

## Description of a New Species of Ponyfish (Teleostei: Leiognathidae: Equulitini: *Photolateralis*) from the Gulf of Oman

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### ABSTRACT

A new species belonging to the leiognathid genus *Photolateralis*, collected from the coastal waters of Oman, is described herein. *Photolateralis* is unique among leiognathid genera in possessing a species-specific translucent midlateral flank stripe that may be comprised of either multiple independent translucent windows (*P. stercorarius*, *P. moretoniensis*, and the new species) or a continuous translucent lateral band (*P. antongil*). *Photolateralis polyfenestrus*, new species, is distinguished from congeners by the presence of a short, composite midlateral stripe comprised of three small, rounded translucent windows (vs. numerous windows in both *P. stercorarius* and *P. moretoniensis*, or a continuous translucent stripe in *P. antongil*), and that is confined to the midflank (vs. extending a majority of the length of the flank in congeners). The new species is further distinguished from both *P. moretoniensis* and *P. antongil* by a shallower body, and from both *P. stercorarius* and *P. moretoniensis* by a pigmentation pattern above the lateral midline comprised primarily of larger rounded blotches (vs. smaller sinuous lines and markings comprising a vermiculated pattern). *Photolateralis polyfenestrus* is characterized by a lower jaw that is deep and convex in lateral view (vs. mostly straight in congeners, excluding *P. antongil*), and that forms an angle of between 60°–70° to horizontal (vs. less than 45° in congeners, excluding *P. antongil*). The only other species of *Photolateralis* reported from the Western Indian Ocean is *P. antongil*, to date only known from the coastal waters of Madagascar, whereas both *P. stercorarius* and *P. moretoniensis* have ranges restricted to the western Pacific and extending into the eastern Indian Ocean.

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## INTRODUCTION

The genus *Photolateralis* was recently described by Sparks and Chakrabarty (2015) to encompass members of Leiognathidae that are characterized by a species-specific translucent midlateral flank stripe. *Photolateralis* currently comprises three species, *P. stercorarius* (Evermann and Seale, 1907), *P. moretoniensis* (Ogilby, 1912), and *P. antongil* (Sparks, 2006), not including the new species described herein. This characteristic flank stripe may either be comprised of multiple independent translucent windows (*P. stercorarius*, *P. moretoniensis*, and the new species) or is a continuous translucent lateral band (*P. antongil*), through which bacterially mediated luminescence is presumably transmitted from the light organ via clearing of the silvery lateral lining of the gas bladder (Sparks et al., 2005; Sparks, 2006; Sparks and Chakrabarty, 2015). All members of *Photolateralis* were formerly placed in *Equulites* (Kimura et al., 2008; Chakrabarty et al., 2011a, 2011b), and *Photolateralis* shares the presence of translucent lateral flank regions with its sister genus *Equulites*, although the morphology of these translucent regions differ substantially between the two genera. *Photolateralis* is recovered as the sister group to *Equulites*, and together these two genera comprise the tribe Equulitini (Chakrabarty et al., 2011a, 2011b), which is the sister taxon to the tribe Nuchequulini within the subfamily Gazzinae (Chakrabarty and Sparks, 2015).

Members of *Photolateralis* can be distinguished from their sister taxon *Equulites*, as well as other members of the family, by both external and internal features of their light-organ system. Externally, male members of *Equulites* are characterized by an expansive and translucent triangular, cornucopia-shaped, or trapezoidal patch on the flank (Sparks and Chakrabarty, 2007: fig. 1), versus a continuous or composite midlateral stripe comprised of multiple independent translucent windows in *Photolateralis* (Sparks and Chakrabarty, 2015: fig. 3). In *Photolateralis*, the translucent lateral stripe is either lacking entirely in females, or is considerably less developed (note: only the holotype, a male, is known for the new species). Both *Equulites* and *Photolateralis* exhibit lateral clearing (= translucence) of the guanine-lined internal gas bladder surface, and the extent of clearing corresponds to the location of the translucent external patches or stripe. Lateral gas bladder clearing in *Equulites*, however, is far more extensive, extending the full length of the gas bladder, whereas in *Photolateralis* clearing is restricted to the posterior region of the gas bladder (see Sparks et al., 2005: figs. 4, 5; Sparks and Chakrabarty, 2015: figs. 2, 4). Male members of *Photolateralis* exhibit a moderately enlarged donut-shaped light organ that extends at most only slightly posteriorly into the gas bladder space, whereas the light organ in male members of *Equulites* is greatly enlarged, with paired dorso-lateral lobes extending posteriorly well into the gas bladder space (less *E. leuciscus*) (see Sparks and Chakrabarty, 2015: figs. 2, 4).

Based on a number of taxonomically comprehensive family-level phylogenetic hypotheses that have been generated in recent years, we now have a better understanding of leiognathid diversity, intrafamilial relationships, and the evolution of their unique light-organ system (Sparks and Dunlap, 2004; Sparks et al., 2005; Chakrabarty et al., 2011a, 2011b). As a result of these phylogenetic studies, extensive fieldwork, and detailed morphological comparisons, several new leiognathid genera and species have recently been described (e.g., see Chakrabarty

and Sparks, 2008; Sparks and Chakrabarty, 2015; Suzuki and Kimura, 2017). In the present study, a new species belonging to *Photolateralis* is described from material collected in the Gulf of Oman.

## MATERIALS AND METHODS

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). The first caudal vertebra is here defined as the first vertebra bearing a definite hemal spine (Hubbs and Lagler, 1949). 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.

Morphology of the light-organ system was examined in situ (new species) or in isolation via dissection to permit detailed anatomical comparisons. Sex of the holotype was confirmed via dissection. Osteological and soft tissue features were analyzed using standard film and digital radiographs, high-resolution digital images, MRIs (Chakrabarty et al., 2011a), examination of whole alcohol-preserved specimens, specimens cleared-and-stained (C&S) for bone and cartilage (following the protocol of Taylor and Van Dyke, 1985), and dry skeletal (S) preparations. Specimens examined are listed under Material Examined in appendix 1. Institutional abbreviations are as listed in Leviton et al. (1985) and Sabaj Pérez (2014).

## RESULTS

### SYSTEMATIC ACCOUNT

#### *Photolateralis polyfenestrus*, new species

Figures 1, 2; table 1

**HOLOTYPE:** AMNH 267152, 66.8 mm SL, male; Sultanate of Oman: Gulf of Oman, Fish Market, 23° 36' N; 058° 33' E; Z. Baldwin, July 2008.

**DIAGNOSIS:** *Photolateralis polyfenestrus* is distinguished from congeners by the presence of a short, composite midlateral stripe comprised of three small, rounded translucent windows that are peppered with chromatophores (vs. numerous windows in both *P. stercorarius* and *P. moretoniensis*, or a continuous translucent stripe in *P. antongil*) and is confined to the midflank (vs. extending most to entire the length of the flank in congeners). The new species is further distinguished from both *P. stercorarius* and *P. moretoniensis* by a pigmentation pattern above the lateral midline comprised of larger rounded blotches and markings (vs. smaller sinuous lines and markings forming a vermiculate pattern), and both *P. moretoniensis* and *P. antongil* by a shallower body. *Photolateralis polyfenestrus* exhibits a lower jaw that is deep and convex in lateral view (vs. mostly straight in congeners, less *P. antongil*), and that forms an angle of between 60°–70° to horizontal (vs. less than 45° in congeners, less *P. antongil*). The only other species of *Photolateralis* reported from the western Indian Ocean is *P. antongil*, to date only known from the coastal waters of Madagascar, and whereas both *P. stercorarius* and *P. moretoni-*

*ensis* have more extensive ranges, nevertheless they are restricted to the western Pacific and extending into the eastern Indian Ocean.

**DESCRIPTION:** Proportional measurements and meristic data presented in table 1 and internal osteological features can be visualized in figure 2. A moderately shallow-bodied and elongate leiognathid. Body laterally compressed. Lateral snout outline straight with a protuberance above upper lip. Mouth small and terminal in position. Premaxilla long and protruding along dorsal margin. Posterior margin of maxilla exposed, reaching to level of vertical through anterior margin of orbit. Lower jaw deep and noticeably convex in lateral view, forming angle of  $60^{\circ}$ – $70^{\circ}$  to horizontal. Mild preorbital protuberance due to protrusion of both frontal and lateral ethmoid ossifications. Predorsal head profile weakly sloping and straight. Nuchal spine (exposed rising dorsal aspect of the supraoccipital crest) very slightly protruding and distal tip exposed. Nuchal spine with distinct median keel. Eye large. Anterior nasal pore small and round; posterior foramen much larger and crescent shaped, partially encircling anterior pore. Two short and stout postnasal spines present on lateral ethmoid, located posterior to nasal foramina and just rostradorsal of orbit. Postnasal spines followed posteriorly by well-developed supraorbital ridges that converge posteriorly. One supraneural present with strong anterior process. Preopercular margin smooth, not serrate, along ventral and ventrocaudal margins. Dorsal and ventral body profiles mildly rounded, with ventral profile more convex than dorsal. Dorsal-fin origin located well posterior to vertical through pelvic-fin origin. Anal-fin origin located at about level of vertical through the last (= 8th) dorsal-fin spine/first dorsal-fin ray. Caudal peduncle slender and shallow. Total vertebral count 23: 10 precaudal + 13 caudal. Neural and hemal spines of vertebral centrum PU4 weakly expanded distally and bladelike. Thirteen elongate and triangular outer gill rakers arrayed along lower limb (= 5th ceratobranchial) of first gill arch.

**Fins:** Dorsal fin with VIII spines and 16 branched rays. First dorsal-fin spine greatly reduced in length and somewhat robust. Second through fourth dorsal-fin spines elongate and robust; second spine longest. Second dorsal-fin spine moderately, but not exceedingly, elongate compared to third and fourth. Third and fourth dorsal-fin spines serrate along anterior margin “lock” into groove on posterior margin of preceding spine when erect (fig. 2). Dorsal-fin spines five through eight feeble, considerably 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. Third anal-fin spine serrate on anterior margin “locks” into groove on posterior margin of second spine when erect (fig. 2). Spinous dorsal and anal fins with asquamate basal sheath. Eighteen total pectoral-fin rays. Pelvic fins short, not reaching first anal-fin spine when adducted (i.e., a significant gap present). Eight upper and seven lower branched caudal-fin rays.

**Dentition:** Two distinct rows of extremely closely set, elongate and recurved conical teeth present in both upper and lower jaws. Upper jaw teeth somewhat larger and more recurved than those of lower jaw. Lips fleshy, and teeth embedded.

**Squamation:** Body scales cycloid. Head and opercular region asquamate. Chest fully scaled, except along ventral midline. Scales conspicuous. Squamation extends anteriorly, ventral to

TABLE 1. Morphometric and Meristic Data for Holotype of *Photolateralis polyfenestrus*.

Character	Holotype
Standard length (mm)	66.8
Percentage of SL	
Head width (max.)	13.2
Head length	27.7
Body depth	35.9
Caudal peduncle length	5.4
Caudal peduncle width	2.3
Caudal peduncle depth	5.8
Pectoral-fin length	19.5
Predorsal length	41.5
Preanal length	53.4
Prepelvic length	33.1
Percentage of HL	
Snout length	33
Orbit diameter	34.6
Upper jaw length	22.7
Lower jaw length	58.4
Interorbital width	30.8
Caudal peduncle length/width	2.4
Caudal peduncle length/depth	0.9
Gill rakers (lower limb 1st arch)	13
Vertebrae (precaudal + caudal)	10 + 13 = 23
Dorsal fin	VIII 16
Anal fin	III 14

opercle, to approximately anterior margin of chest. Lateral line arched and complete, located well dorsal to lateral midline. Pored scales in lateral line highly embedded and difficult to visualize and count. Pores well developed. All fins asquamate, except for caudal fin, which bears several rows of cycloid scales of reduced size, particularly centrally on fin.

**PIGMENTATION IN PRESERVATIVE:** Body ground coloration olive to light brown above lateral midline, and silvery, guanine covered below midline (fig. 1). Pigmentation pattern above lateral midline characteristically blotchy and mottled, comprised of darker brown roundish blotches and broad lines over olive to light brown background. Blotches variable in size and somewhat closely arranged, particularly rostradorsally. Body just ventral to lateral midline peppered with melanophores. Opercle, interopercle, and lacrimal iridescent silvery with golden hue. Preopercle, subopercle, and cheek iridescent and silvery. Short, composite, midlateral stripe present, comprised of three oblong dark gray translucent windows studded with chromatophores, and appearing much darker than surrounding region due to concentration of

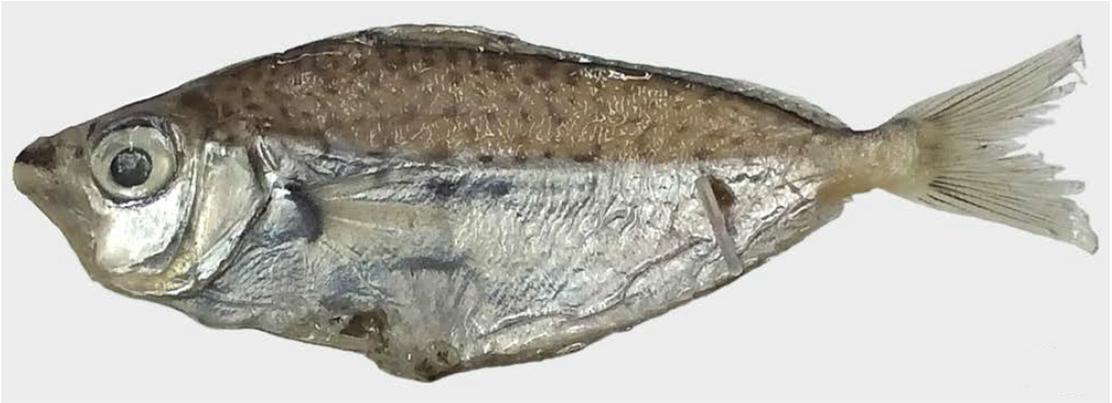


FIG. 1. *Photolateralis polyfenestrus*, new species, holotype, AMNH 267152, male, 66.8 mm SL; Sultanate of Oman: Gulf of Oman, Mutrah Fish Market. Note: Specimen has field tag on posterior flank and anteriormost midlateral window is obscured behind pectoral-fin rays in image.

melanophores. Stripe located at midflank, beginning about level of terminal adducted pelvic-fin rays. Lips grayish. Lower jaw and gular region grayish. Snout with large black patch above upper lip. Two distinct black blotches present anterior to orbit; dorsal blotch covering anterior portion of postnasal spines on lateral ethmoid. Dorsal and ventral margins of orbit lined in black pigment. Interorbital region and nape grayish anteriorly to grayish-brown posteriorly. Large, oblong dark brown marking posterior to orbit and dorsal to opercle. Chest and belly silvery; silvery along ventral midline. Dorsal and anal fins hyaline to pale yellowish-white, with a slight concentration of black pigment distally on dorsal-fin spines. Base of dorsal fin black; becoming more prominent (i.e., darker) posteriorly. Pectoral and pelvic fins yellowish tan. Caudal peduncle pale tannish yellow with blackish saddle on dorsal margin. Base of caudal fin pale yellow. Caudal fin yellowish to olive proximal to base, becoming translucent to white distally. Membrane of caudal fin with concentration of black pigment, creating series of thin, black radiating lines, particularly near base.

**LIGHT-ORGAN SYSTEM (LOS):** In *Photolateralis* the light-organ system is internally characterized by a moderately enlarged, donut-shaped, and conspicuously spotted light organ in males that extends only slightly posteriorly into the gas bladder. In contrast, in members of *Equulites*, its sister taxon, the dorsolateral lobes of the light organ in males are greatly enlarged, heavily pigmented, and extend posteriorly well into the gas bladder. Internally, male members of *Photolateralis* exhibit posterolateral clearing of the silvery gas bladder lining, corresponding in extent to the external translucent lateral stripe or windows on the flank. The light-organ system in the new species is similar to that described for males of other members of *Photolateralis* (see Sparks, 2006; Sparks and Chakrabarty, 2015). In the new species, lateral clearing of the gas bladder lining corresponds to the three external translucent midlateral windows, the anteriormost window located at about the midpoint of the adducted pectoral-fin rays. Externally, members of *Photolateralis* are distinguished from all other leiognathids by the presence of a translucent flank stripe, which, depending on the species, may be comprised of either

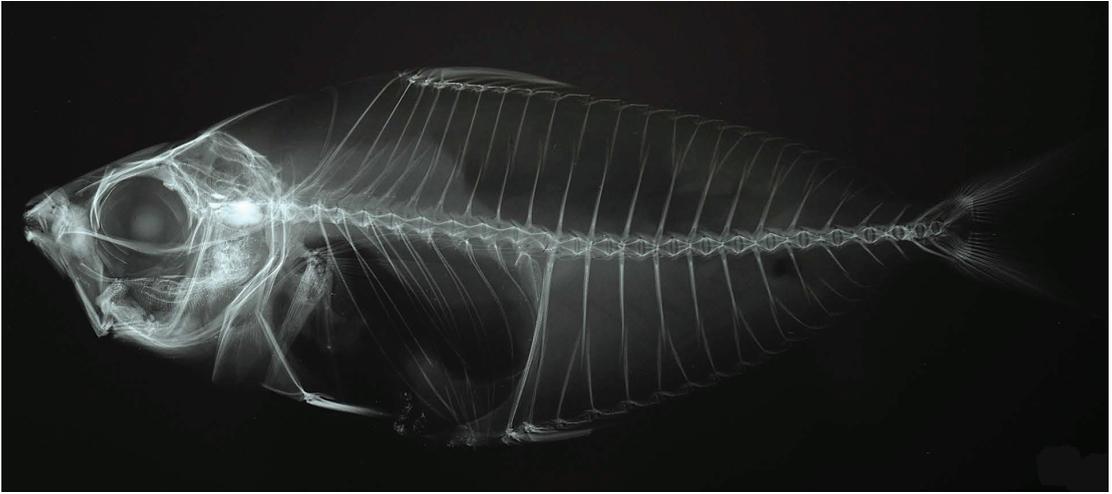


FIG. 2. Radiograph of *Photolateralis polyfenestrus*, new species, holotype, AMNH 267152, male, 66.8 mm SL; Sultanate of Oman: Gulf of Oman, Mutrah Fish Market.

multiple independent translucent windows (*P. stercorarius*, *P. moretoniensis*, and the new species) (figs. 1, 3A–C), or a continuous midlateral band (*P. antongil*) (fig. 3D). In *Photolateralis*, the translucent lateral stripe is either lacking entirely in females, or is considerably less well developed.

**DISTRIBUTION:** Known only from a single specimen acquired at a fish market (23° 36' N; 058° 33' E) in northeastern Oman, Sultanate of Oman. The new species is presumably more widespread in the region as well as in the Gulf of Oman. Extensive recent surveying and collecting in the adjacent portion of the Persian (Arabian) Gulf did not result in any additional observations of this species (personal obs.).

**ETYMOLOGY:** Named in reference to the characteristic translucent midlateral windows, which are rounded and appearing spotlike. The specific epithet, *polyfenestrus*, is used as an adjective.

## DISCUSSION AND COMPARISONS

As many as 10 leiognathid species have been reported to occur in the coastal waters of Oman (Randall, 1995; Al-Jufaili et al., 2010, Froese and Pauly, 2019). In addition, recent studies have confirmed the occurrence of both *E. elongatus* (Jayabalan et al., 2010; Jawad et al., 2013), which had previously been reported from Oman, and *E. klunzingeri* (Jawad et al., 2012), new record, from the coastal waters of Oman. Although both of these species are shallow-bodied, elongate ponyfishes, they are characterized by an expansive translucent triangular or trapezoidal patch on the flank in males (Sparks and Chakrabarty, 2007: fig. 1a, d).

The only species *Photolateralis polyfenestrus* could potentially be misidentified as and confused with (and that has been reported to occur in the region) is the species commonly referred to as *Leiognathus oblongus* or *Equulites oblongus* (Valenciennes, 1835) (fig. 4). Note, we use *Equulites oblongus* for convenience only, as there are no external apomorphic features that can

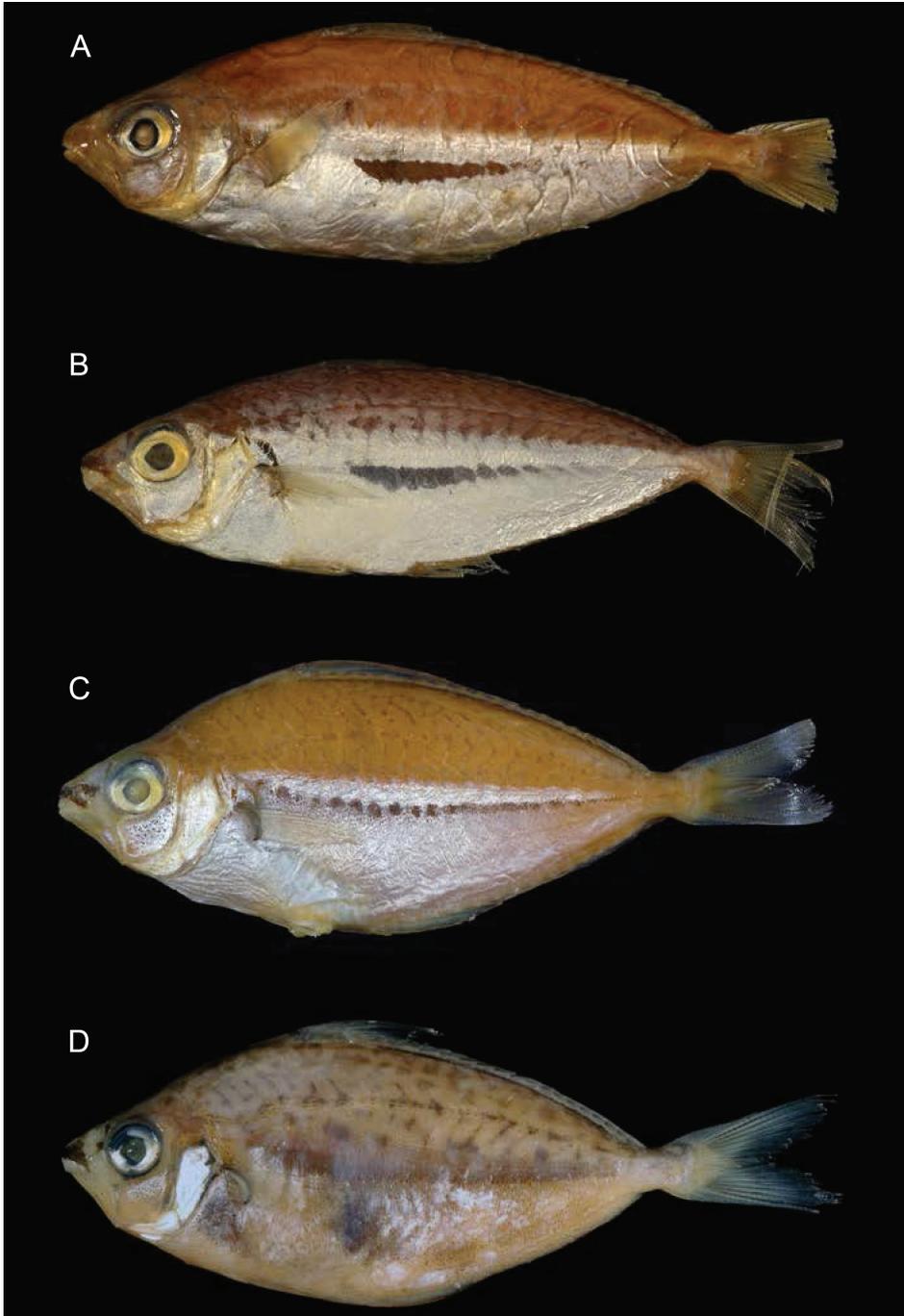


FIG. 3. Species of *Photolateralis* illustrating phenotypic variability of translucent midlateral flank stripe characteristic of genus. (A) *P. stercorarius*, USNM 55906, holotype, 83.8 mm SL, Philippines. (B) *P. stercorarius*, SIO 96-96, non-type, 98.2 mm SL, Philippines. (C) *P. moretoniensis*, AMS I.22983001, nontype, 76.9 mm SL, Australia. (D) *P. antongil*, AMNH 236544, holotype, 75.0 mm SL, Madagascar.



FIG. 4. *Equula oblonga*, holotype, MNHN A-6754, 61.8 mm SL; Timor, Indonesia.

be identified on the holotype to place the species in *Equulites*. The holotype of *E. oblongus* is intact, nondissected, and lacking any evidence of translucent flank patch(es) or a stripe that would allow one to place it in the genus *Equulites*. Based on overall body shape, including lateral profile of the lower jaw and remaining flank pigmentation pattern above the lateral midline in preservation, we believe the holotype of *E. oblongus* (MNHN A-6754) should actually be placed in *Photolateralis*.

We further note, however, that specimens attributed to *E. oblongus* (from Oman) are much deeper bodied than the holotype of *E. oblongus*, exhibit a very different pigmentation pattern on the flank above the lateral midline, and lack the translucent lateral windows or stripe that characterize the new species, and members of *Photolateralis* in general (compare figs. 1 and 3 with fig. 4; also see Randall, 1995: 193, fig. 486). Based on external morphology, the specimen shown by Randall and identified as *E. oblongus* (1995: fig. 486) appears to be a female *E. leuciscus*. *Equulites leuciscus* is a widespread species in the Indo-West Pacific, with a range reportedly extending from East Africa and Madagascar, to northern Australia and New Caledonia, to Vietnam, Taiwan, and China (personal obs.); Froese and Pauly, 2019), but that has not previously been reported from Oman.

The original description of *E. oblongus* is insufficient for distinguishing this species from other members of Equulitini, despite the holotype (MNHN A-6754) being in relatively good condition (fig. 4). In addition to the translucent lateral flank windows present in the new species, *P. polyfenestrus* can easily be distinguished from the holotype of *E. oblongus* by flank pigmentation pattern above the lateral midline (few large, roundish blotches in *E. oblongus* vs. a more blotchy and variable pattern in the new species, comprised of numerous smaller and more irregular dark, roundish markings), a deeper body, a straight predorsal profile (vs. rounded in *E. oblongus*), and a much deeper and concave (vs. relatively straight and short in *E. oblongus*) lateral lower jaw profile (figs. 1–2, 4).

Upon first examining the holotype of *P. polyfenestrus* in 2008, and noting its unique translucent midlateral flank patches, we realized that we had a new species in hand. Ideally, we would have liked to have located additional specimens prior to describing the new species, however, as part of our ongoing morphological studies of Leiognathidae, we searched museum collections unsuccessfully for additional specimens since the collection of the holotype in 2008. We feel that it is prudent to describe the new species at this time, given how distinct it is from other members of *Photolateralis*, since it appears that additional specimens referable to the new species do not exist in accessible museum collections. We anticipate that, with intensified collecting efforts in the region, additional specimens attributable to the new species will be collected.

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## APPENDIX 1

### MATERIAL EXAMINED

*Aurigequula fasciata*: AMNH 15520; AMNH 237140; AMNH 241338; CAS 1872; UMMZ 240504; AMNH 240597; AMNH uncat.; USNM 191962; USNM 191966; WHT PC-195; WHT PC-196; WHT PC-197. *Aurigequula longispina*: MNHN A-0579, holotype; AMNH 219296; AMNH 242135; AMNH uncat. (SI-87); AMS I.20907036; AMS I.22974001; AMS 22981001; AMS 23044001; USNM 324651; ZRC 50950. *Aurigequula striata*: SU 22909; WHT PC-183; WHT PC-184; WHT PC-192; WHT PC-193; WHT PC-194.

*Deveximentum hanedai*: FUMT P 8701, paratype, 1 ex. *Deveximentum indicium*: AMNH 239272; AMNH 239290; AMNH 241326; AMNH 242615; ANSP 76147; ANSP 87160; UMMZ 240127; USNM 139559; USNM 395666. *Deveximentum insidiator*: ZMB 1676, syntypes, 2 ex.; AMNH 240594; ANSP 51324; ANSP 62128; ANSP 87838; CAS 29894; UMMZ uncat. *Deveximentum mazavaaoka*: AMNH 251200, holotype; AMNH 231398, paratype, 1 ex., AMNH 236061, paratype, 1 ex., AMNH 244283, paratypes, 43 ex., AMNH 244293, paratypes, 12 ex., AMNH 244306, paratype, 1 ex., AMNH 245638, paratypes, 10 ex., AMNH 253842, paratype, 1 ex., AMNH 253843, paratypes, 5 ex., ANSP 53115, paratype, 1 ex., ANSP 54891, paratypes, 5 ex., ANSP 88786, paratype, 1 ex., USNM 373273, paratypes, 7 ex., USNM 373282, paratypes, 17 ex. *Deveximentum megalolepis*: UMMZ 240135. *Deveximentum ruconium*: AMNH 239277; AMNH 241293; AMNH 241322; ANSP 77437; ANSP 87141; CAS-SU 29895; UMMZ 225240; UMMZ uncat.; USNM 151406.

*Equulites absconditus*: AMNH 249306, holotype; AMNH 239270, paratype, 1 ex.; AMNH 242666, paratypes, 97 ex.; LSUMZ 13236, paratype, 1 ex.; LSUMZ 13339, paratypes, 21 ex.; NTUM 5698, paratypes, 2 ex. *Equulites 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. *Equulites klunzingeri*: NMW 68277, syntypes, 4 ex.; NMW 68280, syntypes, 2 ex.; NMW 76008, syntypes, 4 ex.; NMW 76009, syntypes, 4 ex.; AMNH 44488; AMNH 44491; AMNH 44493. *Equulites laterofenestra*: USNM 387899, holotype; USNM 228508, paratypes, 4 ex.; AMNH 238682, paratypes, 2 ex.; AMNH 241277; AMNH 241311; AMNH 241315; AMNH 241352; WHT PC-132; WHT PC-133; WHT PC-188. *Equulites leuciscus*: BMNH 1858.4.21.243, holotype; AMNH 237149; AMNH 239270; AMNH 240587; AMNH 240589; AMNH 241278; AMNH 241313; AMNH 242666; AMS I.22967001; AMS I.22978004; AMS I.34365015; ANSP 27525 (holotype of "*Leiognathus*" *vermiculatus*); UMMZ 240125; UMMZ uncat.; USNM 76609;

USNM 191979; USNM 191991; USNM 307917; USNM 373280; QM I.878 (holotype of “*Equula longispina*”). *Equulites rivulatus*: AMNH 34850; UMMZ 182938; UMMZ 240144; UMMZ uncat.

*Eubleekeria jonesi*: ZSI (CMFRI.T 100/1), uncatalogued holotype; AMNH 241302; AMNH 241339; AMNH 241359; UMMZ 235095; UMMZ 240134; UMMZ 240505; UMMZ uncat.

*Eubleekeria kupanensis*: UMMZ 243701. *Eubleekeria splendens*: AMNH 241339; ANSP 59963; ANSP 27530; ANSP 47486 (holotype of “*Leiognathus philippinus*”); ANSP 47487; CAS 1485; CAS 38789; CAS 56438; CAS 56441; MNHN A-6724; UMMZ 191202; UMMZ 240130, UMMZ uncat.; USNM 190258; USNM 190263; WHT PC-136; WHT PC-137; WHT PC-166; WHT PC-191.

*Gazza achlamys*: CAS-SU 21652, paratype, 1 ex.; CAS-SU 22853, paratype, 1 ex.; 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. *Gazza rhombea*: USNM 332347, paratype, 1 ex.; USNM 350467, paratype, 1 ex. *Gazza squamiventralis*: USNM 345525, holotype; USNM 345526, paratype, 1 ex.; AMNH 237137.

*Karalla daura*: AMNH 241316; ANSP 89582; USNM 100291; USNM 373281; WHT PC-131;

WHT PC-170; WHT PC-187. *Karalla dussumieri*: MNHN A-6721, syntype, 1 ex.; AMNH 234763; WHT PC-130; WHT PC-134; WHT PC-135; WHT PC-161; WHT PC-162; WHT PC-190.

*Leiognathus equulus*: ZMUC P48219, lectotype (dry skin; photographs and radiographs examined); ZMUC P48220, paralectotype (dry skin, photograph and radiograph examined); ZMB 8756 (holotype of “*Leiognathus edentulus*”); AMNH 59535; AMNH 88039; AMNH 237139; AMNH 242134; 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, 1 ex., paratype; UMMZ 240362, 1 ex, paratype.; UMMZ 240360.

*Nuchequula blochii*: MNHN A-6757, syntype, 1 ex.; MNHN A-6759, syntype, 1 ex.

*Nuchequula decora*: AMNH 231297, AMS I.22990002. *Nuchequula mannusella*:

AMNH 238753, holotype; AMNH 238754, paratypes, 15 ex.; AMNH 238755, paratypes; 16 ex.; AMNH 238756, paratypes, 15 ex.; AMNH 238757, paratypes, 14 ex.; AMNH 238758, paratypes; 20 ex.; AMNH 238759, paratypes, 9 ex.; AMNH 238760, paratypes, 13 ex.; AMNH 238761, paratypes, 1 ex.; AMNH 238762, paratype, 1 ex.; AMNH 238763, paratypes; 1 ex.; AMNH 238764, paratype, 1 ex.; AMNH 238765, paratypes, 29 ex.; ASIZP0062322, paratype, 1 ex.; ASIZP0060823, paratype; 1 ex.; ASIZP0059839, 2 ex.; ASIZP0065686. *Nuchequula nuchalis*: RMNH 1287, holotype; AMNH 26819; AMNH 34861, AMNH 26819; AMNH 238766; CAS-SU 4757; UMMZ 240143. *Nuchequula pan*: CUMZ 2528.2.9.1, holotype; CUMZ 2528.2.9.2, paratype, 1 ex.; CUMZ 2528.2.9.3, paratype, 1 ex.; USNM 276536, paratype, 1 ex.

*Photolateralis antongil*: AMNH 236544, holotype; AMNH 236545, paratypes, 3 ex.

*Photolateralis moretoniensis*: QM I.1583, syntype, 1 ex.; AMS I.21700001; AMS I.22983001; LSUMZ 13646, LSUMZ 13647, LSUMZ 13648, LSUMZ 13656, LSUMZ 13657, LSUMZ 13658.

*Photolateralis stercorarius*: USNM 55906, holotype; USNM 126395, cotype; ANSP 33289, paratype, 1 ex.; CAS 42171, paratype; CAS 17678; CAS-SU 20004, paratype; AMNH uncat.; SIO 00-13; SIO 96-96; UMMZ 240138; UMMZ uncat.; USNM 191996; ZRC 50951.

*Photopectoralis aureus*: SIO 83-132; UMMZ 240129; UMMZ 240309; UMMZ uncat.; USNM

373277. *Photopectoralis bindus*: AMS I.34367021, CAS 51097; UMMZ 240131; UMMZ 240142; UMMZ uncat.; USNM 373284; MNHN A-6763 (syntype of "*Equula*" *brevirostris*). *Photopectoralis cf. bindus*: AMNH 237147. *Photopectoralis hataii*: UMMZ uncat. *Photopectoralis cf. hataii*: AMNH 89922. *Photopectoralis panayensis*: UMMZ 240300, holotype; UMMZ 240301, paratypes, 4 ex.; UMMZ 240302, paratypes, 5 ex.; UMMZ 240303, paratypes, 8 ex.; UMMZ 240304, paratypes, 16 ex.; UMMZ 240137; UMMZ uncat.



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