



Diagnoses for *Leiognathus* Lacepède 1802, *Equula* Cuvier 1815, *Equulites* Fowler 1904, *Eubleekeria* Fowler 1904, and a New Ponyfish Genus (Teleostei: Leiognathidae)

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Diagnoses for *Leiognathus* Lacepède 1802, *Equula* Cuvier 1815, *Equulites* Fowler 1904, *Eubleekeria* Fowler 1904, and a New Ponyfish Genus (Teleostei: Leiognathidae)

PROSANTA CHAKRABARTY¹ AND JOHN S. SPARKS¹

ABSTRACT

Recent phylogenetic work on ponyfishes has delimited and revealed the interrelationships of major leiognathid clades. To begin to recognize a monophyletic taxonomy for Leiognathidae we diagnose, delimit, and describe a number of ponyfish genera to reflect our current knowledge of their phylogenetic history. *Equula* Cuvier, 1815, is resurrected from synonymy with *Leiognathus* Lacepède, 1802, and comprises *E. fasciata* and *E. longispinis*. Members of *Equula*, the sister group to all other members of Leiognathidae, are large-bodied ponyfishes characterized by conspicuous round yellow blotches on the flank. The genus *Leiognathus* Lacepède, 1802, the sister group to the remaining members of Leiognathidae less *Equula*, is herein restricted to a clade comprising *Leiognathus equulus*, *L. robustus*, and *L. striatus*. The subgenus *Equulites* Fowler, 1904, comprising *E. leuciscus*, *E. klunzingeri*, and *E. laterofenestra*, is removed from synonymy with *Leiognathus* and is elevated to generic rank. The subgenus *Eubleekeria* Fowler, 1904 is removed from synonymy with *Leiognathus* and is likewise elevated to generic rank. *Eubleekeria* encompasses the “*Leiognathus*” *splendens* species complex, which is recovered as the sister group to *Photopectoralis*. To remedy the paraphyly of the remaining species placed within *Leiognathus* we describe a new genus, *Karalla*, which is recovered as the sister group to *Nuchequula*.

INTRODUCTION

Our knowledge of leiognathid intrarelationships has increased substantially due to the

publication of several recent family-level phylogenetic analyses (Ikejima et al., 2004; Sparks and Dunlap, 2004; Sparks et al., 2005). It is noteworthy that all studies recover a

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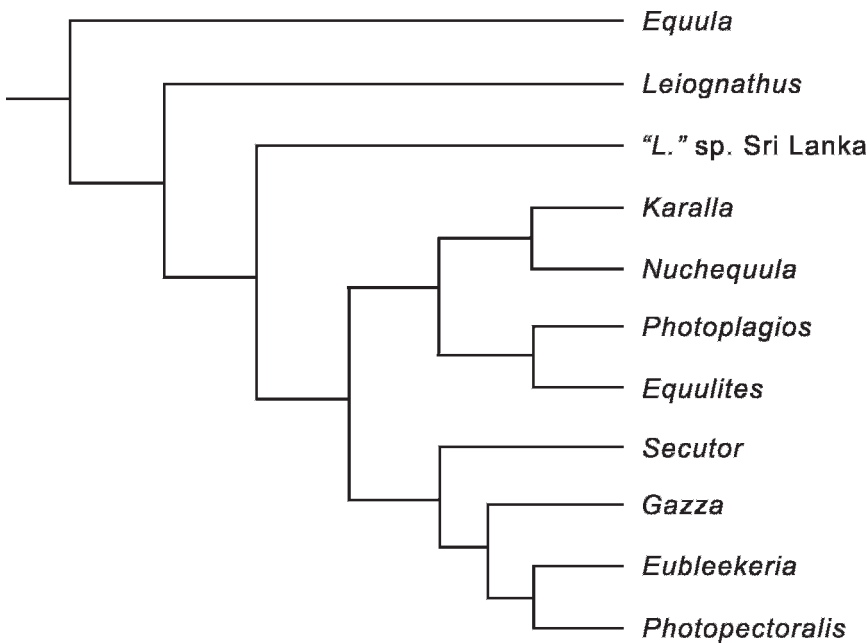


Fig. 1. Generic-level phylogeny for Leiognathidae based on Sparks et al. (2005) and Chakrabarty et al. (MS).

paraphyletic *Leiognathus* Lacepède, 1802. To begin to achieve a monophyletic taxonomy for Leiognathidae, a number of new genera have recently been described or resurrected from synonymy including: *Nuchequula* Whitley, 1932 (elevated to generic rank by Chakrabarty and Sparks, 2007), *Photoplagios* Sparks et al., 2005, and *Photopectoralis* Sparks et al., 2005.

Members of Leiognathidae are nondescript, silvery, generally small (<200 mm SL), laterally compressed fishes. Their mouths are highly protractible either dorsally, rostrally, or most commonly, ventrally. They possess five branchiostegals, VII–IX dorsal-fin spines (mode VIII) and 15–17 branched rays (mode 16), three anal-fin spines and 13–15 branched rays (mode 14), and 24 (10 precaudal + 14 caudal) vertebral centra. These counts are consistent within the family and do not vary among species. Uniquely, all leiognathids possess a circumesophageal light organ that contains symbiotic luminescent bacteria (*Photobacterium*), whose light the fish co-opt for photic communication and predator avoidance (Hastings, 1971; McFall-Ngai and Dunlap, 1983). Most species are sexually

dimorphic with regard to the light organ and associated structural features that facilitate the transmission of bacterially generated luminescence (i.e., the light-organ system: LOS; Sparks et al., 2005). Males of many species have a translucent lateral patch or patches on the head region or flank from which light is emitted (Sparks et al., 2005). Additional apomorphic anatomical features for the family include: broad, extremely thin cleithrum that is sheetlike ventrally; two distinct bony prongs along the anterior margin of the cleithrum (see below); broad and platelike neural and hemal spines on fourth preural centrum; and one or two unique spinous processes on the lateral ethmoid.

On the basis of a rigorous phylogenetic hypothesis for Leiognathidae, we continue instituting taxonomic changes here by resurrecting previously synonymized genera, naming novel genera, and by restricting *Leiognathus* Lacepède, 1802, to a monophyletic group (Sparks et al., 2005; Chakrabarty et al., ms; fig. 1). *Leiognathus* has historically been a catchall genus whose monophyly had not been tested until recently. Figure 1 depicts a generic-level phylogeny for Leiognathidae

based primarily on the analysis of Sparks et al., 2005.

MATERIALS AND METHODS

Osteological features were examined using radiographs, specimens cleared and stained (C&S) for bone and cartilage (following Taylor and Van Dyke, 1985), and dry skeletal (S) preparations. Comparative materials are listed in Material Examined. Light organs were examined in situ or isolated via dissection to permit detailed morphological comparisons. Morphometric measurements were recorded to the nearest 0.1 mm using dial calipers. Standard length (SL) and body depth (BD) are used throughout.

INSTITUTIONAL ABBREVIATIONS

AMNH	American Museum of Natural History, New York
AMS	Australian Museum, Sydney
ANSP	Academy of Natural Sciences, Philadelphia
ASIZ	Academia Sinica Institute of Zoology, Taipei
BMNH	British Museum of Natural History, London
CAS	California Academy of Sciences, San Francisco
CUMZ	Chulalongkorn University Museum of Zoology, Bangkok
LACM	Los Angeles County Museum of Natural History, Los Angeles
MCZ	Museum of Comparative Zoology, Cambridge
MNHN	Muséum National d'Histoire Naturelle, Paris
NMW	Naturhistorisches Museum, Wien
QM	Queensland Museum, Brisbane
RMNH	Nationaal Natuurhistorisch Museum, Leiden
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C.
UMMZ	University of Michigan Museum of Zoology, Ann Arbor
WHT	Wildlife Heritage Trust, Colombo, Sri Lanka
ZMB	Universitat Humboldt, Museum für Naturkunde, Berlin
ZMUC	Københavns Universitet Zoologisk Museum, Copenhagen
ZRC	Raffles Museum of Biodiversity Research, Singapore

SYSTEMATIC ACCOUNTS

Leiognathus Lacepède, 1802

Figure 2

TYPE SPECIES: *Leiognathus equulus* (Forsskål, 1775).

OTHER INCLUDED SPECIES: *Leiognathus robustus* Sparks and Dunlap, 2004, *L. striatus*, James and Badrudeen, 1990.

DIAGNOSIS: Members of *Leiognathus* are distinguished from all other leiognathids by a combination of large adult body size (>150 mm SL), the absence of large round blotches of pigment on the flank, and the presence of a strongly ventrally protracting mouth.

REMARKS: Members of *Leiognathus* can be further distinguished from all other ponyfishes, except *Equula*, by the presence of a nonsexually dimorphic light organ. The absence of flank pigmentation or the possession of faint yellowish or grayish-yellow vermiculate lines or vertical bars on the dorsal flank also distinguishes members of *Leiognathus* from all other ponyfishes, except *Equula*. Members of *Leiognathus* can be further distinguished from members of *Equula* by the presence of a strongly concave lower jaw profile (versus straight or nearly straight in *Equula*). All explicit phylogenetic studies of Leiognathidae to date have recovered a paraphyletic *Leiognathus* (Ikejima et al., 2004; Sparks and Dunlap, 2004; Sparks et al., 2005; Chakrabarty et al., ms). In accordance with the results of these studies, we restrict the name *Leiognathus* to the clade containing the type species, *Leiognathus equulus* (Forsskål, 1775) (see Sparks and Dunlap, 2004), and two other described species, *Leiognathus robustus* Sparks and Dunlap, 2004, and *Leiognathus striatus* James and Badrudeen, 1990, a species rarely mentioned in the literature and even more rarely encountered in museum collections. This restricted concept of *Leiognathus* is recovered as the sister group to all other members of Leiognathidae, less *Equula* (fig. 1). Other ponyfish species in the literature currently referred to *Leiognathus*, but not included in our restricted concept of this genus, are provided novel or resurrected generic assignments below on the basis of apomorphic



morphological features. The lineage labeled “*L.* sp. Sri Lanka” in figure 1 is recovered as a member of *Leiognathus* in Chakrabarty et al. (MS). The taxonomy of this group is further dealt with in that manuscript rather than here, because the species-level status of “*L.*” sp. Sri Lanka cannot be determined due to a lack of morphological vouchers (only a tissue sample was available to Sparks et al., 2005).

Leiognathus striatus can be distinguished from its congeners by the presence of an extremely deep body with a strongly convex dorsal profile (owing to the presence of a pronounced occipital hump) and a pigmentation pattern on the dorsal flank comprising broad yellow vertical bars. *Leiognathus robustus* can be distinguished from its congeners by the absence of a pronounced occipital hump and the presence of a mildly sloping predorsal profile (see Sparks and Dunlap, 2004). *Leiognathus equulus* is distinguished from congeners by the combination of a strongly sloping predorsal profile with a pronounced occipital hump and the absence of yellow vertical bars on the flank.

Equula Cuvier, 1815

Figure 3

Leiognathus fasciatus complex Clade I: Sparks et al., 2005.

TYPE SPECIES: *Equula longispinis* Valenciennes, in Cuvier and Valenciennes, 1835.

OTHER INCLUDED SPECIES: *Equula fasciata* (Lacepède, 1803).

DIAGNOSIS: Members of *Equula* can be distinguished from all other leiognathids by the presence of a series of round yellow blotches arrayed horizontally along the flank.

REMARKS: Members of *Equula* can be further distinguished from all other pony-

fishes, except *Leiognathus*, by the presence of a nonsexually dimorphic light organ.

Sparks et al. (2005) recovered a clade they referred to as the “*Leiognathus fasciatus* complex” (Clade I in that study) as the sister group to the remaining members of Leiognathidae. The “*Leiognathus fasciatus* complex” of Sparks et al. (2005) included two nominal species, *Leiognathus fasciatus* and *L. longispinis*. The oldest available name for this group is *Equula* Cuvier, 1815, which is henceforth removed from synonymy with *Leiognathus* and assigned to this clade. Tortonese (1973) considered *Equula* Cuvier, 1815, to be a junior synonym of *Leiognathus* Lacepède, 1802, but this synonymy was not based on an explicit comparative analysis. Because of the influence of the work of Cuvier and Valenciennes (1835), many species of leiognathids were initially described as members of *Equula*, and for much of the early part of the last century most leiognathid species were considered to be members of this genus.

The two species of *Equula* can be easily distinguished from each other by the presence of a markedly elongate (≥ 60 – 100% of BD) second anal-fin spine in *E. longispinis* (vs. $< 50\%$ of BD in *E. fasciata*), a feature lacking in all other leiognathids (Jones, 1985; Sparks, 2006a).

A homonym, *Equula longispina* De Vis, 1884 exists for *Equula longispinis* Valenciennes, in Cuvier and Valenciennes, 1835, which is objectively invalid and was provided the replacement name of *Leiognathus hastatus* Ogilby, 1912 (Eschmeyer, 2007). *Leiognathus hastatus* Ogilby, 1912 (= *Equula longispina* De Vis, 1884) is considered to be a synonym of *Photoplagios leuciscus* (Günther, 1860; see Hoese and Bray, 2006, and Eschmeyer, 2007). *Leiognathus smithursti* (Ramsay and Ogilby, 1886) was recently deemed a junior

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Figs. 2–6. Coloration of ponyfishes. **2A**, *Leiognathus equulus*, AMNH 242134, 182.7 mm SL; coloration in life. **2B**, *Leiognathus robustus*, UMMZ 242144, holotype, 183.4 mm SL; coloration in preservation. **2C**, *Leiognathus striatus*, WHT PC-183, 173.6 mm SL; coloration in life. **3A**, *Equula longispinis*, AMNH 242135, 160.6 mm SL; coloration in life. **3B**, *Equula fasciata*, AMNH uncat., 119.2 mm SL, coloration in life. **4A**, *Equulites leuciscus*, AMNH uncat., ca. 80 mm SL; coloration in life. **4B**, *Equulites laterofenestra*, AMNH 241311, 100.1 mm SL; coloration in life. **5**, *Eubleekeria splendens*, WHT PC-166, 68 mm SL, type species of genus; coloration in life. **6A**, *Karalla daura*, WHT PC-187, 97.8 mm SL, type species of genus; coloration in life. **6B**, *Karalla dussumieri*, MNHN A-6721, holotype; coloration in preservation.

synonym of *Equula longispinis* (Sparks, 2006a).

Equulites Fowler, 1904

Figure 4

Photoplagios in part: Sparks et al., 2005; Sparks, 2006b; Sparks and Chakrabarty, 2007.

TYPE SPECIES: *Equulites leuciscus* (Günther, 1860).

OTHER INCLUDED SPECIES: *Equulites khun-zingeri* (Steindachner, 1898), *E. laterofenestra* (Sparks and Chakrabarty, 2007).

DIAGNOSIS: Members of *Equulites* are distinguished from all other leiognathids by the combination of an expansive translucent triangular, cornucopia-shaped or trapezoidal patch on the flank in males, a greatly elongate and feeble second dorsal-fin spine (more pronounced in males), and a pigmentation pattern on the dorsal flank comprising speckles and vermiculate markings or broad oblong markings that occasionally form open circular patterns.

REMARKS: *Equulites* was described by Fowler (1904: 516–517) as a subgenus of *Leiognathus* to encompass his newly described species *Leiognathus vermiculatus* Fowler, 1904, and *L. virgatus* Fowler, 1904. *Leiognathus virgatus*, a deep-bodied species, was subsequently synonymized with *Leiognathus* (now *Photopectoralis*) *bindus* (Valenciennes, 1835) by Woodland et al. (2001), whereas *Leiognathus vermiculatus* was synonymized with *L.* (now *Equulites*) *leuciscus* by Jones (1985: 590–591), a synonymy further corroborated by Sparks (2006b: 13). Herein we elevate *Equulites*, a strongly supported monophyletic assemblage (Sparks et al., 2005: fig. 1) comprising three nominal species, to generic rank. *Equulites* is a widespread genus, with members' distributions spanning nearly the entire geographic range of the family. Members of *Equulites* are sexually dimorphic with respect to light-organ volume and shape, with those of males being considerably larger than similarly sized conspecific females. Males also possess an expansive translucent triangular flank patch and corresponding clearing of the guanine-lined gas bladder, features lacking entirely in females.

Members of *Equulites* can easily be distinguished from *Photoplagios*, to which they were formerly assigned (Sparks et al., 2005), by pigmentation pattern on the dorsal flank (vermiculate and highly mottled in *Equulites* vs. much larger and more sparse oval blotches in *Photoplagios*; see Sparks and Chakrabarty, 2007: fig. 1), length of the second dorsal-fin spine (markedly elongate in *Equulites*), and degree of sexual dimorphism and morphology of the light organ (dorsal lobes of males moderately enlarged in males and extending only slightly into the gas bladder chamber in *Equulites* vs. dorsal lobes of males greatly enlarged and extending posteriorly well into the gas bladder chamber in *Photoplagios*). Sparks and Chakrabarty (2007: 627) present a number of diagnostic species-level features to distinguish members of this clade from congeners.

Eubleekeria Fowler, 1904

Figure 5

Leiognathus splendens complex: Kimura et al., 2005.
Clade H: Sparks et al., 2005.

TYPE SPECIES: *Eubleekeria splendens* (Cuvier, 1829).

OTHER INCLUDED SPECIES: *Eubleekeria jonesi* (James, 1971), *E. kupanensis* (Kimura and Peristiawady, 2005, in Kimura et al., 2005), *E. rapsoni* (Munro, 1964).

DIAGNOSIS: Members of *Eubleekeria* are distinguished from all other leiognathids by the combination of a vermiculate dorsal flank pigmentation pattern, black markings in the membrane of the spinous dorsal fin, and the presence of chest scales.

ETYMOLOGY: *Eubleekeria* was named in honor of the prolific Dutch ichthyologist Pieter Bleeker by Fowler (1904: 516). Russell (1803) illustrated the fish that was later described as *Equula splendens* Cuvier, 1829 (who provided the binomial in a footnote referring to Russell's illustration), providing it with the common name "Goomorah Karah".

REMARKS: *Eubleekeria* was described by Fowler (1904: 516–517) as a subgenus of *Leiognathus* to encompass *Leiognathus splendens* (Cuvier, 1829) and *Leiognathus spilolus* Fowler, 1904, which was later synonymized

with *L. splendens* by Kimura et al. (2005). Sparks et al. (2005: fig. 1) recovered “Clade H” (herein *Eubleekeria*) as the sister group to *Photopectoralis*. Herein we elevate this monophyletic assemblage to generic rank. Members of *Eubleekeria* are sexually dimorphic with respect to light-organ volume, with those of males being considerably larger than similarly sized conspecific females. Kimura et al. (2005) presented the following combination of characters in their diagnosis of this group: body deep (42–60% SL); mouth protracting ventrally; jaw teeth slender, minute; 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. Unfortunately, all of these features are more broadly distributed within Leiognathidae, and provide no diagnostic information for *Eubleekeria*. In addition, we find the mouth to protract only slightly downward in these species, as opposed to strongly downward as is the case with most other members of the family. The shape of the snout in *Eubleekeria* also appears to be unique, owing to the combination of a shorter snout length than in most leiognathids (25–30% of HL; similar to *Photopectoralis bindus*, and members of *Gazza* and *Secutor*) and an orbital ridge that protrudes strongly dorsally. The four species of *Eubleekeria* can be distinguished by squamation pattern (on the cheek, chest, and predorsal region) as well as the extent of the dark blotch on the spinous portion of the dorsal-fin membrane (see Kimura et al., 2005, for diagnostic species-level features).

Karalla, new genus

Figure 6

Clade G, in part: Sparks et al. 2005.

TYPE SPECIES: *Karalla daura* (Cuvier, 1829).

OTHER INCLUDED SPECIES: *Karalla dussumieri* (Valenciennes, in Cuvier and Valenciennes, 1835).

DIAGNOSIS: Members of *Karalla* are distinguished from all other leiognathids by either the presence of a deep golden coloration on the flank or a weakly retrognathous lateral snout outline.

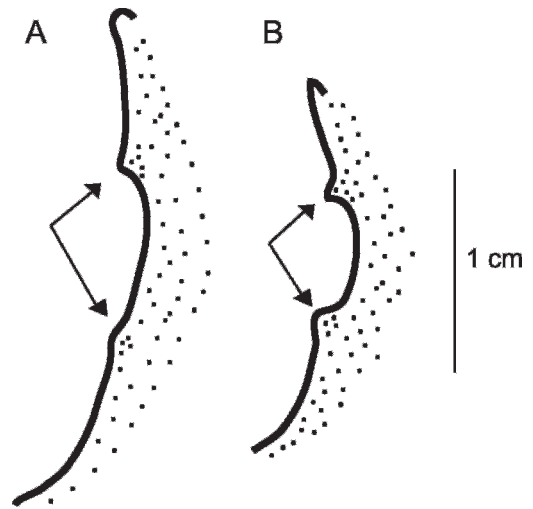


Fig. 7. Lateral view of anterodorsal margin of left cleithrum showing two pronglike protuberances as observed in (A) *Eubleekeria splendens*, CAS 56441, 95.7 mm SL, and more highly developed state in (B) *Karalla daura*, ANSP 89582, 85.1 mm SL.

ETYMOLOGY: *Karalla* is the local name for ponyfishes in Sri Lanka and the surrounding region where members of this genus commonly occur. This generic epithet is gender-neutral.

REMARKS: *Karalla* can be further distinguished from other leiognathids by the combination of a scaled nuchal region, an elongate rhomboid body, and the presence of two well-developed (vs. weak) prongs on the anterodorsal margin of the cleithrum (fig. 7). The presence of two prongs on the anterodorsal margin of the cleithrum is a synapomorphy of Leiognathidae; however, this feature is more prominent in *Karalla* than most other genera (fig. 7). Members of *Karalla* also possess a distinct golden or deep yellowish-green coloration in life that differs from the bright yellow coloration of some species of *Nuchequula*.

The relationship between *Karalla* and *Nuchequula* was unresolved in the analysis of Sparks et al. (2005; *Karalla daura* was recovered as more closely related to *Nuchequula* than to *K. dussumieri*); however, members of both genera were recovered together as a monophyletic group in that study. *Nuchequula* is recovered with strong support as the sister group to *Karalla* in the

phylogenetic analysis of Chakrabarty et al. (ms). This clade comprising *Karalla* and *Nuchequula* is in turn recovered as the sister group to *Photoplagios* (fig. 1). *Karalla* can be easily distinguished from *Nuchequula* by the absence of a prominent nuchal marking, whereas the presence of a nuchal marking is a synapomorphy of the latter genus (Chakrabarty and Sparks, 2007).

Karalla daura can easily be distinguished from all other leiognathids by the presence of enlarged fleshy lips and by the presence of a broad, golden horizontal stripe along the midline of the flank, which surrounds the entire lateral line from the orbit to the caudal peduncle, and is as deep as the arc of the lateral line vertically (fig. 6A). In contrast, *K. dussumieri* lacks a distinct golden stripe. Instead, a diffuse golden coloration is present on the flank punctuated by dark, yellow-green vermiculate lines over the dorsal half of the body. In addition, *K. daura* also possesses a large dark blotch on the spinous dorsal-fin membrane, a feature lacking in *K. dussumieri* (fig. 6B).

MATERIAL EXAMINED

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.

Equula 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. *Equula longispinis*: 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.

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*).

Eubleekeria jonesi: 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.

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; *Leiognathus striatus*: SU 22909; WHT PC-

183; WHT PC-184; WHT PC-192; WHT PC-193; WHT PC-194.

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 par*: 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.

Photopectoralis aureus: 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.

Photoplagios antongil: AMNH 236544, holotype; AMNH 236545, paratypes, 3 ex. *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. *Photoplagios moretoniensis*: QM I.1583, syntype, 1 ex.; AMS I.21700001; AMS I.22983001. *Photoplagios rivulatus*: AMNH 34850; UMMZ 182938; UMMZ 240144; UMMZ uncat. *?Photoplagios* ("*Leiognathus*") *oblonga*: MNHN A-6754, holotype. *?Photoplagios* ("*Leiognathus*") *parviceps*:

MNHN A-0580, syntype, 1 ex. *?Photoplagios* sp.: MNHN 1988-0327. *Photoplagios stercorearius*: USNM 55906, holotype; USNM 126395, cotype; ANSP 33289, paratype, 1 ex.; CAS 42171, paratype; CAS 17678; CAS-SU 20004, paratype; UMMZ 240138; UMMZ uncat.; USNM 191996; ZRC 50951.

Secutor indicus: UMMZ 240127; UMMZ uncat. *Secutor insidiator*: CAS 29894; UMMZ uncat. *Secutor megalolepis*: UMMZ 240135. *Secutor ruconius*: CAS-SU 29895; UMMZ 225240; UMMZ uncat.

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