

REDISCRPTION OF PONYFISHES (TELEOSTEI: LEIOGNATHIDAE) OF SRI LANKA AND THE STATUS OF *AURIGQUULA* FOWLER 1918

Prosanta Chakrabarty^{1*}, Thasun Amarasinghe² and John S. Sparks³

¹Museum of Natural Sciences, Louisiana State University, Baton Rouge, Louisiana, USA 70803

²146, Kendalanda, Homagama, Sri Lanka

³American Museum of Natural History, Department of Ichthyology, Central Park West at 79th St.,
New York, New York, USA 10024

Accepted 28 November 2008

ABSTRACT

The ponyfishes of Sri Lanka are redescribed from recent collections. Comparisons are made among species in a Principal Components Analysis. Sri Lanka's proximity to the type localities of many inadequately described ponyfish species makes it ideal for the rediscovery and redescription of populations consistent in features with those from the original descriptions. Many ponyfish species were described over a hundred years ago (sometimes over 200 years ago) without designation of type material and using vague and non-apomorphic features. The descriptions made here will allow for comparison with those earlier descriptions and leiognathid specimens from localities throughout their range. These comparisons may lead to the discovery of new species and to a better understanding of the relationships within the group. In addition, *Aurigequula* Fowler, 1918 is resurrected from synonymy with *Leiognathus* Lacepède, 1802 to replace a previously established invalid name. *Aurigequula* comprises, *A. fasciata* and *A. longispinis*.

Key words: Leiognathids, ponyfish, Sri Lanka, taxonomy

INTRODUCTION

Leiognathidae is represented by a high diversity of species in Sri Lanka. There are at least 13 species present representing approximately a quarter of the nominal species. There are 17 species listed in the Food and Agriculture Organization's (FAO) guide to Sri Lanka's fisheries resources (De Bruin *et al.*, 1995); however, several of these are dubious identifications, such as *Leiognathus berbis*, *Leiognathus brevirostris*, *Leiognathus smithursti*, and *Leiognathus lineolatus* (Sparks, 2006a and 2006b; Chakrabarty and Sparks, 2007). *Gazza achlamys* is the only leiognathid species currently recognized as valid that was originally described from Sri Lanka, although many have been described from nearby India. The 13 species reviewed here were collected from March 30th to April 6th of 2007. During these dates PC and TA traveled along Western and Southern Sri Lanka visiting over twenty sites ranging from large commercial fish markets to roadside vendors and individual fisherman (Fig. 1). The northern-most point visited was Kalpitiya Lagoon (08°58'44.8"N;

079°49'57.1"E), the southern-most point Matara (05°56'50.2"N, 080°32'55.3"E), and the eastern-most locality was Hambantota (06°07'27.2"N, 081°07'31.1"E). Collections from more Northeastern localities could not be made due to the current political situation, which has made travel in this region unsafe. Most of the ponyfish species collected have long established scientific names associated with them. However, a few of these names are incorrectly attributed to Sri Lankan species and reflect species from other countries; these species require new names and descriptions. Advances in our understanding of the phylogenetic relationships of ponyfishes has necessitated the description of several new generic names in order to begin to recognize a monophyletic taxonomy (Sparks *et al.*, 2005; Chakrabarty and Sparks, 2007; Kimura *et al.*, 2008; Chakrabarty and Sparks, 2008). The genus *Leiognathus*, which formally contained a majority of ponyfish species, was paraphyletic. Updated generic names are used throughout this study. The 13 species collected during this expedition are reviewed here to illustrate local variation, and in some cases these taxa may represent undescribed species.

*Corresponding author's email: prosanta@lsu.edu

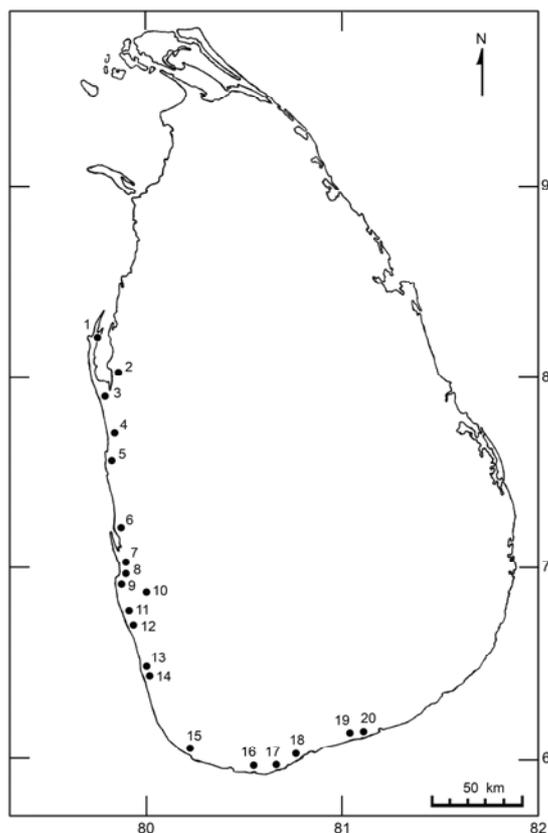


Figure 1. Map of Sri Lanka illustrating sites where collections were made. (1) Kalpitiya, (2) Puttalam, (3) Madurankuliya, (4) Arachchikattuwa, (5) Chilaw, (6) Negambo, (7) Wattala, (8) Colombo, Cargills Supermarket, (9) Colombo, St. John's Fish Market, (10) Pannipitiya, (11) Moratuwa, (12) Panadura, (13) Maggona, (14) Beruwala, (15) Galle, (16) Matara, (17) Dikwella, (18) Tangalle, (19) Hambantota, Karagan Levaya and (20) Hambantota.

MATERIALS AND METHODS

Specimens were collected in markets or directly from local fisherman. Collections or observations not reported in detail here were also made of the following fish families: Carangidae, Bagridae, Cichlidae, Clupeidae, Coryphaenidae, Engraulidae, Plotosidae, Rachycentridae,

Scombridae, Scorpaenidae, Serranidae, and various families in Elasmobranchii. Comparative materials are listed in MATERIAL EXAMINED. Morphometric measurements were recorded to the nearest 0.1 mm using dial calipers and follow Hubbs and Lagler (2004). Standard length (SL) is used throughout. 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. Materials referred to in this paper were deposited in the collection of the Wildlife Heritage Trust of Sri Lanka, now housed in the National Museum of Sri Lanka, Colombo.

For the Principal Components Analysis (PCA) of shape, digital images were taken from the left side of each specimen. Only specimens that were unbent and of adult size were used in this analysis. Landmarks (putatively homologous points on anatomical structures) were chosen in order to best represent the external shape of the body (Fig. 2). The program TPSDIG2 (Rohlf, 2006) was used to digitize the landmarks on the images. Generalized Least Squares (GLS) Procrustes superimposition was performed to remove size from the data. In the optimal superimposition, the distance minimized is the Procrustes distance, calculated as the square root of the summed squared distances between homologous landmarks (Goodall, 1991; Rohlf and Slice, 1990). This superimposition, and the PCA, was performed using PCAGEN (Sheets, 2001).

One hundred and four specimens were examined for the Principal Components Analysis, *Gazza achlamys* (n=4), *Gazza minuta* (n=7), *Leiognathus equulus* (n=11), *Leiognathus striatus* (n=5), *Photopectoralis bindus* (n=9), *Karalla daura* (n=8), *K. dussumieri* (n=12), *Aurigequula fasciata* (n=3), *Eubleekeria splendens* (n=13), *Nuchequula* sp. (n=13), *Equulites laterofenestra* (n=7), *Secutor ruconius* (n=9), *Secutor insidiator* (n=3).

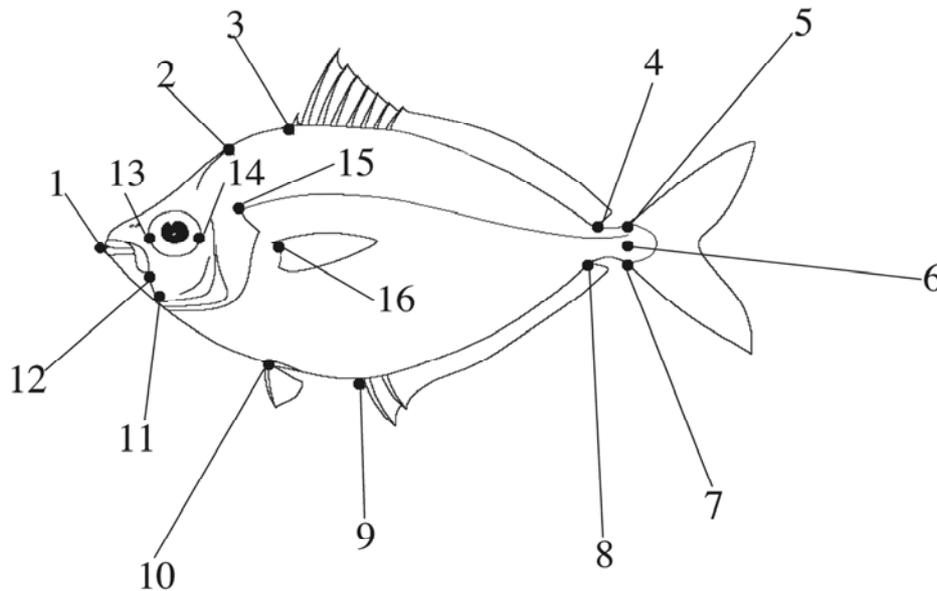


Figure 2. Landmarks used for Principal Components Analysis: (1) rostral tip of premaxilla, (2) posterior end of nuchal spine, (3) anterior insertion of dorsal fin, (4) posterior insertion of dorsal fin, (5) dorsal insertion of caudal fin, (6) midpoint of caudal border of hypural plate, (7) ventral insertion of caudal fin, (8) posterior insertion of anal fin, (9) anterior insertion of anal fin, (10) dorsal base of pelvic fin, (11) ventral end of lower jaw articulation, (12) posterior end of maxilla, (13) anterior margin through midline of orbit, (14) posterior margin through midline of orbit, (15) dorsal end of opercle, (16) dorsal base of pectoral fin. Base figure modified from Nelson (2006).

RESULTS

Morphometric measurements are presented in Tables 1A-1D. Results of the Principal Components Analysis is shown in Figure 3. The plot of PC1 versus PC2 separates *Secutor insidiator* and *S. ruconius* from all other species along PC2. The two species of *Gazza* form independent clusters from each other. *Aurigequula fasciata* and *Leiognathus striatus* also notably form independent clusters on this plot. Principal component (PC) 1 explains 42% of the variation among specimens; most of the variation along this axis is explained by body depth, particularly in the anterior portion of the body from the snout to the anal-fin origin. Principal component 1 separates shallower bodied species such as (listed here from more shallow to deeper bodied); *Equulites laterofenestra*, *Gazza minuta*, *Karalla daura*, *K. dussumieri* and *Nuchequula sp.*, from more deep-bodied species like *Secutor ruconius*, *Eubleekeria splendens*, *Photopectoralis bindus*, *Gazza achlamys*, *Aurigequula fasciata*, *Leiognathus equulus* and *L. striatus*. *Secutor insidiator* is recovered as having an intermediate position along PC1 with specimens that are both deep-bodied and a single shallow bodied specimen; this specimen (PC-145) has an

unusual body shape for a *Secutor*. Principal component 2 explains 33% of the variation among specimens; most of the variation along this axis is explained by the position of the upper and lower jaws. Principal component 2 also explains variation in the distance between the pelvic and anal fins and snout length. Principal component 2 strongly separates the species of *Secutor*, which are characterized by upturned mouths and short snouts, from the remainder of the sampled species. Most of the remaining leiognathid species overlap along PC2.

Principal component 3 explains only 6% of the variation among specimens; most of the variation along this axis is explained by overall head length and depth. Most species overlap along this axis; however, species of *Gazza* and *Secutor* form independent clusters in the plot of PC2 versus PC3 (not shown). Also notable is that *Photopectoralis bindus* forms an independent cluster on this plot separate from all other species. This species, like *Gazza*, has a mouth that protracts forward (instead of upward like *Secutor* or downward like all other Sri Lankan species collected during this expedition), but is not a large-eyed piscivore like members of that genus.

Table 1A. Morphometric measurements of species of ponyfish: *Gazza alchemys*, *G. minuta*, *Secutor ruconius* and *S. insidiator*.

	<i>Gazza alchemys</i> (n=3)	<i>G. minuta</i> (n=7)	<i>Secutor ruconius</i> (n=3)	<i>S. insidiator</i> (n=1)
Standard length (mm)	65 – 72.8	76 – 93.5	47.2 – 61	68.5
Percentage of SL				
Head length	33.7 (33.2 – 34.3)	33.4 (30.1 – 35.2)	27.9 (26.5 – 30.5)	26.9
Body Depth	50.7 (50.1 – 51.5)	40.1 (38.2 – 42.0)	58.6 (57.0 – 59.7)	47.6
Predorsal length	44.1 (41.1 – 47.4)	43.1 (36.6 – 46.3)	41.5 (38.1 – 44.6)	37.5
Preanal length	58.1 (57.2 – 59.6)	61.1 (56.8 – 64.4)	62.2 (60.7 – 63.7)	55.9
Prepelvic length	43.7 (43.5 – 43.9)	43.8 (37.6 – 48.4)	50.7 (48.3 – 53.7)	42.0
Head width (max.)	15.8 (13.6 – 17.0)	19.8 (14.1 – 35.8)	13.2 (12.5 – 14.0)	13.7
Caudal peduncle length	9.9 (9.8 – 10.1)	6.9 (5.7 – 8.4)	7.6 (7.4 – 7.9)	8.9
Caudal peduncle width	4.1 (3.4 – 5.0)	3.8 (3.1 – 4.2)	3.5 (2.6 – 4.2)	4.5
Caudal peduncle depth	6.6 (6.5 – 6.7)	5.8 (4.9 – 6.6)	6.1 (5.1 – 6.8)	5.0
Pectoral-fin length	24.0 (21.4 – 27.4)	16.0 (6.1 – 18.5)	20.5 (19.7 – 21.2)	6.9
Pelvic-fin length	17.4 (14.4 – 22.2)	12.0 (9.8 – 15.4)	6.5 (5.4 – 7.4)	8.8
Percentage of HL				
Snout length	27.4 (25.0 – 31.1)	31.6 (29.6 – 34.2)	28.2 (24.3 – 30.9)	27.7
Orbit diameter	44.0 (43.2 – 44.6)	38.1 (32.3 – 41.1)	39.1 (35.2 – 43.8)	38.0
Upper jaw length	57.3 (56.8 – 58.0)	50.5 (46.6 – 54.5)	40.1 (37.7 – 43.1)	36.4
Lower jaw length	70.5 (68.0 – 74.8)	39.6 (31.3 – 66.4)	67.0 (62.3 – 69.9)	52.7
Interorbital width	34.5 (29.0 – 40.5)	35.8 (31.3 – 41.4)	44.1 (43.2 – 45.2)	38.0

Table 1B. Morphometric measurements of species of ponyfish: *Nuchequula sp.*, *Karalla daura* and *K. dussumieri*.

	<i>Nuchequula sp.</i> (n=4)	<i>Karalla daura</i> (n=7)	<i>K. dussumieri</i> (n=7)
Standard length (mm)	68.2 – 79.5	65 – 97.8	72.3 – 101.5
Percentage of SL			
Head length	31.1 (29.6 – 32.7)	29.7 (28.1 – 31.4)	31.8 (30.3 – 33.4)
Body Depth	42.3 (41.7 – 43.1)	42.7 (39.8 – 45.5)	42.9 (41.8 – 43.8)
Predorsal length	46.5 (45.2 – 49.8)	48.0 (45.3 – 55.0)	47.8 (45.4 – 49.3)
Preanal length	56.6 (54.5 – 58.3)	53.1 (40.9 – 56.3)	57.5 (54.9 – 62.8)
Prepelvic length	38.7 (35.6 – 40.9)	42.3 (37.5 – 54.1)	38.2 (33.8 – 40.0)
Head width (max.)	14.4 (14.2 – 14.7)	15.2 (14.5 – 16.0)	17.2 (16.6 – 17.6)
Caudal peduncle length	7.9 (7.0 – 9.1)	7.9 (5.1 – 9.1)	7.9 (6.3 – 10.1)
Caudal peduncle width	3.9 (2.6 – 4.4)	3.8 (3.0 – 5.4)	4.2 (3.6 – 5.5)
Caudal peduncle depth	5.7 (5.1 – 6.1)	6.5 (5.8 – 7.4)	6.0 (5.7 – 6.8)
Pectoral-fin length	18.4 (17.4 – 19.2)	19.3 (17.3 – 21.6)	20.8 (18.0 – 22.1)
Pelvic-fin length	12.7 (11.7 – 14.1)	14.1 (10.7 – 20.1)	14.6 (10.7 – 16.5)
Percentage of HL			
Snout length	31.5 (28.5 – 33.6)	33.4 (30.5 – 36.7)	36.9 (32.9 – 39.9)
Orbit diameter	34.8 (30.8 – 37.4)	33.7 (27.3 – 38.6)	32.9 (28.3 – 35.6)
Upper jaw length	45.0 (44.4 – 45.5)	35.8 (29.6 – 43.1)	39.7 (34.6 – 44.6)
Lower jaw length	39.6 (31.6 – 57.9)	45.0 (34.0 – 53.2)	32.4 (26.2 – 47.6)
Interorbital width	32.7 (30.3 – 36.6)	35.2 (33.2 – 37.4)	30.2 (26.2 – 34.1)

Table 1C. Morphometric measurements of species of ponyfish: *Photopectoralis bindus*, *Equulites laterofenestra* and *Eubleekeria splendens*.

	<i>Photopectoralis bindus</i> (n=7)	<i>Equulites laterofenestra</i> (n=7)	<i>Eubleekeria splendens</i> (n=7)
Standard length (mm)	62.7 – 71.9	65.7 – 81.8	76.8 – 106.3
Percentage of SL			
Head length	29.2 (28.0 – 31.3)	29.5 (27.4 – 35.4)	30.0 (27.9 – 30.8)
Body Depth	56.0 (50.7 – 58.3)	36.0 (33.9 – 38.6)	51.9 (49.8 – 56.5)
Predorsal length	43.0 (38.8 – 46.1)	43.1 (39.7 – 45.2)	49.5 (46.6 – 52.9)
Preanal length	56.9 (54.4 – 59.9)	55.5 (52.4 – 60.1)	55.2 (52.3 – 57.9)
Prepelvic length	42.2 (40.8 – 43.1)	40.5 (36.5 – 58.1)	37.7 (35.7 – 39.4)
Head width (max.)	16.0 (13.1 – 28.0)	14.1 (13.4 – 14.7)	16.5 (15.1 – 18.6)
Caudal peduncle length	8.2 (6.3 – 10.0)	7.2 (6.0 – 10.1)	10.5 (6.8 – 18.3)
Caudal peduncle width	3.6 (3.0 – 4.8)	4.0 (2.9 – 4.6)	3.8 (3.2 – 4.7)
Caudal peduncle depth	6.2 (4.8 – 7.0)	5.6 (5.1 – 6.1)	7.3 (6.4 – 8.3)
Pectoral-fin length	20.3 (17.7 – 22.8)	16.9 (14.7 – 19.7)	22.5 (21.4 – 23.8)
Pelvic-fin length	10.8 (8.2 – 12.8)	11.2 (10.0 – 12.4)	13.4 (11.6 – 15.5)
Percentage of HL			
Snout length	27.1 (25.0 – 30.0)	33.2 (30.2 – 38.9)	29.4 (26.7 – 31.7)
Orbit diameter	38.4 (33.5 – 44.2)	33.4 (27.2 – 38.9)	41.1 (39.0 – 43.2)
Upper jaw length	42.8 (34.2 – 57.8)	42.8 (31.1 – 55.6)	39.4 (37.0 – 42.2)
Lower jaw length	43.8 (36.5 – 57.5)	35.1 (28.0 – 47.2)	40.0 (31.1 – 52.2)
Interorbital width	40.7 (36.0 – 47.2)	33.4 (28.0 – 38.0)	38.2 (31.1 – 47.0)

Table 1D. Morphometric measurements of species of ponyfish: *Leiognathus equulus*, *Aurigequula fasciata* and *Leiognathus striatus*.

	<i>Leiognathus equulus</i> (n=7)	<i>Aurigequula fasciata</i> (n=3)	<i>Leiognathus striatus</i> (n=3)
Standard length (mm)	92 – 128.8	112.3 – 124.6	89.5 – 173.6
Percentage of SL			
Head length	31.8 (29.8 – 34.5)	32.0 (30.9 – 33.9)	33.2 (31.9 – 35.1)
Body Depth	57.3 (53.9 – 61.8)	54.8 (53.2 – 57.1)	59.5 (57.9 – 60.7)
Predorsal length	52.5 (50.5 – 54.0)	52.1 (51.3 – 53.5)	54.1 (52.8 – 55.2)
Preanal length	58.2 (56.6 – 60.2)	57.7 (56.5 – 58.4)	59.2 (54.9 – 66.5)
Prepelvic length	43.1 (37.2 – 50.5)	42.0 (40.5 – 42.9)	39.6 (37.4 – 40.7)
Head width (max.)	16.1 (15.2 – 17.6)	15.9 (14.7 – 17.3)	18.8 (14.9 – 32.4)
Caudal peduncle length	8.3 (6.8 – 10.6)	8.0 (7.7 – 8.4)	8.3 (7.0 – 9.3)
Caudal peduncle width	4.2 (3.6 – 4.7)	4.6 (4.5 – 4.7)	4.3 (4.0 – 4.8)
Caudal peduncle depth	6.9 (6.5 – 7.1)	6.7 (6.4 – 7.1)	6.8 (6.1 – 7.3)
Pectoral-fin length	22.0 (20.1 – 24.1)	22.7 (22.5 – 22.9)	20.5 (18.7 – 21.5)
Pelvic-fin length	16.6 (15.0 – 18.1)	13.2 (12.9 – 13.4)	15.0 (12.3 – 18.1)
Percentage of HL			
Snout length	34.9 (33.3 – 37.3)	32.9 (32.0 – 34.0)	37.4 (33.0 – 41.7)
Orbit diameter	34.6 (30.0 – 37.6)	34.5 (32.9 – 35.5)	31.1 (28.6 – 33.9)
Upper jaw length	38.9 (35.0 – 41.3)	40.5 (38.4 – 43.4)	38.7 (34.6 – 42.4)
Lower jaw length	40.0 (25.7 – 60.0)	49.3 (45.0 – 51.6)	34.6 (25.8 – 50.3)
Interorbital width	36.8 (25.7 – 43.5)	34.0 (28.0 – 37.1)	31.3 (25.8 – 35.2)

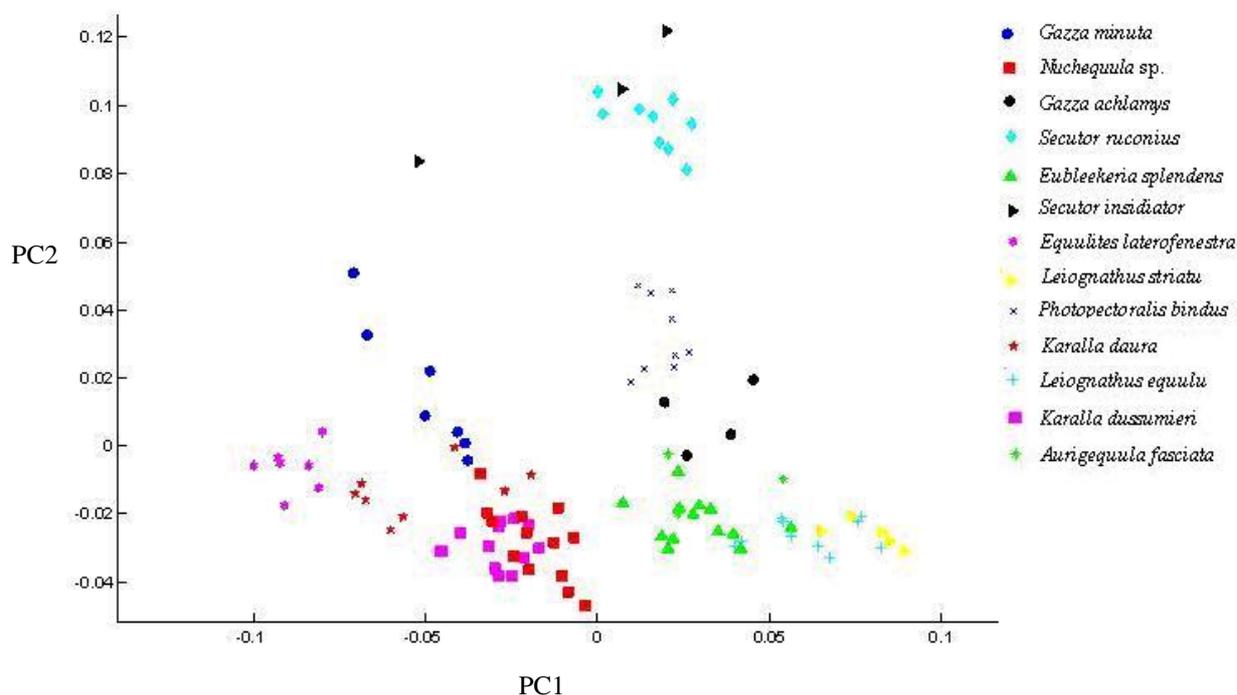


Figure 3. Results of the Principal Components Analysis. Plot of PC1 versus PC2.

KEY TO SRI LANKAN LEIOGNATHIDAE

- (1) Mouth protracts dorsally, extremely laterally compressed.....2
 (1b) Mouth protracts ventrally or anteriorly.....3
- (2) Dorsal flank pigmentation composed of about 10 vertical bars.....*Secutor ruconius*
 (2b) Dorsal flank pigmentation composed of large spots and dashes.....*Secutor insidiator*
- (3) Mouth with large caniniform teeth.....4
 (3b) Mouth with small, inconspicuous teeth.....5
- (4) Elongate to rhomoid shaped (BD < 47 % of SL).....*Gazza minuta*
 (4b) Deep bodied (BD > 50% of SL).....*Gazza achlamys*
- (5) Deep bodied (BD > 50% of SL).....9
 (5b) Elongate bodied (BD < 45 % of SL).....6
- (6) Large lips, prominent black markings on dorsal fin.....*Karalla daura*
 (6b) No black markings on dorsal fin.....7
- (7) Greenish-yellow tint to body with dark vertical vermiculate lines present
 on the dorsal flank*Karalla dussumieri*
 (7b) No prominent vermiculate lines or greenish pigmentation.....8
- (8) Prominent black nuchal marking.....*Nuchequula sp.*
 (8b) Body silvery-white, males with a large trapezium or cornucopia
 shaped translucent patch.....*Equulites laterofenestra*

- (9) Large adult body size (typically reaching >120 mm SL).....10
 (9b) Small adult body size (typically less than 100 mm SL).....12
- (10) No broad yellow markings on dorsal flank.....*Leiognathus equulus*
 (10b) Prominent yellow vertical lines present on dorsal flank, markedly
 long dorsal fin spine.....11
- (11) Large nuchal hump, broad unbroken yellow bands on dorsal flank.....*L. striatus*
 (11b) Broad yellow bands become rounded dashes along the
 midline.....*Aurigequula fasciata*
- (12) Dorsal-fin membrane with bright orange pigmentation.....*Photopectoralis bindus*
 (12b) Dorsal-fin membrane with black pigmentation, lateral line scales yellow-
 orange.....*Equulites splendens*

SYSTEMATIC ACCOUNTS

Aurigequula Fowler, 1918

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

Equula Cuvier, 1815 (incorrectly raised from synonymy by Chakrabarty and Sparks, 2008)

Type Species: *Clupea fasciata* Lacepède, 1803=
Aurigequula fasciata (Lacepède, 1803)

Other Includes Species: *Aurigequula longispinis* (Valenciennes, in Cuvier and Valenciennes, 1835)

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

Remarks: For additional comments on this genus see description of *Equula* in Chakrabarty and Sparks (2008). The authors incorrectly assigned the wrong type species to *Leiognathus*. The correct type species is *Leiognathus argenteus* Lacepède 1802 (see Eschmeyer, 2008; Sparks and Dunlap, 2004). The same specimen was used to describe the type species of both *Equula* and *Leiognathus*, making these genera objective synonyms and identical. Therefore, we resurrect *Aurigequula* Fowler, 1918 from synonymy with *Leiognathus*. *Aurigequula* was established by Fowler (1918) as a subgenus for *Leiognathus fasciatus*, the type species by monotypy. Whitley (1932) raised *Aurigequula* to a genus and added *A. longispinis*. James (1975) later listed this genus in synonymy with *Leiognathus* (Sparks, 2006b). Here *Aurigequula* is resurrected, and comprises the two species that we recover as sister taxa in our phylogenetic

analyses and that comprised this genus according to Whitley (1932), *A. fasciata* and *A. longispinis*.

Aurigequula fasciata (Lacepède, 1803)

Description: *Aurigequula fasciata* is a large, robust, and deep-bodied ponyfish. The dorsal and ventral profiles are equally convex. This species has a forward pointing mouth that opens strongly downward when protracted. The lower jaw profile is slightly concave. The mouth can extend about 15-20% of the SL. The greatest body depth is reached at the vertical from the dorsal-fin origin to the pelvic-fin origin. The dorsal- and pelvic-fin origins are located along the same vertical. The anal-fin origin is at a vertical with the first or second dorsal fin-ray. The dorsal head profile is strongly concave with a large hump in the nuchal region. There is strong concavity dorsal to the orbit formed by this hump and the slightly convex dorsal profile in the region extends from the mouth to the area dorsal to the orbit. The dorsal ridge of the orbit never reaches the dorsal head outline. The lips are somewhat fleshy but thin. The posterior margin of the maxilla is exposed and reaches the vertical through the anterior margin of the pupil. The teeth are small and villiform. The lateral line is complete and includes about 50 to 60 scales. The chest is asquamate; the entire triangular region between the margin of the opercle, the pectoral fin base, and the posterior margin of the pelvic fin is asquamate. The remainder of the body is scaled except the head. The nuchal region is fully scaled except along the dorsal-most margin. There is a large axillary scale on both the pelvic and anal fins. The second dorsal-fin spine is twice to nearly three times longer than the third. The second dorsal fin-spine is

about 70-90% of the BD. The second anal-fin spine is elongate, but not remarkably so relative to the third, (about 30-60% longer), and is between 20-50% of the BD.

Pigmentation: The entire body is silvery. The head and asquamate chest region are silvery-white. The fin-spines are silvery. There is a light yellow tint to the membrane of all fins, particularly the membrane between the anal-fin rays. There is little coloration in the caudal fin. Their dorsal flank has a pigmentation pattern of 10-15 broad yellow vertical lines that extend slightly ventral to the lateral line. Ventral to the lateral line and near the midline of the flank, the lines break into broad rounded dashes. The pectoral-fin axil and the base of the pectoral fin have a strong yellow coloration. The pelvic fins are white. The large axillary scales on the pelvic and anal fins are silvery-white. There is a concentration of melanophores on the snout dorsal to the lips.

Remarks: *Aurigequula fasciata* is not common, it was found only at Galle beach (SRI-15-2007) and there were only three individuals found. This species can reach up to 21 cm in length (De Bruin *et al.*, 1995) and the largest individual collected measured 125 mm SL. The local name, *wali*, refers to the long spine on the dorsal fin of this species.

Secutor insidiator (Bloch, 1797)

Description: *Secutor insidiator* is a strongly laterally compressed ponyfish. The body depth ranges from somewhat elongate to quite deep-bodied. The ventral profile is much more convex than the dorsal. It has an upwardly turned mouth and the lower jaw is straight and nearly vertical; the lower jaw profile is at a right angle with the remainder of the body. The mouth can extend about 15-20% of the SL. The snout is very short. The greatest body depth is reached at the vertical from the dorsal-fin origin to the pelvic-fin origin. The dorsal- and pelvic-fin origins are located along the same vertical. The pelvic fins are very short. The anal-fin origin is at a vertical with the last dorsal-fin spine. There is a slight concavity at the orbit preceding an elevation to the dorsal-fin origin. The lips are thin and not fleshy. The posterior margin of the maxilla is exposed, reaching a vertical through the anterior part of the orbit. The teeth are small and villiform. The lateral line is incomplete, extending from the posterior margin of the opercle and terminating anterior to the caudal

peduncle. The lateral line includes about 40 scales. The eyes are small (about 35% of SL). There is a strong concavity dorsal to the orbit, formed by the exposed rising dorsal aspect of the supraoccipital crest (*i.e.*, nuchal spine) which extends from dorsal to the orbit to the dorsal-fin origin. There are no scales on the chest or nuchal region and most of the remainder of the body appears asquamate as well, although scales in this region may be highly deciduous and lost in preservation.

Pigmentation: The entire body is silvery. The membrane of the spinous region of the dorsal fin is black from about 1/4 the length of the second dorsal-fin spine to the distal margin of the fin. There are dark vertical markings comprising incomplete circular bands and vertical dash-like objects. There are clear regions between these circles and dashes. There is a dark stripe of melanophores at the midline of the flank. There is a black region in the posterior margin of the lower jaw and ventral to the orbit. There is a black line of concentrated melanophores extending from the pectoral-fin axil to about the posterior margin of the pelvic fin. The second and third dorsal- and anal-fin spines are about the same length. The second dorsal-fin spine is about 35% of the BD and the second anal-fin spine about 25% of the BD.

Remarks: *Secutor insidiator* was collected at only two sites and there were far fewer individuals at those sites relative to *S. ruconius*. This species is more elongate than its congener and has a flank pattern of circular bands and vertical dash-like objects that are separated by pigment-less regions. These circular bands and vertical dash-like objects are less frequently separated by pigment-less regions in *Secutor ruconius*, creating an appearance of longer vertical lines on the flank. *Secutor insidiator* can reach up to 11cm in length (De Bruin *et al.*, 1995); the largest collected in this study was 69 mm SL. The local name *kasi peththa* refers to the perceived coin shaped body of this species.

Secutor ruconius (Hamilton-Buchanan, 1822)

Description: *Secutor ruconius* is a strongly laterally compressed and deep-bodied ponyfish. The ventral profile is much more convex than the dorsal. It has an upwardly turned mouth and the lower jaw is straight and nearly vertical; it is at a right angle with the remainder of the body. The mouth can extend about 15-20% of the SL. The snout is very short. The greatest body depth

is reached at the vertical from the dorsal-fin origin to the pelvic-fin origin. The dorsal- and pelvic-fin origins are located along the same vertical. The pelvic fins are very short. The anal-fin origin is at a vertical with the first dorsal-fin ray. There is a very strong concavity at the orbit preceding a rise in the dorsal profile of the head to the dorsal-fin origin. The anterior half of the body up to the vertical through the dorsal-fin origin, is nearly circular. The lips are thin and not fleshy. The posterior margin of the maxilla is exposed, and is directly anterior to the orbit. The teeth are small and villiform. The lateral line is incomplete, extending from the posterior margin of the opercle and terminating anterior to the caudal peduncle. The lateral line includes about 30 to 40 scales. The eyes are small. There are no scales on the chest or nuchal region and most of the remainder of the body appears asquamate as well, although scales in these regions may be highly deciduous in preservation. The second dorsal- and anal-fin spines are slightly (20-40%) longer than the third spines. The second dorsal-fin spines are about 30-40% of the BD, and the second anal-fin spine about 10-20% of the BD.

Pigmentation: The entire body is silvery. The membrane of the spinous region of the dorsal fin has concentrated melanophores from about 1/4 the length of the second dorsal spine to the distal margin of the fin. There are dark vertical markings comprising incomplete circular bands and vertical dash-like objects, these markings are connected forming about 10 vertical bars (versus unconnected circular bands and dashes in *Secutor insidiator*). This dorsal pattern is more lightly pigmented than the black of *S. insidiator*. The dorsal pattern is a greenish yellow. There is a black region in the posterior margin of the lower jaw and ventral to the orbit. There is a black line of concentrated melanophores extending from the pectoral-fin axil to about the posterior margin of the pelvic fin. The base of the dorsal fin has a strong silvery guanine line.

Remarks: This species was collected at three sites and also observed at two others, and was common at those sites. This species is deeper bodied than its congener and has a flank pattern composed of vertical lines made up of interconnected circular and vertical dash-like objects that are not separated by unpigmented regions and that is more lightly pigmented. This species can reach up to 8 cm in length (De Bruin *et al.*, 1995); the largest collected in this study was 61 mm SL. The local name *kasi peththa* refers to the perceived coin shaped body of this species.

The taxonomic history of this species is complicated. The Catalog of Fishes (Eschmeyer, 2008) currently recognizes this species as valid. No types exist and some refute whether the original description refers to a member of *Secutor* (Mochizuki and Hayashi, 1989). This genus requires a revision to sort out problematic taxa that is beyond the scope of this publication.

Gazza minuta (Bloch, 1797)

Description: *Gazza minuta* is a rhomboid-shaped and robust (*i.e.*, not laterally compressed) ponyfish with a large head. The dorsal and ventral profiles are equally convex. The mouth protracts forward and can extend about 15-20% of the SL. The lower jaw profile is straight. The snout is short. The greatest body depth is reached at the vertical from the dorsal-fin origin to the pelvic-fin origin. The pelvic-fin origin is slightly anterior to the dorsal. The anal-fin origin is at a vertical from the last dorsal-fin spine. The dorsal head profile is straight. The lips are somewhat fleshy. The posterior margin of the maxilla is exposed and reaches the vertical through the anterior margin of the pupil. The most anterior teeth are large and caniniform. The lateral line is complete and includes about 45 scales. The eyes are large. There are no scales on the chest or nuchal region and most of the remainder of the body appears scaled except the head. The dorsal- and anal-fin spines are weak.

Pigmentation: The body is silvery-white. The pelvic-fin spine is silvery. The membrane of the spinous region of the dorsal fin has scattered melanophores, which extend from about 1/4 the length of the second dorsal-fin spine to its distal margin. There is no obvious dorsal flank pigmentation pattern. There is a black region along the posterior margin of the lower jaw in some specimens. The pectoral-fin axil is black and the pectoral fin is yellowish. The dorsal and anal-fin membranes are yellowish. The pelvic-fin axillary scale is large and silvery.

Remarks: This species was collected at four of the 20 sites (and observed at two others) and was relatively abundant. *Gazza minuta* is not as deep bodied as its local congener. *Gazza minuta* can reach up to 14 cm in length (De Bruin *et al.*, 1995); the largest individual from this collection measured 94 mm SL. The common local name of this species is *dath karralla* referring to its large teeth. The second and third dorsal- and anal-fin spines are about equal length and the first spines are greatly reduced in length.

Gazza achlamys Jordan and Starks, 1917

Description: *Gazza achlamys* is a somewhat laterally compressed and deep-bodied ponyfish with a large head. The dorsal and ventral profiles are about equally convex. The lower jaw profile is concave. The mouth can extend about 15-20% of the SL and it protracts forward. The snout is short. The greatest body depth is reached at the vertical from the dorsal-fin origin to the pelvic-fin origin. The dorsal- and pelvic-fin origins are located along the same vertical. The anal-fin origin is at a vertical from the last dorsal-fin spine. The dorsal head profile is straight. The lips are thin and not fleshy. The posterior margin of the maxilla is exposed and reaches the vertical through the anterior margin of the pupil. The anterior-most teeth are large and caniniform. The lateral line is complete and includes about 40 to 45 scales. The eyes are large. There are no scales on the chest or nuchal region and most of the remainder of the body appears scaled except the head.

Pigmentation: The entire body is silvery. The membrane of the spinous region of the dorsal fin has concentrated melanophores, from about 1/4 the length of the second dorsal spine to its distal margin. There is no obvious dorsal flank pigmentation pattern. There is a black region along the posterior margin of the lower jaw in some specimens. The pectoral-fin axil is black. The anal-fin spines are yellowish, and the membrane of the fin is clear. The pelvic-fin axillary scale is large and silvery. The dorsal- and anal-fin spines are weak. The second and third dorsal- and anal-fin spines are about equal length and the first spines are greatly reduced in length. The second dorsal-fin spine is about 40-50% of the body depth whereas the second-anal fin spine is about 35-40% of the BD.

Remarks: This species was found at only two sites and was common only at Beruwala-Maggon (SRI-12). *Gazza achlamys* is more deeper bodied than *G. minuta*. *Gazza achlamys* can reach up to 17 cm in length (De Bruin *et al.*, 1995). The common local name of this fish is *dath karralla* referring to its large teeth.

Eubleekeria splendens (Cuvier, 1829)

Description: *Eubleekeria splendens* is a robust and deep-bodied ponyfish. The dorsal and ventral profiles are equally convex (the ventral profile is more convex in smaller individuals). The snout is short. The mouth opens slightly

downward when protracted. The lower jaw profile is straight. The mouth can extend about 8-15% of the SL. The greatest body depth is reached at the vertical from the dorsal-fin origin to the pelvic-fin origin. The dorsal- and pelvic-fin origins are located along the same vertical. The anal-fin origin is at a vertical with the last dorsal-fin spine. There is a slight concavity at the orbit preceding a slight rise in the dorsal head profile to the dorsal-fin origin. The dorsal head profile is slightly convex. The eyes are large and the dorsal ridge of the orbit may extend to the dorsal head outline (more so in smaller individuals). The lips are thin and not fleshy. The posterior margin of the maxilla is exposed, reaching between the verticals of the anterior margin of the orbit and the pupil. The teeth are small and villiform. The lateral line is complete and includes about 40 scales. The chest is fully scaled; the nuchal region is scaled except along the dorsal margin. Most of the remainder of the body is scaled except the head.

Pigmentation: The entire body is a silvery-white, particularly ventral to the midline of the flank. The membrane of the spinous region of the dorsal fin has scattered melanophores from about 1/2 the length of the second dorsal-fin spine to its distal margin. In some individuals this region appears black but in others there is only a light scattering of melanophores except for the distal margin. Their dorsal flank has a pigmentation pattern of dark vertical vermiculate lines that form zigzags (or curves). There is a thin silvery line at the midline, which is sometimes dashed. The pectoral-fin axil is black. There is a strong yellow-orange tint to the lateral line scales, particularly in larger individuals. There is a slight yellow tint to the caudal, dorsal, anal and pectoral fins, which fades soon after death. The pelvic fins are white. There is a black marking on the snout dorsal to the lip. The second and third dorsal- and anal-fin spines are about the same length (second spine about 10% of the BD), whereas the first spines are greatly reduced in length. The second dorsal-fin spine is about 30% of the BD.

Remarks: *Eubleekeria splendens* was abundant at all four sites (out of 20 total sites) where it was found. Large individuals were purchased at the commercial St. John's Market (SRI-2-2007). The collections from Waddala (SRI-10-2007) exhibited much more black in the dorsal-fin membrane than individuals from the other collections. This species can reach up to 14cm in length (De Bruin *et al.*, 1995); the largest individual from this collection measured 106

mm SL. The local name *mas karralla* refers to the perceived fleshy body of this species.

Karalla daura (Cuvier, 1829)

Description: *Karalla daura* is a rhomboid-shaped and robust ponyfish. The dorsal and ventral profiles are equally convex. This species has a shallow head with a somewhat pointed snout. It has a forward pointing mouth that opens strongly downward when protracted. The lower jaw profile is straight. The mouth can extend about 10-15% of the SL. The greatest body depth is reached at the vertical from the dorsal-fin origin to the pelvic-fin origin. The pelvic-fin origin is located slightly anterior to the vertical through the dorsal-fin origin. The anal-fin origin is at a vertical with the last dorsal-fin spine. The dorsal head profile is straight. The eyes are relatively small and the dorsal ridge of the orbit does not protrude dorsally. The lips are fleshy and the largest of any species in the family. The posterior margin of the maxilla is exposed, reaching a vertical through the anterior margin of the orbit. The teeth are small and villiform. Due to the expanded lips, the teeth are not exposed. The lateral line is complete and includes about 30-40 scales. The nuchal region is scaled, but the chest and head are asquamate; most of the remainder of the body is scaled.

Pigmentation: The entire body is silvery except for a broad golden-yellow horizontal band extending from the orbit (including the dorsal half of the eye), across the lateral line, and terminating on the caudal peduncle. The dorsal 1/2 of the membrane of the spinous dorsal fin is black. The spines of the dorsal fin are silvery. The membrane and spines of the anal fin are yellow. The pelvic-fin spine is silvery. The pectoral-fin axil is black. The distal margins of the anterior and posterior lobes of the caudal fin are yellow. The dorsal flank has a faint pigmentation pattern of thin vermiculate lines. There is a black region on the snout dorsal to the mouth. The second and third dorsal- and anal-fin spines are about the same length whereas the first spines are greatly reduced in length. The second dorsal-fin spine is about 50% of the BD.

Remarks: This species is common, but not abundant and was found at six locations. It is a popular food fish and was often found in the local supermarkets. This species can reach up to 14 cm in length (De Bruin *et al.*, 1995) and the largest individual in this study measured 98 mm

SL. The local name *thel karalla* refers to the perceived "oily" properties of this species.

Karalla dussumieri (Valenciennes, 1835)

Description: *Karalla dussumieri* is an elongate and robust ponyfish. The dorsal and ventral profiles are equally convex. This species has a pointed snout and the upper jaw extends rostral to the lower. It has a mouth that opens strongly downward when protracted. The lower jaw profile is straight. The mouth can extend about 10-15% of the SL. The greatest body depth is reached at the vertical from the dorsal-fin origin to the pelvic-fin origin. The dorsal- and pelvic-fin origins are located along the same vertical. The anal-fin origin is at a vertical with the last dorsal-fin spine. The dorsal head profile is straight. The eyes are not large. The lips are somewhat fleshy. The posterior margin of the maxilla is exposed and extends to the vertical of the anterior margin of the pupil. The teeth are small and villiform. The lateral line is complete and includes about 50 scales. The chest and nuchal region are fully scaled as is most of the remainder of the body except the head.

Pigmentation: The entire body is silvery with a greenish-yellow tint to the dorsal flank and dorsal portion of the head and particularly ventral to the midline of the flank (see Fig. 4G). Often ventral to the pectoral fin at a diagonal angled towards the midpoint of the pelvic fin is a yellow outlined band of concentrated chromatophores. A similar band is present in species of *Nuchequula*. The membrane of the spinous region of the dorsal and the anal fins are a light yellow. There are some lightly scattered melanophores in the membrane of the dorsal fin. The spines of the dorsal fin are silvery. Their dorsal flank has a pigmentation pattern of dark vertical vermiculate lines that form zigzags and that can be slightly curved. These lines extend slightly ventral to the lateral line. There is a thin silvery line, sometimes dashed, at the midline of the flank. The pectoral-fin axil is black. Occasionally there is a strong greenish-yellow tint to the lateral-line scales. There is a black region on the snout dorsal to the mouth. The second and third dorsal- and anal-fin spines are about the same length whereas the first spines are greatly reduced in length. The second dorsal-fin spine is about 45% of the BD and the second anal-fin spine is about 35% of the BD.

Remarks: This species is very common and was abundant at many sites. It is perhaps the most

popular food fish sold at markets. *Karalla dussumieri* can reach up to 14cm in length (De Bruin *et al.*, 1995). The local name *katu karalla*

refers to the perceived “spiny” (*i.e.*, boney) properties of this species relative to other ponyfish.

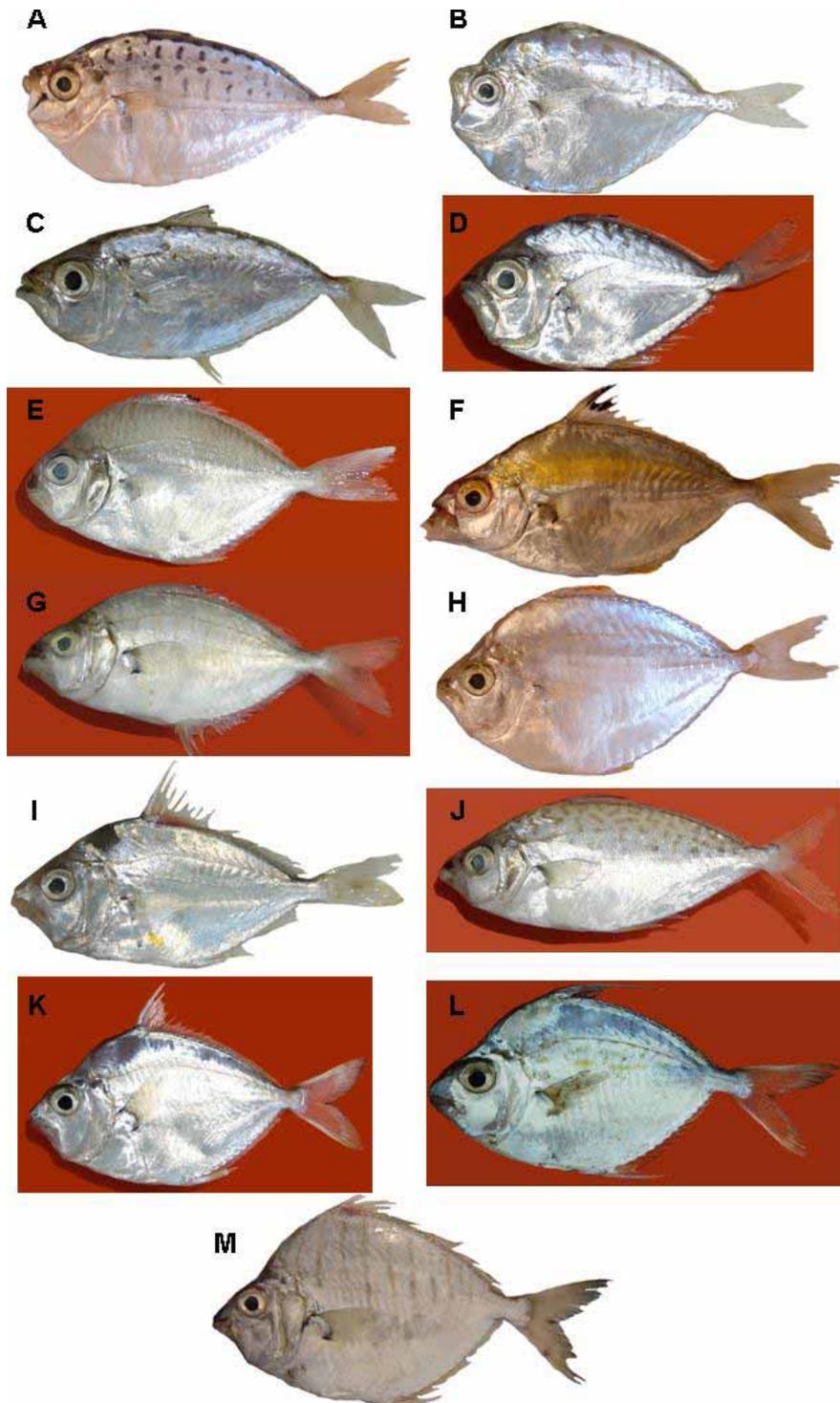


Figure 4. Leionathid species from Sri Lanka: (A) *Secutor insidiator*, (B) *Secutor ruconius*, (C) *Gazza minuta*, (D) *Gazza achlamys*, (E) *Eubleekeria splendens*, (F) *Karalla daura*, (G) *Karalla dussumieri*, (H) *Photopectoralis bindus*, (I) *Nuchequula* sp., (J) *Equulites laterofenestra*, (K) *Leiognathus equulus*, (L) *Aurigequula fasciata*, (M) *Leiognathus striatus*.

Photopectoralis bindus (Valenciennes, 1835)

Description: *Photopectoralis bindus* is a deep-bodied and relatively laterally compressed ponyfish. The ventral profile is more convex than the dorsal. This species has a short snout. The mouth extends forward when protracted about 10-15% of the body length. The lower jaw profile is straight. The greatest body depth is reached at the vertical from the dorsal-fin origin to the pelvic-fin origin. The dorsal- and pelvic-fin origins are located along the same vertical. The anal-fin origin is at a vertical with the last dorsal-fin spine. The dorsal head profile is straight. The eyes are not large. The lips are thin and not fleshy. The posterior margin of the maxilla is exposed and reaches the vertical through the anterior margin of the orbit. The teeth are small and villiform. The lateral line is complete and includes about 50 scales. The chest and nuchal region are asquamate; the remainder of the body is scaled except the head. The second and third dorsal- and anal-fin spines are about the same length whereas the first spines are greatly reduced in length.

Pigmentation: The entire body is silvery-white with some yellowish pigment on the head. In males with a flank patch, the region behind the pectoral fin is translucent whereas in females it is covered in silvery-white guanine as is the remainder of the body. The pectoral-fin axil is yellow with some melanophores. There is a strong concentration of melanophores on the snout dorsal to the mouth. The dorsal 1/2 of the spinous dorsal-fin membrane is bright orange. The region ventral to the orange pigment is lined with melanophores. The dorsal-fin spines are silvery. There is some light yellow pigment on the caudal, pectoral and anal fins. There is less guanine on the dorsal part of the body than ventrally, with a concentration at the midline of the flank. The midline of the flank is more silvery than the areas dorsal and ventral and in some specimens there are black horizontal dashes along the midline of the flank. The dorsal flank pigmentation pattern comprises semi-circle markings sometimes forming full circles or oval shapes. These markings are dark yellow in color. The second and third dorsal- and anal-fin spines are about the same length, the first spines are greatly reduced in length, the second dorsal-fin spine is 35-40% of the BD. The second anal-fin spine is about 20-25% of the BD.

Remarks: This is the only member of *Photopectoralis* collected. This species was collected at only two sites, although it was

somewhat abundant at Galle beach (SRI-15-2007). This species can reach up to 11cm in length (De Bruin *et al.*, 1995); the largest individual collected in this study measured 72 mm SL. *Photopectoralis bindus* collected by PC and JSS in Taiwan and Thailand differed in the size of their translucent light organ patch, body depth and dorsal pigmentation pattern; these populations may represent distinct species. The Sri Lankan populations may represent the species as it was described by Cuvier, because of its proximity to the type locality. The translucent window near the pectoral-fin axil is completely covered by the pectoral fin when the fin is adpressed. There is no translucent patch in females. The local name, *handa pana*, refers to the strong concentration of melanophores on the snout.

Nuchequula sp.

Description: *Nuchequula* sp. is a medium sized, elongate and somewhat laterally compressed ponyfish. The ventral profile is slightly more convex than the dorsal. This species has a pointed snout. The mouth extends forward when protracted about 15-20% of the body length. The lower jaw profile is strongly convex. The greatest body depth is reached at the vertical from the dorsal-fin origin to the pelvic-fin origin. The pelvic-fin origin is slightly anterior to the vertical through the dorsal-fin origin. The anal-fin origin is at a vertical with the last dorsal-fin spine. The dorsal-fin spines are weak. The dorsal head profile is nearly straight with a slight concavity dorsal to the orbit. The lips are thin and not fleshy. The posterior margin of the maxilla is exposed and extends to the vertical through the anterior part of the orbit. The teeth are small and villiform. The lateral line is complete and includes about 50 scales. The chest and nuchal region are asquamate (although nuchal scales are occasionally present), whereas the remainder of the body is scaled except the head.

Pigmentation: The entire body is silvery-white ventral to the midline of the flank and silvery to bluish gray dorsal to the midline of the flank and on the head. There is a concentration of melanophores dorsal to the mouth. There is some yellow pigment on the anal and pectoral fins. There is yellow pigment on the membrane on the distal half of the spinous dorsal and anal fins. The dark grey nuchal spot is large, rounded, and occasionally triangular. There is often a round translucent region near the center. There is

a yellowish diagonal marking between the pectoral fin and pelvic fin, which is spotted with concentrated melanophores. The second dorsal- and anal-fin spines are slightly (20%-30%) longer than the third spines. The second dorsal-fin spine is about 50-60% of the BD. The second anal-fin spine is about 40% of the BD.

Remarks: This species was collected at five sites but was not abundant at any. *Nuchequula* was elevated to generic rank by Chakrabarty and Sparks (2007) and includes all ponyfish species with a dark nuchal marking. This species is often identified as *Leiognathus brevirostris* (De Bruin *et al.*, 1995); however, the holotype of *Leiognathus brevirostris* is a deep-bodied specimen of *Photoplagios bindus* that does not resemble this *Nuchequula* species (Chakrabarty and Sparks, 2007).

Kimura *et al.* (2008b) recognized several new *Nuchequula* species. Among these, *Nuchequula gerreoides* (Bleeker, 1851) is given a distribution that includes Sri Lanka. Unfortunately we are unable to link the Sri Lankan specimens we collected with any described *Nuchequula* species.

Equulites laterofenestra Sparks and Chakrabarty, 2007

Description: *Equulites laterofenestra* is a medium sized and elongate ponyfish. The ventral profile is slightly more convex than the dorsal. This species has a pointed snout. The mouth extends forward when protracted about 7-15% of the body length. The lower jaw profile is straight. The greatest body depth is reached at the vertical from the dorsal-fin origin to the pelvic-fin origin. The pelvic-fin origin is slightly anterior to the vertical through the dorsal-fin origin. The anal-fin origin is at a vertical with the last dorsal-fin spine. The dorsal head profile is straight. The lips are thin and not fleshy. The posterior margin of the maxilla is exposed and reaches the vertical through the anterior part of the pupil. The teeth are small and villiform. The chest and head are asquamate the remainder of the body (including the nuchal area) is scaled. In males, a translucent patch is present; translucent scales occur in the region of the patch.

Pigmentation: The entire body is silvery-white. The dorsal flank has less guanine than present ventrally, and appears clear when viewed dorsally. The flank pigmentation pattern is comprised of dark, relatively broad, lines (not

vermiculate) that sometimes form open circular patterns. Along the midline of the flank, there is a translucent row of five to seven oval patches (in both males and females). There is a concentration of melanophores dorsal to the mouth. There is some yellow pigment on the anal-fin membrane and the spinous dorsal and caudal fins. The pectoral fin is yellowish with some silver on the pelvic spines. The male flank patch is a four-sided trapezium (quadrilateral) or cornucopia that extends from the base of the pectoral fin to the midpoint of the body (Fig. 5). It is similar to the patch in *Equulites leuciscus*, but more rectangular or rounded rather than triangular. The second dorsal- and anal-fin spines are slightly (15%-30%) longer than the third spines. The second dorsal- and anal-fin spines are about 40-45% of the BD.

Remarks: Although only one male was collected female specimens of this species were common. This unequal sex ratio may be explained by females forming and being captured in large groups while males were not, but it may also be explained by an unequal number of males being born relative to females. Neither explanation is acceptable without further biological investigation.

Leiognathus equulus (Forsskål, 1775)

Description: *Leiognathus equulus* is a large, robust, and rhomboid shaped ponyfish. The dorsal and ventral profiles are equally convex. This species has a forward pointing mouth that opens strongly downward when protracted. The lower jaw profile is concave. The mouth can extend about 15% of the SL. The greatest body depth is reached at the vertical from the dorsal-fin origin to the pelvic-fin origin. The dorsal- and pelvic-fin origins are located along the same vertical. The anal-fin origin is at a vertical with the first dorsal-fin ray. The dorsal head profile is straight with a slight hump in the nuchal region. The dorsal ridge of the orbit never reaches the dorsal head outline. The lips are somewhat fleshy but thin. The posterior margin of the maxilla is exposed and extends between the verticals of the anterior part of the orbit and the pupil. The teeth are small and villiform. The lateral line is complete and includes about 50 to 60 scales. The chest is asquamate; the entire triangular region between the margin of the opercle, the pectoral-fin base, and the posterior margin of the pelvic fin is asquamate. Most of the remainder of the body is scaled except the head. The nuchal region is asquamate along the

dorsal margin. The asquamate region broadens near the posterior margin of the nuchal spine in a characteristic curve (Fig. 6). There is a large axillary scale on the pelvic and anal fins, within which the spines can be retracted. The second dorsal- and anal-fin spines are elongate relative to the third, but not dramatically so.

Pigmentation: The entire body is silvery with a yellowish tint to most of the body posterior to the head. The head and asquamate chest are silvery-white. The dorsal-fin spines are silvery. There dorsal flank has a pigmentation pattern of light but relatively broad vertical lines that extend to about the midline of the flank. The pectoral-fin axil is black, but there is no pigment at the base of the pectoral fin. There is a yellow

tint to the lateral line scales. There is a strong yellow tint to the fins, particularly the anal fin, which can be orange in color. The caudal fin is yellowish throughout. The pelvic fins are white. There is a concentration of melanophores on the snout dorsal to the lip. The large axillary scales on the pelvic and anal fins are silvery. There is a strong concentration of guanine on the head and asquamate region on the dorsal margin of the nuchal region, creating a solid, smooth, armor plate-like appearance. The second dorsal-fin spine is about 50% longer than the third and is about 40% of the BD. The second anal-fin spine is also about 40% of the BD. The first spine in both the dorsal and anal fins are greatly reduced in length.



Figure 5. Translucent flank patch in *Equulites laterofenestra* males.



Figure 6. Asquamate region in: (A) *Leiognathus equulus*, (B) *Aurigequula fasciata* and (C) *Leiognathus striatus*.

Remarks: *Leiognathus equulus* was found only at four sites and large individuals were rare. This species can reach up to 24 cm in length (De Bruin *et al.*, 1995) and the largest individual collected in this study measured 129 mm SL. *Leiognathus equulus* was abundant only at Moratuwa (SRI-20-2007) where local fisherman commonly caught juveniles in the brackish waters. Individuals larger than 100 mm SL are rarely found in these waters. *Leiognathus equulus* is the type species of *Leiognathus*. This species can be distinguished from the other large leiognathid species like *Aurigequula fasciata* and *Leiognathus striatus* by shorter second dorsal- and anal-fin spines, an asquamate scale nuchal region, a more straight dorsal head profile, and pigmentation pattern. The local name, *mas karalla*, refers to the fleshy body of this species.

Leiognathus striatus James and Badrudeen 1990

Description: *Leiognathus striatus* is a large, robust, and very deep-bodied ponyfish superficially resembling *Aurigequula fasciata*. The dorsal profile is much more convex than the ventral profile. This species has a forward pointing mouth that opens downward when protracted. The lower jaw profile is concave. The mouth can extend about 10-15% of the SL. The greatest body depth is reached at the vertical from the dorsal-fin origin to the pelvic-fin origin. The dorsal- and pelvic-fin origins are located along the same vertical. The anal-fin origin is at a vertical with the first or second dorsal-fin ray. The anterior tip of the snout is blunt and squared-off. The dorsal head profile slopes upward anterior to the orbit where the dorsal ridge of the orbit reaches the dorsal head outline and slopes steeply dorsally with a very large hump to the dorsal-fin origin. The lips are somewhat fleshy but thin. The posterior margin of the maxilla is exposed and reaches the vertical through the anterior margin of the orbit. The teeth are small and villiform. The lateral line is complete and includes about 50 to 60 scales. The chest is asquamate; the entire triangular region between the margin of the opercle, the pectoral-fin base, and the midpoint of the pelvic fin is asquamate. The remainder of the body is scaled except the head. The nuchal region asquamate over a large area along the dorsal margin. This unscaled region forms a straight diagonal line and does not dip as in *Leiognathus equulus* (Fig. 6). There is a large axillary scale on the pelvic and anal fins, within which the spines can retract. The second dorsal-fin spine is twice to

nearly three-and-a-half times longer than the third. The second dorsal-fin spine is about 50-80% of the BD. The second anal-fin spine is elongate but not remarkably so, and is between 30-100% longer than the third (20-40% of the BD).

Pigmentation: The entire body is silvery. The head and asquamate chest regions are silvery-white. The fin spines are silvery. There is a light yellow tint to the membrane in all fins particularly the membrane between the anal-fin rays. There is little coloration in the caudal fin. The dorsal flank has a pigmentation pattern of 10-15 broad golden- yellow vertical lines that extend to the midline of the flank (never forming circular dashes as in *Aurigequula fasciata*). The pectoral-fin axil and the base of the pectoral fin lacks pigment. The pelvic fins are white. The large axillary scales on the pelvic and anal fins are silvery-white. There is a concentration of melanophores on the snout dorsal to the upper lip. There is a yellow tint to the opercular region.

Remarks: This species is not common and was only collected at two sites (a total of five individuals were collected). This species can be distinguished from *Aurigequula fasciata* by the coloration and pigmentation pattern on the dorsal flank (golden-yellow vertical lines that extend to the midline of the flank versus lighter yellow lines that break into spots ventral to the lateral line), the much larger hump on the head, the more blunt squared snout, and the asquamate nuchal region. *Leiognathus striatus* can also be distinguished from *Aurigequula fasciata* by the lack of a yellowish marking behind the pectoral fin. This species is rarely mentioned in the literature and even more rare in collections.

DISCUSSION

Many leiognathid species were described from material collected in the coastal waters of India by Cuvier and Valenciennes, among other researchers, in the early to mid 1800s. Unfortunately, the lack of type specimens and rudimentary descriptions for many of these species has made identification of recent Leiognathid collections difficult. These initial taxonomic problems led to the creation of widespread "umbrella" species. These umbrella taxa contain several superficially similar looking species (often with distinct features) together having a widespread distribution. Because of the lack of adequate type material and descriptions there is no adequate method for determining

which populations represent the species as it was described. Regional variation in populations often represent new species.

The Sri Lankan material from this expedition is important because it entails the first study of many of these species from near their type locality since the work of Day (1865). Day's studies aided in our understanding of the material described by Cuvier and Valenciennes, but comparative material from his work is no longer available.

Species reported from Sri Lanka in recent field guides (De Bruin *et al.*, 1995) that were not collected in this study include *Nuchequula blochii*, *Leiognathus berbis* (*nomen dubium*; see Chakrabarty and Sparks, 2007), *Equulites elongatus*, "*Leiognathus*" *lineolatus* (*nomen dubium*; see Sparks 2006a), "*Leiognathus*" *smithursti* (= *Equula longispinis*; see Sparks, 2006b). These remaining species may perhaps be found in Sri Lanka during other parts of the year, or in localities not visited (including most of the eastern coast of the island).

One apparently new species was discovered during this study (*Nuchequula* sp.). This species awaits comparison with material from other localities before there can be formal description. Because Sri Lankan law forbids the removal of such biological material, direct comparisons with outside material will be impossible. Further comparisons will be made from photographs, detailed field notes, and DNA analysis (Chakrabarty and Sparks, 2008).

ACKNOWLEDGEMENTS

Rohan Pethiyagoda kindly provided resources during this trip and also stored and cataloged specimens at the Wildlife Heritage Trust (WHT) of Sri Lanka. Logistical help while in Sri Lanka was also provided by Kelum Manamendra-Arachchi. Dr. William Eschmeyer was also extremely helpful in resolving some taxonomic issues related to leiognathids. This research was supported by a grant (DEB-0444842) from the National Science Foundation (USA).

REFERENCES

Chakrabarty, P. and Sparks, J.S. (2007). Phylogeny and taxonomic revision of *Nuchequula* Whitley 1932 (Teleostei:

Leiognathidae), with the description of a new species. *American Museum Novitates* **3588**: 1 – 28.

Chakrabarty, P., and Sparks, J.S. (2008). Diagnoses for *Leiognathus* Lacepède 1802, *Equula* Cuvier 1815, *Equulites* Fowler 1904, *Eubleekeria* Fowler 1904, and a New Ponyfish Genus (Teleostei: Leiognathidae). *American Museum Novitates* **3623**: 1-11.

Day, F. (1865). *The Fishes of Malabar*. Bernard Quaritch, London.

De Bruin, G.H.P., Russel, B.C. and Bogusch, A. (1995). *FAO species identification field guide for fishery resources of Sri Lanka*. Rome, FAO.

Eschmeyer, W.N. (ed.) (2008). Catalog of Fishes. Electronic version available at <http://www.calacademy.org/research/ichthyology/catalog/fishcatsearch.html>

Fowler, H.W. (1918) New and little known fishes from the Philippine Islands. Proceedings of the Academy of Natural Sciences Philadelphia **70**: 2-71.

Goodall, C. (1991). Procrustes methods in the statistical analysis of shape. *Journal of the Royal Statistical Society, Series B (Methodological)* **53**: 285--339.

Hubbs, C.L. and Lagler, K.F. revised and updated by G.R Smith (2004). *Fishes of the Great Lakes Region*. Ann Arbor: University of Michigan Press.

James, P.S.B.R. (1975). A systematic review of the fishes of the family Leiognathidae. *Journal of the Marine Biological Association of India* **17**: 138-172.

James, P.S.B.R., and Badrudeen, M. (1991). A new species of silverbelly *Leiognathus striatus* (Family Leiognathidae: Pisces) from the Gulf of Mannar, India and redescription of *Leiognathus fasciatus* (Lacepède). *Journal of the Marine Biological Association of India* **32**: 217–226.

Kimura, S., Motomura, H. and Iwatsuki, Y. (2008). *Equulites* Fowler 1904, a senior synonym of *Photoplagios* Sparks, Dunlap, and Smith 2005 (Perciformes: Leiognathidae). *Ichthyological Research* **55**: 204-205.

Kimura, S., Kimura R. and Ikejima, K. (2008b). Revision of the genus *Nuchequula* with

- descriptions of three new species (Perciformes: Leiognathidae). *Ichthyological Research* **55**: 22-42.
- Mochizuki, K. and Hayashi, M. (1989). Revision of the leiognathid fishes of the genus *Secutor*, with two new species. *Science Report of the Yokosuka City Museum* **37**: 83-95.
- Rohlf, F.J. (2006). *TPSDIG2.2.05*. State University of New York, Stony Brook, NY, <http://life.bio.sunysb.edu/morph/>.
- Rohlf, F.J. and Slice, D.E. (1990). Extensions of the Procrustes method for the optimal superimposition of landmarks. *Systematic Zoology* **39**: 40--59.
- Sheets, H.D. (2001). *PCAGEN*. Canisius College, Buffalo, NY, <http://www2.canisius.edu/~sheets/morphsoft.html>.
- Sparks, J.S. and Dunlap, P.V. (2004). A clade of non-sexually dimorphic ponyfishes (Teleostei: Perciformes: Leiognathidae): Phylogeny, taxonomy, and description of a new species. *American Museum Novitates* **3459**: 1-21.
- Sparks, J.S., Dunlap, P.V. and Smith, W.L. (2005). Evolution and diversification of a sexually dimorphic luminescent system in ponyfishes (Teleostei: Leiognathidae), including diagnoses for two new genera. *Cladistics* **21**: 305-327.
- Sparks, J.S. (2006a). A new species of ponyfish (Teleostei:Leiognathidae:*Photoplagios*) from Madagascar, with a phylogeny for *Photoplagios* and comments on the status of *Equula lineolata* Valenciennes. *American Museum Novitates* **3526**: 1-20.
- Sparks, J.S. (2006b). *Leiognathus longispinis* (Valenciennes, in Cuvier and Valenciennes, 1835), a senior synonym of *Leiognathus smithursti* (Ramsay and Ogilby, 1886) (Teleostei:Leiognathidae) *Copeia* **2006**: 539-543.
- Sparks, J.S. and Chakrabarty, P. (2007). A new species of ponyfish (Teleostei:Leiognathidae: *Photoplagios*) from the Philippines. *Copeia* **2007**: 622 – 629.
- Whitley, G.P. (1932). Some fishes of the family Leiognathidae. *Memoirs of the Queensland Museum* **10**: 99-116.

Appendix. List of localities sampled and species of Leiognathids collected.

SRI-1-2007, Cargills Supermarket, Colombo - *Karalla daura*, *Karalla dussumieri*.

SRI-2-2007, St. John's Fish Market, Colombo; (06°56'26.5"N; 079°51'11.7"E) - *Gazza minuta*, *Eubleekeria splendens*, *Karalla dussumieri*, *Leiognathus equulus*, *Nuchequula* sp., *Equulites laterofenestra*, *Secutor insidiator*, *S. ruconius*.

SRI-3-2007, Panadura (06°43'37.6"N; 079°54'03.6"E) - no ponyfish collected.

SRI-4-2007, Puttalam Main Fish Market (08°01'49.5"N; 079°49'42.0"E) - *Karalla dussumieri*, *Nuchequula* sp., *Equulites laterofenestra*.

SRI-5-2007, Kalpitiya Lagoon (08°58'44.8"N; 079°49'57.1"E) - *Nuchequula* sp.

SRI-6-2007, Madurankuliya Fish Market (07°54'32.4"N; 079°49'22.0"E) - no ponyfish collected.

SRI-7-2007, Arachchikattuwa town (07°39'53.9"N; 079°50'13.6"E) - *Karalla daura*.

SRI-8-2007, Chilaw Main Market (07°34'39.5"N; 079°47'22.8"E) - *Leiognathus equulus*.

SRI-9-2007, Negambo Fish Market (07°12'36.7"N; 079°49'53.6"E) - *Gazza achlamys*, *G. minuta*, *Eubleekeria splendens*, *Karalla daura*, *K. dussumieri*, *Secutor ruconius*.

SRI-10-2007, Wattala Fish Market (06°59'41.7"N; 079°52'25.8"E) - *Gazza minuta*, *Eubleekeria splendens*, *Secutor insidiator*.

SRI-11-2007, Pannipitiya Fish Shop - *Gazza minuta*, *Karalla dussumieri*, *Photopectoralis bindus*, *Secutor insidiator*.

SRI-12-2007, Beruwala-Maggonna Fishing Village (06°30'19.4"N; 079°58'42.7"E) - *Gazza minuta*, *Karalla daura*.

SRI-13-2007, Beruwala Harbor (06°28'34.9"N; 079°58'56.9"E) - *Gazza achlamys*, *Karalla daura*, *Leiognathus striatus*.

SRI-14-2007, Dikwella Fishery Port, (06°08'32.2"N; 080°05'56.8"E) - *Karalla dussumieri*, *Nuchequula* sp., *Equulites laterofenestra*.

SRI-15-2007, Galle Beach Front, (06°01'50.0"N; 080°14'27.9"E) - *Aurigequula fasciata*, *Leiognathus equulus*, *Leiognathus striatus*, *Photopectoralis bindus*.

SRI-16-2007, Matara Fair, (06°01'50.0"N; 080°14'27.9"E) - *Eubleekeria splendens*, *Nuchequula* sp.

SRI-17-2007, Tangalle, (06°01'29.1"N; 080°47'53.7"E) - *Secutor ruconius*.

SRI-18-2007, Hambantota Fish Market (06°07'27.2"N; 081°07'31.1"E) - *Karalla dussumieri*.

SRI-19-2007, Hambantota, Karagan Levaya (06°07'11.8"N; 081°06'04.2"E) - no ponyfish collected.

SRI-20-2007, Moratuwa Fishing Pier (06°46'26.8"N; 079°53'29.4"E) - *Leiognathus equulus* (observed but not collected).