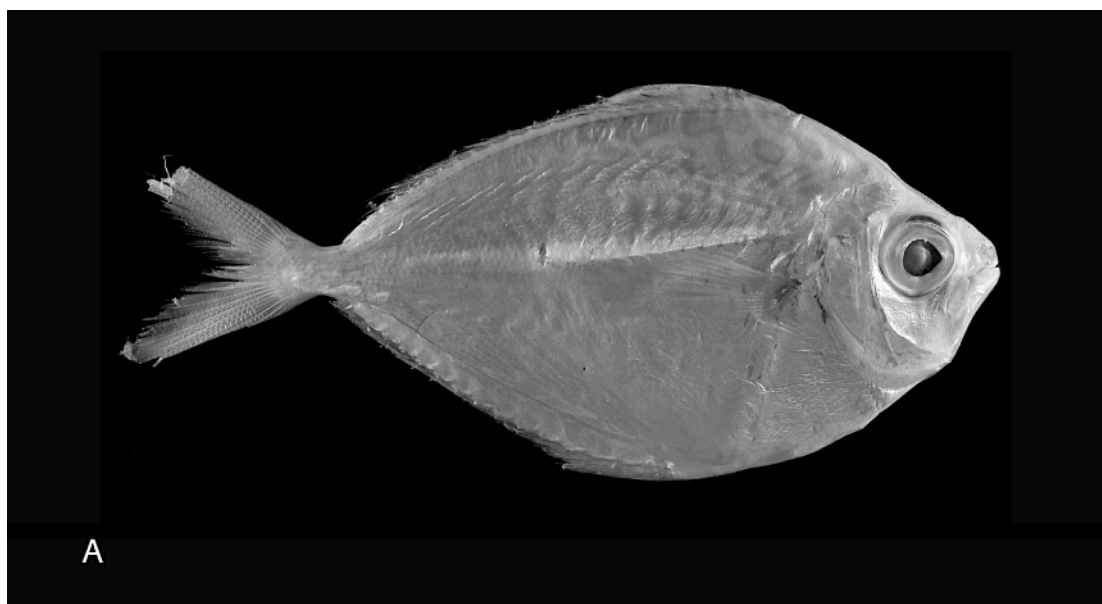


Fig. 6. *Photopectoralis* (L.) *bindus*. (A) *Photopectoralis bindus* male in preservation, UMMZ uncat. (PVD 00-01/18a), 66.5 mm SL; Philippines. (B) Illustration of Bindoo karah reproduced from Russell (1803: vol. 1, 50, pl. 64), upon which Valenciennes, in Cuvier and Valenciennes, 1835 based his description of *Equula bindus*.

oblonga. I have examined the holotype of *E. oblonga* from Timor (MNHN A-6754, 61.8 mm SL; fig. 7), which is in relatively good shape, and I find the species to be quite distinct from *L. bindus*, a species described

as having a “rhombic body” (Russell, 1803: vol. 1, 50). (Valenciennes, in Cuvier and Valenciennes, 1835 described *E. bindus* based on Bindoo karah Russell, 1803 [vol. 1, 50, pl. 64 ; reproduced in fig. 6B].) *Equula oblonga*



Fig. 7. *Equula oblonga*, holotype, MNHN A-6754, 61.8 mm SL; Timor, Indonesia.

(MNHN A-6754, holotype), as its name suggests, is a very elongate ponyfish (“its height is three times and a half in its overall length”) that exhibits a midlateral stripe (“side line”), a feature lacking in *L. bindus* (Valenciennes, in Cuvier and Valenciennes, 1835). According to Jones (1985: 575), body depths as a percentage of standard length for the two specimens from the putative syntypic series of *E. lineolata* that were identified as *L. bindus* and designated as lectotypes of *E. lineolata* were 51% and 48%. Evidently, Valenciennes was describing a much more shallow-bodied species than *L. bindus*; something similar in body shape to *E. oblonga* (fig. 7).

Therefore, there is justification under Article 74.2 of the Code (“lectotype found not to have been a syntype”) for rejecting the lectotype designation(s) of Jones (1985) and Bauchot and Desoutter (1989: 21) for specimens attributable to *E. bindus*, not Valenciennes’s *E. lineolata*. Moreover, in the absence of type material corresponding to Valenciennes’s original description of *Equula lineolata*, the status of this taxon remains uncertain. Valenciennes’s original description is not adequate to distinguish the species from congeners (i.e., no diagnostic features were presented), and *Equula lineolata* must be considered a nomen dubium of uncertain placement beyond the family level (i.e., there is no way of knowing exactly what Valenciennes described).

Both Jones (1985: 603–605) and Woodland et al. (2001: 2817, pl. III) included undescribed species in their regional treatments of ponyfishes that warrant comment regarding the status of *Equula lineolata* and specimens traditionally ascribed to this taxon. The species referred to as “*Leiognathus* sp.” by Jones (1985) closely resembles *Photoplagios leuciscus*, with males of this putatively undescribed species possessing a single expansive triangular flank patch. According to Jones (1985: 590), however, the latter species is distinguished from the former by a fully (vs. partly) scaled chest. The presence of a translucent triangular flank patch readily distinguishes “*Leiognathus* sp.” of Jones (1985) from *P. antongil*, which instead possesses a broad darkly pigmented midlateral stripe. However, the species referred to as “*Leiognathus* sp. 1” by Woodland et al. (2001), at least on the basis of the included color plate (pl. III), very closely resembles the overall body shape and pigmentation pattern of *Photoplagios antongil*. From the illustrations presented by Woodland et al. (2001), *P. antongil* can be distinguished from “*Leiognathus* sp. 1” by the absence of two distinct and large dark blotches on the lower flanks, the absence of a darkly pigmented midlateral stripe, and assuming that a male is illustrated by Woodland et al. (2001), by a shorter second dorsal-fin spine. The chest is completely scaled in *P. antongil*, except along the ventral midline, whereas Woodland et al. (2001: 2817)

reported that the anterior portion of the chest ("below head") in "*Leiognathus* sp. 1" is asquamate.

Woodland et al. (2001: 2817) listed "*?Leiognathus lineolatus*" under "Frequent misidentifications" for their "*Leiognathus* sp. 1" and included Madagascar within its range. It is puzzling then that under FAO (Food and Agriculture Organization of the United Nations) names (= common names), Woodland et al. (2001: 2817) listed "Ornate ponyfish" as the English name for this undescribed species, which is the common name of *Leiognathus lineolatus* in the literature (in fact, it is the common name used by Woodland on the FishBase website for *L. lineolatus* [considered there a valid species] [Froese and Pauly, 2005]). Woodland et al. (2001) did not include *L. lineolatus* in their Western Central Pacific FAO contribution on leiognathids, they did not place the species in synonymy with any included species, and they offered no comment regarding its exclusion (as mentioned, the name only appears as a questionable misidentification of an undescribed species referred to as "*Leiognathus* sp. 1" [Woodland et al., 2001: 2817]).

According to references cited in FishBase (Froese and Pauly, 2005), *L. lineolatus* is reportedly widespread, with a range extending from "Durban, South Africa, Madagascar and Pakistan to the Philippines, north to southern Japan and south to northeast Australia." Yet, the species was not mentioned (not even in synonymy) in the most recent FAO guide covering this region (Woodland et al., 2001). It is unclear whether (and, if so, why) Woodland et al. (2001) followed the synonymy of *Equula lineolata* with *Leiognathus bindus* as proposed by Jones (1985) in the FAO publication (although *E. lineolata* is not listed as a junior synonym of *L. bindus* in that contribution) but not on the Fishbase website.

Despite a wealth of discussion and disagreement regarding the identity of *Leiognathus lineolatus* (e.g., Fowler, 1904; James, 1975; Jones, 1985; Woodland et al., 2001), the name continues to be applied without justification to a number of presumably distinct species throughout the Indo-Pacific. Recent researchers seem to have overlooked the troubling fact

that there are no extant types that conform to Valenciennes's original description, which on its own is insufficient to diagnose the species or distinguish it from congeners. Jones (1985) was correct in asserting that the name *Leiognathus lineolatus* (Valenciennes, in Cuvier and Valenciennes, 1835) seems traditionally to have been incorrectly, or at least unjustifiably, used. Jones's (1985) conclusion was based on an absence of specimens in the extant type series that corresponded to what taxonomists had traditionally ascribed to *Leiognathus lineolatus*, regardless of Valenciennes's description (although it remains unclear as to why Jones synonymized *E. lineolata* with *L. bindus*). My interpretation relies on a more literal reading of Valenciennes's original description of *Equula lineolata* and asserts that in the absence of type material that corresponds to this description, as well as the lack of any features in the original description that serve to diagnose *E. lineolata* or distinguish the species from congeners, there is no justifiable alternative but to recognize *Equula lineolata* as a nomen dubium of uncertain placement beyond the family level.

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APPENDIX 1

MATERIAL EXAMINED

Type specimens are listed first, followed alphabetically by museum abbreviation. The notation “(in part)” following some catalog numbers indicates that the alcoholic lot examined was found to contain more than a single species.

Gazza

Gazza achlamys: CAS-SU 21652, paratype; CAS-SU 22853, paratype; UMMZ 240128; UMMZ 240132; UMMZ 240139.

Gazza dentex: MNHN A-578, lectotype.

Gazza minuta: AMNH 220748; AMNH 237136; UMMZ 191542; UMMZ 240126; UMMZ 240140; UMMZ 240141; UMMZ uncat. (PVD 01-02/07a).

Gazza rhombica: USNM 332347, paratype; USNM 350467, paratype.

Gazza squamiventralis: USNM 345525, holotype; USNM 345526, paratype; AMNH 237137.

Gazza n. sp. “Madagascar”: AMNH 236138.

Leiognathus equulus Complex

Leiognathus edentulus: ZMB 8756, holotype (dry skin; photograph and radiographs examined).

Leiognathus edwardsi: USNM 55904, holotype.

Leiognathus equulus: ZMUC P48219, lectotype (dry skin; photographs and radiographs examined); ZMUC P48220, paralectotype (dry skin; photograph and radiograph examined); AMNH 59535; AMNH 88039; AMNH 237139; CAS 57306; CAS-SU 35627; CAS-SU 38781; MNHN A-6723; UMMZ 191520; UMMZ 235029; UMMZ 238805 (in part); UMMZ 240133; UMMZ 240502; UMMZ 240503; UMMZ uncat.

Leiognathus robustus: UMMZ 242144, holotype; AMNH 233607, paratype; UMMZ 240362, paratype; UMMZ 240360.

Leiognathus fasciatus Complex

Leiognathus fasciatus: AMNH 15520; AMNH 237140; CAS 1872; UMMZ 240504; UMMZ uncat.; USNM 191962; USNM 191966.

Leiognathus n. sp. “Madagascar”: AMNH 237141; AMNH 237142; AMNH 237143.

Leiognathus n. sp. “Singapore”: UMMZ 240361.

Leiognathus longispinis (= *L. smithursti*): MNHN A-0579, holotype; AMNH 219296; AMS I.20907036; AMS I.22974001; AMS 22981001; AMS 23044001; USNM 324651.

Leiognathus n. sp. “Sri Lanka”: FRLM uncat.

“*Leiognathus*”

“*Leiognathus*” *daura*: USNM 100291; USNM 373281.

“*Leiognathus*” *decorus*: AMNH 231297; AMNH 234765; AMNH 237144; AMNH 237145; AMNH 237146; AMS I.22990002; AMS I.26927001.

“*Leiognathus*” *dussumieri*: MNHN A-6721, syntype; AMNH 234763.

“*Leiognathus*” *nuchalis*: AMNH 26819; CAS-SU 4757; UMMZ 240143.

“*Leiognathus*” *pan*: USNM 276536, paratype.

“*Leiognathus*” *blochii*: MNHN A-6757, syntype; MNHN A-6759, syntype.

“*Leiognathus*” *jonesi*: UMMZ 240134; UMMZ 240505; UMMZ uncat.

“*Leiognathus*” *philippinus*: ANSP 47486, holotype; ANSP 47487, paratypes; UMMZ 240130.

“*Leiognathus*” *splendens*: CAS 1485; CAS 38789; CAS 56438; CAS 56441; MNHN A-6724; UMMZ 191202; UMMZ uncat.; USNM 190258; USNM 190263.

Photopectoralis

Photopectoralis aureus: UMMZ 240129; UMMZ 240309; UMMZ uncat.; USNM 373277.

Photopectoralis bindus: AMS I.34367021; CAS 51097; UMMZ 240131; UMMZ 240142; UMMZ uncat. (PVD 00-01/18a); UMMZ uncat.

(PVD 99-11/24 75); UMMZ uncat. (PVD 02-03/19a); USNM 373284.

Photopectoralis cf. bindus: AMNH 237147.

Photopectoralis hataii: UMMZ uncat.

Photopectoralis cf. hataii: AMNH 89922.

Photopectoralis panayensis: UMMZ 240300, holotype; UMMZ 240301, paratypes; UMMZ 240302, paratypes; UMMZ 240303, paratypes; UMMZ 240304, paratypes; UMMZ 240137; UMMZ uncat. (PVD 02-03/06a).

Photopectoralis sp. "East China Sea": AMNH 237148.

Photoplagios

Photoplagios elongatus: BMNH 1872.4.6.105, holotype; CAS 52602; LACM 42993-1; LACM 43584-1; SIO 83-55; USNM 55613; UMMZ 226771; UMMZ 240145; UMMZ uncat. (PVD 82-06/19a).

Photoplagios klunzingeri: NMW 68277, syntypes; NMW 68280, syntypes; NMW 76008, syntypes; NMW 76009, syntypes; AMNH 44488; AMNH 44491; AMNH 44493.

Photoplagios leuciscus: BMNH 1858.4.21.243, holotype; AMNH 237149; AMS I.22967001; AMS I.22978004; AMS I.34365015; ANSP 27525, holotype of *Leiognathus vermiculatus*; UMMZ 240125; UMMZ uncat. (PVD 02-01/30a); UMMZ uncat. (PVD 00-10/18 61); USNM 76609; USNM 191991; USNM 373280.

Photoplagios moretoniensis: QM I.1583, syntype; AMS I.21700001; AMS I.22983001.

Photoplagios rivulatus: AMNH 34850; UMMZ 240144; UMMZ uncat. (PVD 82-06/19a).

Photoplagios stercorarius: USNM 55906, holotype; USNM 126395, cotype; ANSP 33289, paratype; CAS 42171, paratype; CAS-SU 20004, paratype; CAS 17678; UMMZ 240138; UMMZ uncat. (PVD 99-11/30a); UMMZ uncat. (PVD 02-03/11a); UMMZ uncat. (PVD 02-03/19 29); UMMZ uncat. (PVD 03-04/07a); USNM 191996.

?*Photoplagios (Leiognathus) berbis*: USNM 228508.

?*Photoplagios (Leiognathus) oblonga*: MNHN NHN A-6754, holotype.

?*Photoplagios (Leiognathus) parviceps*: MNHN A-0580, syntype.

?*Photoplagios* sp.: MNHN 1988-0327, 1 ex. (putative syntype of *Equula lineolata*, and listed as *Leiognathus* sp. by Jones [1985] and Bauchot and Desoutter [1989] due to poor condition; see text for discussion regarding status of type series).

Secutor

Secutor indicus: UMMZ 240127; UMMZ uncat. (PVD 02-03/11a).

Secutor insidiator: CAS 29894; UMMZ uncat.

Secutor megalolepis: UMMZ 240135.

Secutor ruconius: CAS-SU 29895; UMMZ 225240; UMMZ uncat.

Secutor n. sp. "Madagascar": AMNH 232550; AMNH 237150; AMNH 237151; AMNH 237152.

APPENDIX 2

CHARACTER DESCRIPTIONS

Character numbers correspond to those presented in table 1. Characters 1–15 were originally presented and discussed in detail in Sparks et al. (2005).

1. *Circumesophageal light organ*. 0: Absent. 1: Present.
2. *Light organ dimorphic in volume*. 0: Absent. 1: Present.

3. *Dorsolateral lobes of light organ hypertrophied in males; lobes confined to interior of gas bladder lining and extend posteriorly into gas bladder*. 0: Absent. 1: Present.

4. *Dorsolateral lobes of light organ hypertrophied in males; lobes extend laterally, exterior of gas bladder lining, and abut pectoral-axil window*. 0: Absent. 1: Present.

5. *Ventrolateral lobes of light organ hypertrophied in males*. 0: Absent. 1: Present.

6. *Clearing of lateral silvery lining of gas bladder in males*. 0: Absent. 1: Present.

7. *Lateral luminescence via transparent pectoral-axil patch in males*. 0: Absent. 1: Present.

8. *Lateral luminescence via transparent flank patches in males*. 0: Absent. 1: Present.

9. *Morphology of transparent flank patch(es) in males*. 0: Expansive triangular patch. 1: Mid-lateral stripe.

10. *Transparent flank stripe in males*. 0: Continuous. 1: Comprised of numerous, serially arranged, mid-lateral windows, which may be discrete or overlapping.

11. *Lateral luminescence via enlarged transparent opercular patch in males; located anteriorly in opercular cavity and occluded by interopercle*. 0: Absent. 1: Present.

12. *Lateral luminescence via enlarged transparent opercular patch in males; posteriorly positioned in opercular cavity and occluded by subopercle*. 0: Absent. 1: Present.

13. *Silvery, guanine-lined reflective chamber surrounding and extending rostrally and ventrally from contralateral ventral light-organ lobes*. 0: Absent. 1: Present.

14. *Large anteroventrally directed windows present on ventral light-organ lobes, which are oriented into silvery reflective chamber*. 0: Absent. 1: Present.

15. *Silvery, guanine-lined reflective chamber extends rostrally along opercular cavity margin to gular region*. 0: Absent. 1: Present.

16. *Triangular flank patch location and orientation*. 0: Triangular flank patch broadly abuts pectoral-fin base and extends dorsal of lateral midline (Sparks and Dunlap, 2004: fig. 1A). 1: Translucent triangular patch located ventral to lateral midline and at mid-flank; patch does not extend anteriorly to pectoral-fin base (fig. 5). State 0 is restricted to *Photoplagios elongatus* and *P. rivulatus*. State 1 is present in *P. leuciscus*, where the flank patch does not approach the pectoral-fin base, and in *P. klunzingeri*, where only the anterior point of the triangle may approach the base of the pectoral fin.

17. *Distribution of horizontal series of transparent windows*. 0: Extending length of flank. 1: Restricted posterior to vertical through dorsal-fin origin. State 0 is unique to *Photoplagios moretoniensis*. State 1 is unique to *P. stercorarius*.