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Phylogeny and Taxonomic Revision of *Nuchequula* Whitley 1932 (Teleostei: Leiognathidae), with the Description of a New Species

PROSANTA CHAKRABARTY[1] AND JOHN S. SPARKS[1]

ABSTRACT

Nuchequula Whitley 1932, previously considered a subgenus of *Leiognathus* Lacepède 1802, is elevated to generic rank. *Nuchequula* is diagnosed by the presence of a distinct saddle-shaped nuchal marking and by the presence of a pigment-free, mitten-shaped region posteroventral to the pectoral-fin base. The genus comprises five species, *N. blochii*, *N. pan*, *N. nuchalis*, *N. decora*, and a new species described herein. *Nuchequula mannusella*, new species, is distinguished from its congeners by a unique pigmentation pattern on the dorsal fin and morphology of the lower jaw. Redescriptions are provided for the other species. A phylogenetic analysis based on morphological characters, including features of the light-organ system, indicates that *Nuchequula* is monophyletic.

INTRODUCTION

Leiognathidae is in need of taxonomic revision. To date, nearly 80 species have been described; however, only 40 are currently recognized as valid (not including fossil taxa). Recent family-level phylogenetic studies have demonstrated that the largest included genus, *Leiognathus*, is not monophyletic (Ikejima et al., 2004; Sparks and Dunlap, 2004; Sparks et al., 2005). Therefore, there is a need to describe new genera to recognize a monophyletic taxonomy (Sparks and Dunlap, 2004; Sparks et al., 2005). Complicating efforts to clarify the taxonomy of the group is the fact that, for many species, type specimens were either never deposited or have subsequently been lost. The original descriptions of many ponyfish species, including those of Cuvier and Valenciennes who described numerous leiognathids, at best consist of a few sentences restricted to external features (none of which are apomorphic), but often comprise only a footnote providing a new name in reference to an illustration from another source.

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The absence of type material and the rudimentary nature of many original species descriptions have led to the proliferation of nomenclatural problems in the literature. Moreover, the information provided for species in regional faunal inventories (e.g., Food and Agriculture Organization species identification guides) is often not based on reference to type material or original descriptions (Sparks and Chakrabarty, in review).

These nomenclatural problems contribute not only to frequent misidentifications but also to the creation of "wastebasket" species. These taxa frequently comprise multiple species identified under a single name because diagnostic characters have been poorly defined, or not defined at all. Many of these "wastebasket" species are described as exceptionally widespread in distribution, despite the fact that consistent morphological variation is reported among various geographic populations. Consistent geographic variation among allopatric populations should be considered evidence for the presence of undescribed species that are endemic to a portion of the so-called widespread species' range. These "wastebasket" species have essentially taken on a *gestalt* identity of individual researchers in the literature, an identity that is associated with neither the type specimens nor the original species descriptions (Sparks and Chakrabarty, 2007).

Superficially, leiognathids are rather nondescript silvery fishes that possess few external features that can be used to distinguish species. Internally, leiognathids possess a unique light-organ system (LOS), consisting of a circumesophageal light organ and associated structures to facilitate both the transmission and occlusion of bacterially generated luminescence from the light organ. The LOS is highly variable among species and between the sexes (Sparks et al., 2005). Internal sexual dimorphism associated with the LOS and related anatomy has been little explored among leiognathids (Haneda, 1940; McFall-Ngai and Dunlap, 1984; Sparks et al., 2005). The superficial external similarity of leiognathids, rudimentary original descriptions for many species, and propagation of misidentifications in the literature have all contributed to the many taxonomic problems that plague the family. Only through careful study of the name-bearing types, consultation of the original species descriptions, and an understanding of the relationships among species can these taxonomic problems be remedied.

Recently, family-level phylogenetic analyses have provided a better understanding of the diversity of leiognathids (Ikejima et al., 2004; Sparks and Dunlap, 2004; Sparks et al., 2005). These phylogenetic studies have also helped elucidate the limits and relationships of ponyfish genera, and have revealed a great deal of variation in the LOS at the generic and species levels. Leiognathids traditionally have been arrayed in three genera, with the majority of species placed within *Leiognathus* Lacepède 1802; however, *Leiognathus* was not recovered as monophyletic in any recent phylogenetic study. As a result, Sparks et al. (2005) diagnosed two new genera, *Photopectoralis* and *Photoplagios* (based on features of the LOS), as a first step toward solving the paraphyly of *Leiognathus* and clarifying taxonomy within the assemblage. Two other clades, both formerly included in *Leiognathus*, remain without diagnoses and are distinguished from *Leiognathus* sensu strictu by being placed in quotes (i.e., "*Leiognathus*"). Clade G of Sparks et al.'s (2005) phylogeny was recovered as the sister group to *Photoplagios* and is, in part, recognized herein as *Nuchequula*. A phylogenetic analysis of Clade G and *Photoplagios* is included to further explore and clarify the relationships within this assemblage.

Whitley (1932) described *Nuchequula* as a subgenus of *Eubleekeria* Fowler 1904 to include *E.* (*Nuchequula*) *blochii* and *E.* (*N.*) *nuchalis*. *Nuchequula* was subsequently synonymized with *Leiognathus* Lacepède 1802 by James (1975). Whitley (1932) distinguished *Nuchequula* from the subgenus *Eubleekeria* as having "depth more than 2 in length and having a dark nuchal mark" (versus "depth less than, or about, 2 in length with no dark mark on nape"). Whitley (1932) also designated *Equula blochii* as the type species of *Nuchequula*. It is unclear why Whitley (1932) selected *E. blochii* as the type species, because it was one of the few species described at the time that he did not examine. His choice may have been due to the fact that *Equula blochii* Valenciennes, in Cuvier and Valenciennes, 1835 was the oldest available name for any leiognathid species reported to have a nuchal spot (Day, 1875). Notably, a nuchal marking is not mentioned by Valenciennes in the original description of *E. blochii.* The alcohol-preserved syntypes of *E. blochii* (MNHN A-6757, 73.0 mm SL; MNHN A6759, 67.1 mm SL) have lost much of their original pigmentation in preservation; however, a dark brown triangular marking remains beneath the nuchal spine. Whitley (1932) also placed *E. nuchalis* in *Nuchequula*, and in contrast to the information provided for *E. blochii*, he provides a description of the specimens he examined.

Herein we continue our taxonomic studies of Leiognathidae with the resurrection and revision of *Nuchequula* Whitley 1932. *Nuchequula* includes *N. blochii*, *N. pan*, *N. nuchalis*, *N. decora*, and a new species described herein. We address the taxonomy of the species included in *Nuchequula*, with careful consideration of both the available type material and the original species descriptions. For species in which the original descriptions do not provide relevant diagnostic features and for which we lack fresh material (e.g., *N. blochii*, *N. decora*), we defer to subsequent redescriptions of these species from other authors, provided that those descriptions are based on topotypic material and are in agreement with the type series.

MATERIALS AND METHODS

Osteological features of the new species and related taxa 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 to permit detailed morphological comparisons. Morphometric measurements were recorded to the nearest 0.1 mm using dial calipers. Standard length (SL) is used throughout. Vertebral counts exclude the ural centrum (= last half-centrum). Following Hubbs and Lagler (2004), the first caudal vertebra is here defined as the first vertebra bearing a definite hemal spine. Vertebral and fin-spine/ray counts were obtained from radiographs. The terminal dorsal-fin and anal-fin rays, which are branched to the base of the fin, are counted as a single element. Pored scales in the lateral line are counted in series from the dorsal margin of the gill opening to the caudal flexure. Scale counts should be interpreted as approximations, due to high intraspecific variability, irregular arrangement, and 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.

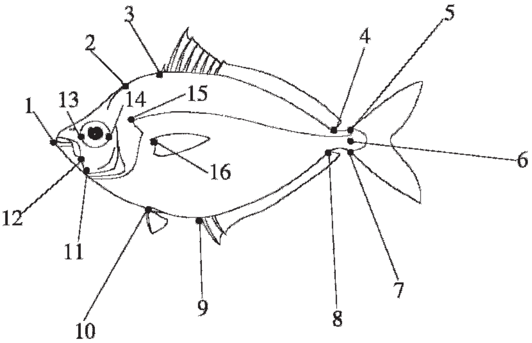

Fig. 1. Landmarks used for PCA: (1) rostral tip of premaxilla; (2) posterior end of nuchal spine; (3) anterior insertion of dorsal fin; (4) posterior insertion of dorsal fin; (5) dorsal insertion of caudal fin; (6) midpoint of caudal border of hypural plate; (7) ventral insertion of caudal fin; (8) posterior 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 eye; (14) posterior margin through midline of eye; (15) dorsal end of opercle; (16) dorsal base of pectoral fin. Base figure modified from Nelson (2006).

For the Principal Component Analysis (PCA) of shape, digital images were taken from the left side of each specimen. Only specimens that were preserved unbent and of adult size were used in this analysis. Landmarks (putatively homologous points on anatomical structures) were chosen to best represent the external shape of the body (fig. 1). 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).

The phylogenetic analysis was conducted in NONA (Goloboff, 1998) via the WINCLADA (Nixon, 2000) interface. For the phylogenetic analysis, 15 morphological features were simultaneously analyzed under the optimality criterion of parsimony (200 random addition replicates of tree bisection–reconnection), with all transformations given equal weight. Only unambiguously optimized morphological transformations are used to diagnose clades.

INSTITUTIONAL ABBREVIATIONS

AMNH	American Museum of Natural History, New York, NY
AMS	Australian Museum, Sydney
ASIZ	Academica Sinica Institute of Zoology, Taipei
BMNH	British Museum of Natural History, London
CAS	California Academy of Sciences, San Francisco, CA
CUMZ	Chulalongkorn University Museum of Zoology, Bangkok
FRLM	Fisheries Research Laboratory, Mie University, Mie-ken
LACM	Los Angeles County Museum of Natural History, Los Angeles, CA
MCZ	Museum of Comparative Zoology, Cambridge, MA
MNHN	Muséum National d'Histoire Naturelle, Paris
NMW	Naturhistorisches Museum, Wien (Vienna)
QM	Queensland Museum, Brisbane
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C.
UMMZ	University of Michigan Museum of Zoology, Ann Arbor, MI
ZMB	Universitat Humboldt, Museum fur Naturkunde, Berlin
ZMUC	Kobenhavns Universitet Zoologisk Museum, Copenhagen

RESULTS

Results of the PCA show that *N. nuchalis*, *N. blochii*, *N. pan*, and the new species form discrete groups on the plot of Principal Component (PC) 1 versus PC2 (fig. 2). PC1 explains 30% of the variation among specimens, whereas PC2 explains 17%, and PC3 explains 12%. PC1 largely explains the variation related to increased body depth, elongation of the head, and shortening of the caudal peduncle. *Nuchequula nuchalis* is highly variable with regard to these shape elements, and specimens are scattered between both extremes along PC1. The types of *N. blochii* and *N. pan* are similarly elongate and do not overlap with any individuals of *N. decora* or the new species along PC1. There is overlap among *N. decora*, *N. nuchalis*, and the new species along PC1. PC2 explains much of the variation due to decreased head depth, particularly due to shortening in the area between the orbit and the posterior margins of the maxilla and lower jaw. PC2 also explains variation due to increased body depth between the nuchal area and the dorsal-fin insertion, as well as the decreased distance between the pelvic- and anal-fin insertions relative to each other and the anterior portion of the body. *Nuchequula nuchalis* and the new species do not overlap along PC2. *Nuchequula nuchalis* has a shallower lower jaw and more anteriorly situated pectoral-, pelvic-, and dorsal-fin origins than the new species. Individuals of *Nuchequula decora* are intermediate and slightly overlapping with both *N. nuchalis* and the new species along PC2.

The phylogenetic analysis of morphological features (table 1) recovered two equally most parsimonious trees with tree lengths of 24, consistency indices of .79, and retention indices of .90. A strict consensus of these two topologies is presented in figure 3. *Nuchequula* and *Photoplagios* are both monophyletic; however, the relationship among these clades and with *"Leiognathus" daura* and *"L." dussumieri* remain unresolved, as they were in the family-level phylogenetic study of Sparks et al. (2005).

SYSTEMATIC ACCOUNTS

Nuchequula Whitley 1932

"*Leiognathus*" Clade G: Sparks et al., 2005 (in part)

TYPE SPECIES: *Nuchequula blochii*.

INCLUDED SPECIES: *N. pan*, *N. nuchalis*, *N. decora*, and *N. mannusella* n.sp.

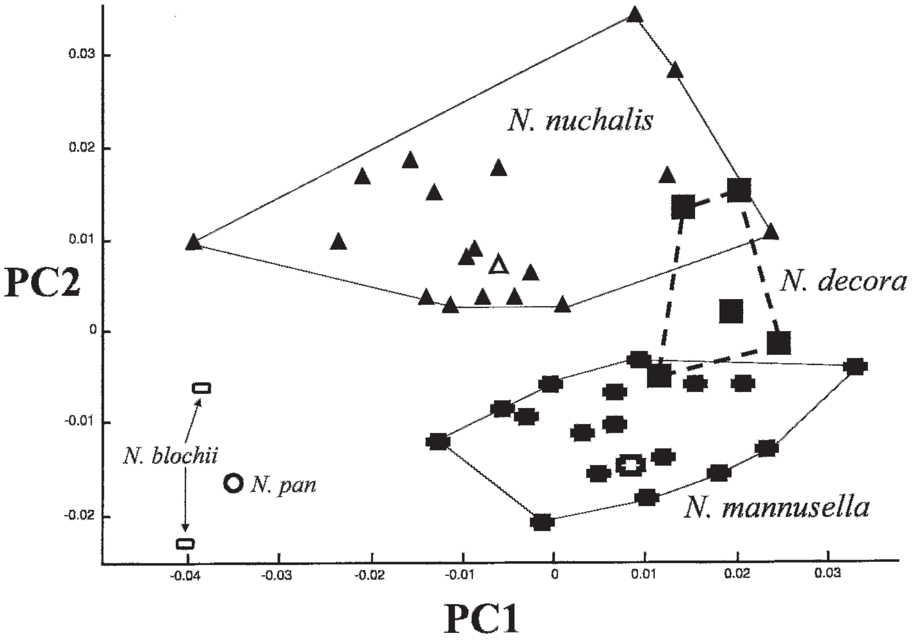

Fig. 2. PCA for species of *Nuchequula* (plot of PC1 versus PC2). Individuals of *Nuchequula mannusella*. are represented by black crosses; *N. decora* (all identified by Jones AMS I.22990002) is represented by squares; and *N. nuchalis* is represented by triangles. Type specimens are represented by open shapes, including *N. blochii* syntypes (rectangles) and *N. pan* paratype (circle). (Only *N. pan* paratype USNM 276536 is included because the holotype and other paratypes of this species were examined at CUMZ and were not available for this analysis.)

DIAGNOSIS: Members of *Nuchequula* are distinguished from all other leiognathids by a darkly pigmented nuchal mark and by a pigment-free, mitten-shaped region ventral and posterior to the pectoral-fin base.

REMARKS: Sparks et al.'s (2005) "Clade G" also included *"Leiognathus" dussumieri* and *"L." daura*. We do not include these species in *Nuchequula* because the relationships of *"L." dussumieri*, and *"L." daura* within Clade G remain unresolved and because both species lack the distinctive nuchal marking that characterizes the genus.

***Nuchequula mannusella*, new species**

figures 4, 5A, tables 2–3

HOLOTYPE: AMNH 238753, 85.5 mm SL; Taiwan: Chiayi County: Tungshih Fish Market: 23°27′1″N, 120°08′19.3″E; TW-6-2006; Prosanta Chakrabarty, Joker K.H. Chiu, John S. Sparks, 22 March 2006.

PARATYPES: AMNH 238754, 15 ex., 72.1–90.1 mm SL; data as for holotype. AMNH 238755, 16 ex., 62.9–89.7 mm SL; data as for holotype. AMNH 238756, 15 ex., 70.2–94.1 mm SL; data as for holotype. AMNH 238757, 14 ex., 64.8–81.2 mm SL; data as for holotype. AMNH 238758, 20 ex., 77.2–86.9 mm SL; data as for holotype. AMNH 238759, 9 ex., 82.1–95.4 mm SL; data as for holotype. AMNH 238760, 13 ex., 75.1–98.5 mm SL; data as for holotype. AMNH 238761, 1 ex., 71.2 mm SL; Taiwan: Hsinchu City: Motorway 3 north from Taichung, one-and-one-half hours from Taichung, West Coast Hwy: Fishing Harbor in Hsinchu: 24°50′55.4″N, 120°55′13.6″E; local fisherman, Prosanta Chakrabarty, Otto Jeng-Di Lee, John S. Sparks, 20 March 2006. AMNH 238762, 1 ex., 53.4 mm SL; data as for holotype. AMNH 238763, 1 ex., 83.0 mm SL; data as for holotype. AMNH 238764, 1 ex., 88.9 mm SL; data as for holotype. AMNH 238765, 29 ex., 73.6–100.9 mm SL; data as for holotype. ASIZP 0062322, 1 ex., 76.2 mm SL; Taiwan: Fenggang:

TABLE 1
Morphological Transformations Used in the Phylogenetic Analysis of *Nuchequula* Species (see fig. 3)

	C1	C2	C3	C4	C5	C6	C7	C8	C9	C10	C11	C12	C13	C14	C15
L. equulus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
L. robustus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
P. elongatus	0	2	1	0	1	2	1	1	1	0	1	1	1	1	0
P. rivulatus	0	2	1	0	1	2	1	1	1	0	1	1	1	1	0
P. leuciscus	0	1	1	0	1	3	1	1	0	1	0	1	1	1	0
P. stercorarius	0	2	1	0	1	3	1	1	0	0	1	1	1	1	0
P. antongil	0	1	1	0	1	3	1	1	1	0	1	1	1	1	0
L. dussumeri	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0
L. daura	0	1	1	0	0	4	0	1	0	0	0	0	0	0	1
N. pan	1	1	0	1	0	5	0	1	0	0	1	0	0	0	1
N. nuchalis	1	1	0	1	0	4	0	1	0	0	1	0	0	0	1
N. blochii	1	1	0	?	0	4	0	1	0	0	0	0	0	0	1
N. decora	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0
N. mannusella	1	1	0	1	0	0	0	1	0	0	0	0	0	0	1

Characters: **C1** = nuchal spot (0 = absent; 1 = present); **C2** = body depth as percentage of standard length (0 = > 50%; 1 = < 40–50%; 2 = < 40%); **C3** = lower jaw profile (0 = concave; 1 = straight); **C4** = pigment-free mitten-shaped region near pectoral fin (0 = absent, scattered melanophores in area; 1 = present); **C5** = concavity above orbit (0 = present; 1 = absent); **C6** = pigmentation pattern on dorsal flank (0 = zigzags, straight, or wavy vertical lines; 2 = circular shapes; 3 = irregular shapes; 4 = absent; 5 = horizontal lines/stripes); **C7** = translucent flank patch (0 = absent; 1 = present); **C8** = adult body size (0 = > 150 mm SL; 1 = < 150 mm SL); **C9** = second dorsal- and anal-fin spines (0 = robust; 1 = feeble); **C10** = second dorsal-fin spine (0 = not considerably more elongate than other spines; 1 = markedly elongate relative to other spines); **C11** = dorsal-fin origin relative to pelvic-fin origin (0 = on vertical through pelvic-fin origin; 1 = posterior to vertical through pelvic-fin origin); **C12** = light organ dimorphic in size (0 = absent; 1 = present); **C13** = dorsal lobes of light organ hypertrophied in males (0 = absent; 1 = present); **C14** = clearing of lateral silvery lining of gas bladder in males (0 = absent; 1 = present); **C15** = dorsal fin markings (0 = absent; 1 = present).

Pingtung: open sea, at 100 m depth: 22°26′N, 120°38′E; J.H. Wu, 1 March 2001. ASIZP 0060823, 1 ex., 90.9 mm SL; Taiwan: Kaoshiung: Shingda Harbor: open sea: 22°87′N, 120°19′E; G.J. Xia, 8 June 2000. SIO 06.261, 2 ex., 83.7–96.2 mm SL; data as for holotype. (Because much of this collection is from a single market locality, different AMNH numbers were assigned to material to reflect the possibility that different vendors sold fish from diverse sources.)

DIAGNOSIS: *Nuchequula mannusella* is distinguished from its congeners by a conspicuously deep lower jaw with a strongly concave profile that is sharply pointed ventrally (versus a slightly concave or straight lower jaw profile). The black dorsal-fin marking of *N. mannusella* is uniquely restricted to the anterior edge of the fin, with some scattered melanophores in the dorsal-fin membrane (versus a large blotch over a larger area on the dorsal fin or an absence of markings on the dorsal fin).

DESCRIPTION: Morphometric and meristic data are presented in table 2, and other comparative features are presented in table 3. *Nuchequula mannusella* is a moderately large (maximum recorded length 101 mm SL), rhomboid-shaped ponyfish. The dorsal and ventral profiles are equally convex. The greatest body depth is reached at the vertical from the dorsal-fin origin to the pelvic-fin origin. There is a concavity above the orbit, formed by the exposed rising dorsal aspect of the supraoccipital crest (i.e., nuchal spine). The dorsal- and pelvic-fin origins are located along the same vertical. The anal-fin origin is located at the vertical from the last (= eighth) dorsal-fin spine. The mouth is terminal and directed strongly ventrally when extended. The lower jaw is deep, and the lateral profile is strongly concave. The lips are thin and only somewhat fleshy. The posterior margin of the maxilla is exposed, reaching the vertical through the anterior part of pupil and the dorsal portion of the lower jaw articulation. The exposed

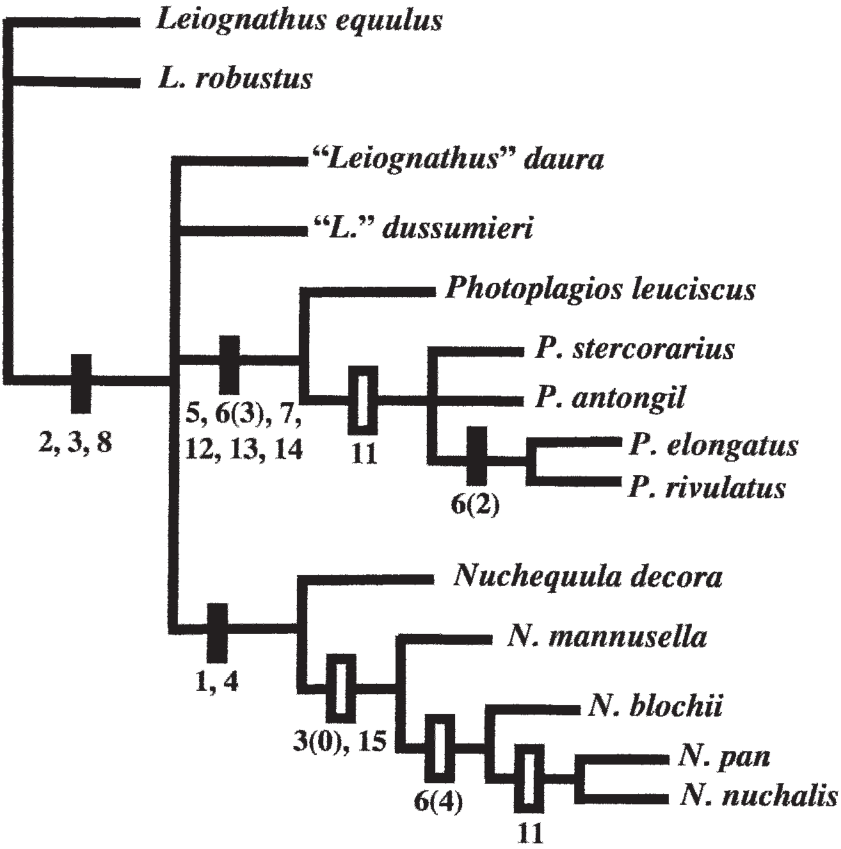

Fig. 3. Strict consensus of two equally most parsimonious topologies based on the analysis of morphological features. The character matrix is presented in table 1. Numbers on branches correspond to apomorphic features that diagnose clades; numbers in parentheses represent the state, other than 1. Solid bars represent unique and unreversed features, whereas open rectangles represent homoplasious characters.

part of maxilla is nearly perpendicular with the mouth when retracted. The eyes are large and circular (~ 10% SL). The sensory pores around the orbit are moderately well developed; some pores posterior to the orbit reach the preopercle. Sensory canals are also present ventral to the orbit and dorsal to the mouth. Two long sensory canals are present ventral to the nuchal spine. Two closely apposed nasal pores are present anterior to the orbit. The anterior nasal pore is smaller and more rounded than the posterior pore. The preopercular margin is strongly serrated along the ventral margin, with 20–25 spines. The supraorbital ridge bears small spines. There are two short and stout postnasal spines present dorsal to the orbit and posterior to the nasal pores. There are 16 elongate and slender gill rakers present on the lower limb of the first gill arch; the rakers are sparsely denticulated (i.e., bearing few teeth). The longest rakers are about the length of the gill lamellae, whereas the shortest are about half the length of the lamellae. There are 23 total vertebrae (10 precaudal + 13 caudal).

Fins: The dorsal fin has VIII spines and 16 rays. The first dorsal-fin spine is much shorter than the other spines, and 15–20% of the second spine. The length of the second and longest dorsal-fin spine is about 40% of body depth and not conspicuously longer than the third or fourth spine. The second and third spines are more robust, particularly at the base, than the remaining spines. The third and fourth spines possess serrations facilitating interlocking with the preceding spine. The

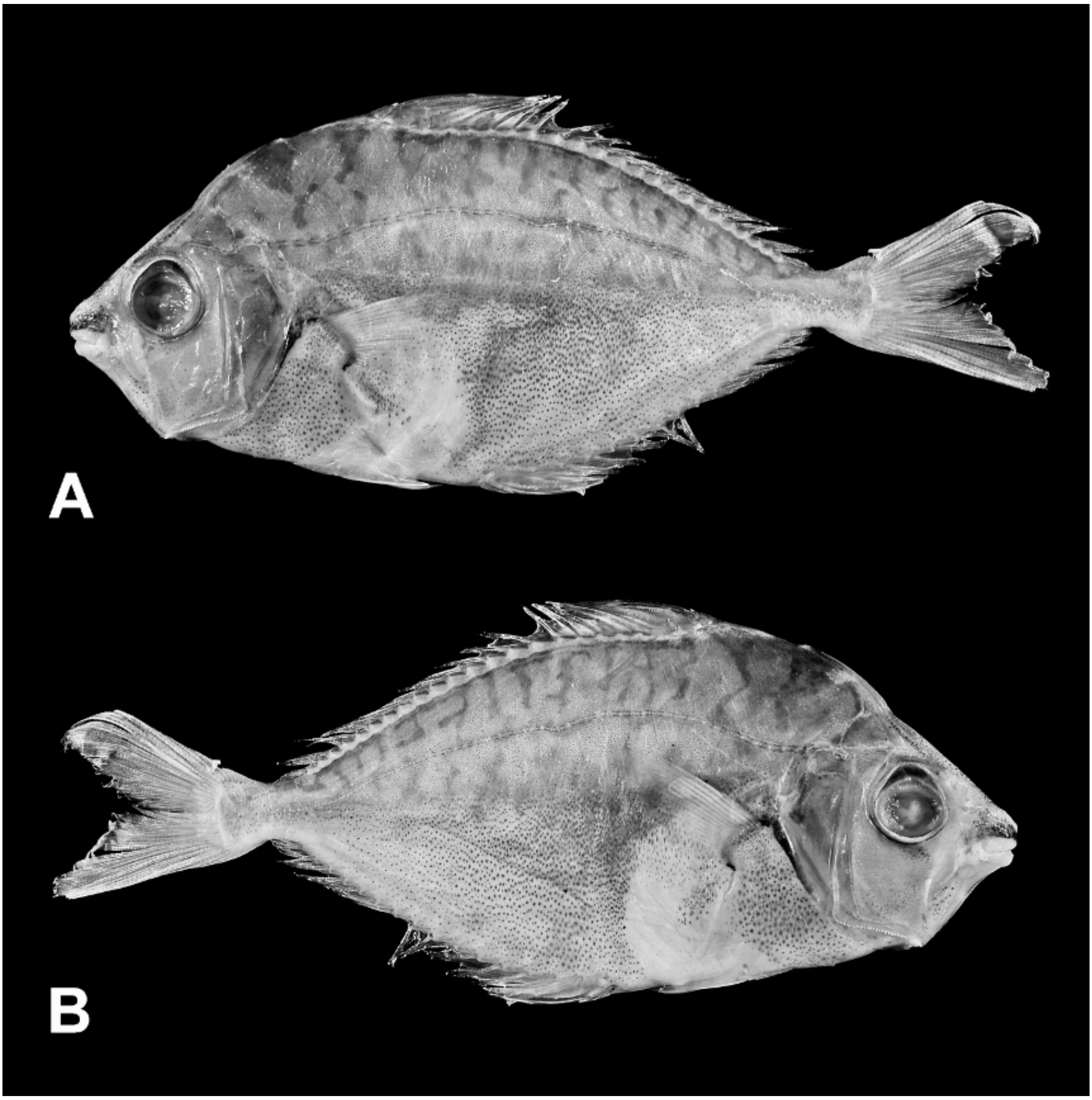

Fig. 4. *Nuchequula mannusella*, new species: (**A**) Holotype, AMNH 238753, 85.5 mm SL, Taiwan. (**B**) Right side of holotype. (**C**) Drawing of holotype. (**D**) Paratype, AMNH 238759, 94.1 mm SL, Taiwan.

anal fin has III spines and 14 rays. The first anal-fin spine is much shorter than the others, 25–35% of the second. The second anal-fin spine is more robust than the other spines; it is only slightly longer than the third and is about 30% of body depth. The third anal-fin spine possesses serrations facilitating interlocking with the second spine. There is a sheath of asquamate tissue that covers the bases of the spinous portions of the dorsal and anal fins. The pelvic fins are short, and do not reach the origin of the anal fin, and have one associated spine. The caudal fin is deeply forked.

Dentition: The teeth are villiform and arrayed in a narrow band of three to five poorly differentiated rows. The teeth in the lower jaw are slightly recurved, whereas those in the upper jaw are strongly recurved and almost parallel with the roof of the mouth.

Squamation: As for all leiognathids, scales are highly deciduous, making accurate counts and observations problematic. The chest and

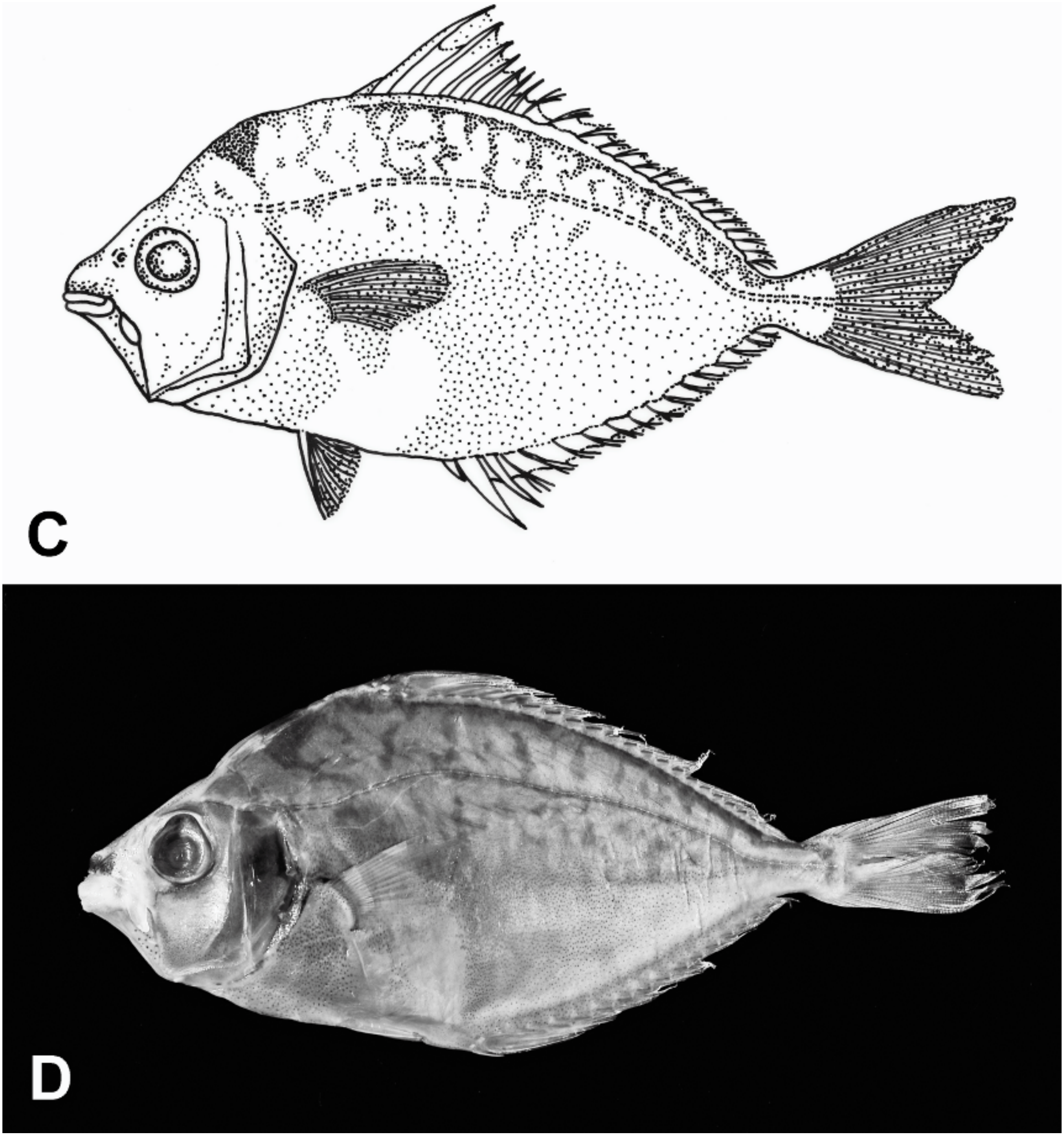

Fig. 4. Continued.

fins are asquamate. Some specimens possess scales on the cheek and in the interpelvic region. There are scales present in the nuchal region and continuing to the ventrum (not including the chest), which extend posteriorly to the caudal peduncle and onto the caudal fin. The lateral line is complete, extending from the posterior edge of the opercle to the posterior margin of the caudal peduncle, and includes about 55 scales. The pores of the lateral line are well developed. The lateral line is horizontal between the posterodorsal margin of the opercle to slightly beyond the pectoral-fin base. The lateral line is arched slightly from the pectoral-fin base posteriorly to the caudal peduncle and is horizontal on the caudal peduncle.

Pigmentation in life: The entire body is silvery (see fig. 5A). The leading edge of the

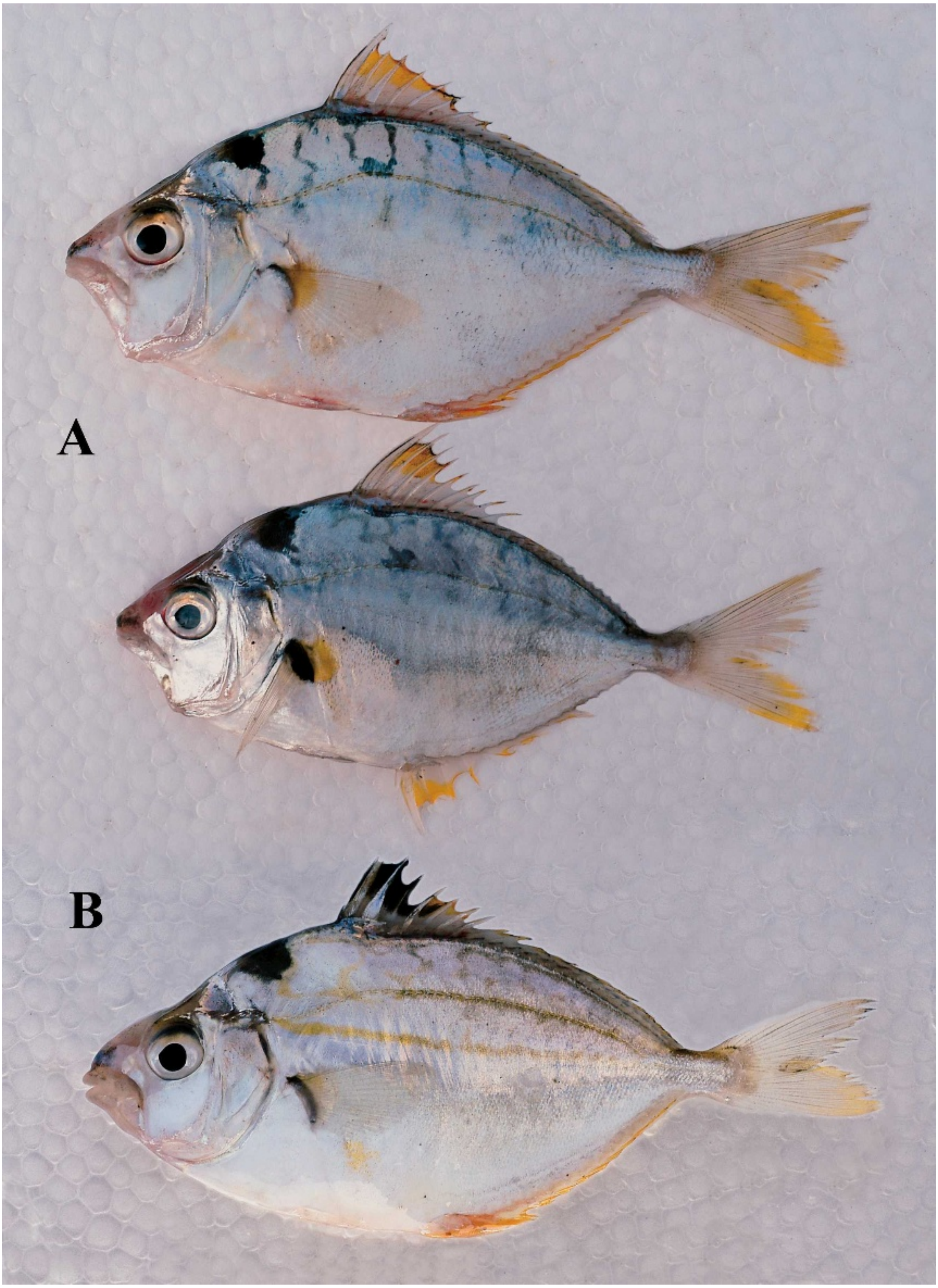

Fig. 5. Fresh material from Tonshi Fish Market, Taiwan. (**A**) Two paratypes of *Nuchequula mannusella*, new species. (**B**) *Nuchequula nuchalis*.

TABLE 2

Morphometric Data for *Nuchequula mannusella* (*N* = 32)

Character	Holotype	Range	Mean	SD
Standard length (mm)	85.5	62.9–90.1	80.3	
Percentage of SL				
Head length	30.5	28.4–32.9	31.0	1.19
Body depth	46.9	41.8–49.4	46.6	1.78
Predorsal length	46.1	35.7–50.1	45.9	3.55
Preanal length	53.5	41.0–60.2	55.3	3.06
Prepelvic length	38.1	32.3–41.0	38.1	1.46
Head width (max.)	13.6	12.2–15.3	14.0	0.59
Caudal peduncle length	7.3	5.3–9.2	7.6	1.05
Caudal peduncle width	2.3	2.3–6.2	3.3	0.68
Caudal peduncle depth	6.2	5.3–7.2	6.2	0.50
Pectoral-fin length	23.5	19.5–26.2	22.5	1.79
Pelvic-fin length	13.5	10.5–15.0	13.0	1.17
Percentage of HL				
Snout length	33.0	29.2–42.1	35.5	3.56
Orbit diameter	31.4	28.3–37.1	31.4	2.00
Upper jaw length	38.7	33.2–50.1	42.5	3.98
Lower jaw length	52.1	47.2–69.0	52.8	4.07
Interorbital width	33.7	28.2–40.9	33.6	3.77
Caudal peduncle length/depth	1.2	0.9–1.6	1.2	0.18
Caudal peduncle length/width	3.1	1.1–3.6	2.4	0.53
Vertebra (precaudal + caudal)	10 + 13	10 + 13		
Dorsal fin	VIII 16	VIII 16		
Anal fin	III 14	III 14		

dorsal fin is black. The spinous region of the dorsal fin is yellow from about three-quarters the length of the second dorsal spine to the distal margin. The entire dorsal fin is yellow distally. The ventral lobe of the caudal fin bears significantly more yellow along its posterior margin than the dorsal lobe. The spinous portion and entire distal margin of the anal fin are yellow. The base of the pectoral fin is yellow. The yellow areas on the fins in some specimens have a reddish hue. The buccal area (mouth, lower jaw) and the region dorsal to the orbit are translucent but sometimes reddish. There is a dark brown or black saddle-shaped, triangular nuchal marking. In some specimens there is a light-blue metallic spangling dorsal to the opercle and a blue ‘‘W’’-shaped marking straddling the dorsal aspect of the lateral line ventral to the spinous portion of the dorsal fin (usually between the fourth and seventh spines). The pectoral-fin axil is black. Dark vertical bands are present on the flanks dorsal to the midline, ranging from broad and nearly straight to vermiculate and moderately curved. These bands sometimes coalesce ventrally.

Pigmentation in preservative: Most specimens comprising the type series have lost their guanine in preservation. Base body coloration is generally tan. In specimens retaining guanine, the body is silvery from slightly above the midline to the ventrum, and the gill covers and suborbital regions are silvery to a vertical through the anterior margin of the orbit. As in life, the dorsal flank markings consist of dark vertical bands that vary from broad and straight to vermiculate and wavy or that form a zigzag pattern. The dorsal markings are most prominent above the lateral line. A dark blotch is present above the upper lip anterior to the nasal pores. The pectoral-fin axil is black or dark brown. Scattered melanophores are present ventrally on the body; they are obscured when guanine is retained. A pigment-free, mitten-shaped region is visible on specimens lacking guanine posterior to the pectoral-fin base and between the pelvic- and anal-fin origins. The pigment-free region is not

TABLE 3
Comparative Features of Species of *Nuchequula* Based on Type Material and Original Descriptions

	N. mannusella	*N. blochii*	*N. pan*	*N. nuchalis*	*N. decora*
Dorsal fin markings (in preservative)	Dark pigment along the anterior edge of the first two spines, some dark pigment scattered along the dorsal-fin membrane of the second through fifth spines.	Described as having a dark spot (Cuvier & Valenciennes 1835). "Black mark in the upper ½ of spinous dorsal fin from the 3rd to 6th spines" (Day 1875). Mark lost in preservative on syntypes.	"Black blotch on spinous dorsal fin distinct" (Wongratana 1988). A dark marking is present on the upper half of spinous dorsal from the second to sixth spine.	"The spiny portion of the dorsal is tinted black towards the top" (Temminck & Schlegel, 1845). Illustration shows a dark spot across the entire upper half of the spinous dorsal.	No markings are noted in the original description by De Vis (1884). Jones (1985) does not illustrate or mention any dark markings in her redescription. None on preserved specimens identified by Jones.
Nuchal spot	Generally triangular but sometimes rounded and usually reaching slightly beyond the posterior edge of the nuchal spine.	Not mentioned in original description (Cuvier & Valenciennes 1835). Syntypes have a large, dark triangular area in the nuchal region. Day's (1875) illustration shows a nuchal spot similar to, but slightly smaller than, that of *N. pan*.	"Blotch on nape diffuse" (Wongratana 1988). A large round spot is present from the nuchal spine ventrally to the area just dorsal to the lateral line.	"A pretty large blackish blotch, diamond-shaped, on top of the head" (Temminck & Schlegel, 1845). The diamond shape is in reference to the blotch viewed dorsally on both sides. Viewed laterally, it is triangular.	Jones (1985) illustrates a U-shaped spot. This dark spot is round but with a small, circular pigmentless area dorsally. The marking is not mentioned in the original description (De Vis, 1884). The nuchal marking is less distinct in preserved material relative to other species.
Body shape	Rhomboid, body depth (BD) 40–50% of SL. Strongly concave lower jaw profile that comes to a point ventrally.	Elongate, BD about 40% SL (syntypes). Lower jaw profile slightly concave.	Elongate (BD less than 43% of SL) (Wongratana 1988). Lower jaw profile slightly concave.	Highly variable (see PCA). Generally rhomboid (like *N. mannusella*) but with a shorter and straighter lower jaw profile.	Rhomboid. Generally more deep-bodied than congeners (43–55% of SL; Jones 1985). Lower jaw profile more or less straight.
Markings on dorsal flank (in preservative)	Dark vertical bands that can be straight or forming a zigzag pattern. Similar to *N. decora*.	None noted in the original description. Day (1875) mentions "vertical zigzag yellow lines on the back and sides, which fade soon after death."	"Diagnosed by series of four broken longitudinal lines on sides dorsally" (Wongratana 1988).	No markings mentioned in the original description. None present on holotype or on other preserved specimens examined.	"Irregular dark brown wavy to zigzag vertical lines" Jones (1985). Lines more numerous and wavy dorsal to lateral line than ventrally.

translucent but is conspicuous because it is the only section ventral to the midline that lacks melanophores. Black pigmentation is present on the leading edge of the dorsal fin, and scattered melanophores are present on the dorsal-fin membrane. A conspicuous black or dark brown triangular (sometimes rounded ventrally) marking is present in the nuchal area. The nuchal mark usually reaches slightly beyond the posterior margin of the nuchal spine and to about the midpoint between the nuchal spine and the lateral line ventrally.

DISTRIBUTION: Currently known only from the coastal waters of Taiwan (Hsinchu, Pingtung, Kaoshiung, and from market collections at Tungshih).

ETYMOLOGY: From the Latin *mannus* (meaning "pony") in reference to the common name for the family, and *sella* (meaning "saddle"), describing the shape of the nuchal marking.

REMARKS: One paratype, AMNH 238761, was collected by a local fisherman using hook and line and observed alive. One of the unusual aspects of the observation was an audible chirping sound made by the fish. Although little can be made of this short observation, it may be important for future reference. Visual communication through bioluminescent flashing is well documented in ponyfishes (Woodland et al., 2002; Sasaki et al., 2003), and the possibility of an auditory component in ponyfish communication would also be noteworthy. Notably, the common name of this fish in Singapore and other parts of the Malay Peninsula is "*kekek*" the onomatopoeic moniker linked to the chirping sound.

Nuchequula blochii (Valenciennes, in Cuvier & Valenciennes, 1835)

figures 6A, 7, tables 3–4

Equula blochii: Valenciennes, in Cuvier and Valenciennes, 1835: 84; Day, 1865: 105; Day, 1875: 238, 241, plate LII, fig. 5.

Eubleekeria (Nuchequula) blochii: Whitley, 1932: 109.

DIAGNOSIS: Distinguished from its congeners, except *Nuchequula pan*, by the presence of scales on the chest. *Nuchequula blochii* is distinguished from *N. pan* by the absence of longitudinal lines on the flank.

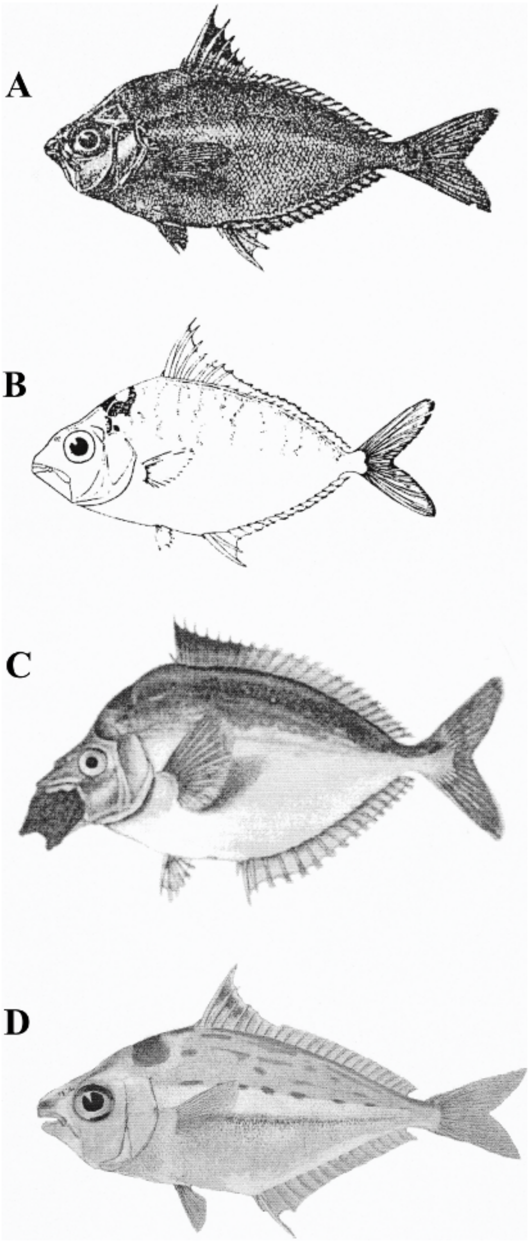

Fig. 6. Illustrations: (**A**) Non-type Indian specimen of *Nuchequula blochii* from Day (1875). (**B**) Non-type Australian specimen of *Nuchequula decora* from Jones (1985). (**C**) Holotype of *Nuchequula nuchalis* from Temminck and Schlegel (1845). (**D**) Holotype of *Nuchequula pan* from Wongratana (1988).

Fig. 7. Syntype of *Nuchequula blochii*, MNHN A=6757, 73.0 mm SL.

DESCRIPTION: Comparative features are presented in table 3; morphometric and meristic data are presented in table 4. *Nuchequula blochii* was described as having an oblong body, a concave lower jaw, and strong dorsal- and anal-fin spines. (We base all elements of this description exclusively on our examination of part of the syntypic series for this species.) The mouth is terminal and directed ventrally when extended. The teeth are villiform and arrayed in a narrow band. Body depth of the syntypes is about 40% of SL. The length of the second dorsal-fin spine is 50% of body depth, and the length of the second anal-fin spine is 46% of body depth (intact in only one specimen). The length of the first dorsal-fin spine is about 15% of the second spine. The length of the first anal-fin spine is 25% of the second. The dorsal- and anal-fin spines are robust (the second and third more so than the others). In lateral view, a slight concavity on the head is present above the orbit. The dorsal and ventral profiles are about equally convex. The caudal fin is deeply forked. The depth of the caudal peduncle is about 6% of SL. The lateral line is complete from the opercle to the posterior margin of the caudal peduncle and parallel with the shape of the back. The lips are thin and not fleshy. The dorsal- and pelvic-fin origins are located along the same vertical. The anal-fin origin is located on the vertical from the eighth dorsal-fin spine. There are 16 rakers on the lower limb of the first gill arch. These rakers are about one-half to three-quarters the length of the gill lamellae. Some scales are scattered along the body (most are apparently lost due to preservation), and scales are still present on the chest and nape. The lateral profile of the lower jaw is concave. Two robust postnasal spines are present dorsal to the orbit and posterior to the nasal pores. The supraorbital ridge is weakly serrated. The width of the body ranges from about 8–12% of SL.

Pigmentation pattern in life: We lack fresh material for study and quote this description from Day (1875), who examined specimens from Malabar, the type locality: "silvery, with a dark brown blotch over nape, and a black mark in the upper half of the spinous dorsal fin from the third to the sixth spines. Vertical zig-zag yellow lines on the back and sides, which fade soon after death: base of pectoral posteriorly dark coloured."

Pigmentation in preservative: Coloration of *N. blochii* was originally described as being similar to that of most other ponyfish species,

TABLE 4

Comparative Morphometric and Meristic Data for *Nuchequula* Species Based on Descriptions in the Literature (marked with asterisk, *) or Our Measurement of Types or Topotypic Material

Character	*N. blochii* (*N* = 2)	*N. decora* (*N* = 5) *Jones 1985	*N. nuchalis* (*N* = 11)	*N. pan* (*N* = 9*) *Wongratana 1985; otherwise *N* = 4
Standard length (mm)	**67.1–73.0**	**39*** (77.2–93.9)	**96.6** (67.9–96.6)	**65.0** (50.0–65.0)*
Percentage of SL				
Head length	**31–32.2**	31.2–32.2	**29.0** (28.5–32.4)	**28.3** (27.1–32.4)*
Body depth	**37.1–38.0**	**45*** (45.8–47.7)	**44.3** (40.4–48.0)	**39.2** (34.2–42.6)*
Predorsal length	**41.7–44.8**	46.4–49.1	**44.4** (40.3–48.0)	**44.6** (42–44.6)*
Preanal length	**52.8–55.6**	53.3–55.3	**53.7** (51.1–60.7)	**56.1** (43.2–56.1)*
Prepelvic length	**37.9–38.4**	37.2–39.8	**36.0** (31.8–41.0)	**36.1** (34.9–39.1)*
Head width (max.)	**13.7–15.2**	14.1–15.3	**13.6** (10.1–15.2)	**14.3** (11.9–15.8)*
Caudal peduncle length	**9.0–9.1**	7.1–10.8	**6.7** (5.6–10.1)	**11.1** (8.1–11.1)
Caudal peduncle width	**2.3–2.8**	2.7–3.7	**3.0** (2.4–3.7)	**3.6** (2.9–5.0)
Caudal peduncle depth	**6.0–6.3**	6.4–7.2	**6.3** (5.2–6.6)	**6.1** (6.0–7.1)*
Pectoral-fin length	**14.9–17.0**	22.3–26.2	**20.6** (19.7–27.1)	**17.1** (17.1–22.6)*
Pelvic-fin length	**13.8–15.2**	12.9–14.3	**10.9** (10.2–15.3)	**11.1** (10.3–13.2)*
Percentage of HL				
Snout length	**29.8–32.8**	31.9–37.3	**36.4** (27.9–41.9)	**29.9** (29.0–33.7)*
Orbit diameter	**28.8–31.1**	28.3–30.3	**30.7** (26.4–34.1)	**33.5** (32–37.4)*
Upper jaw length	**34.4–35.1**	40.7–43.8	**37.5** (33.6–46.5)	**25.6** (24.2–37.8)
Lower jaw length	**48.9–51.0**	53.9–56.7	**48.2** (48.2–61.3)	**51.1** (47.9–64.7)
Interorbital width	**34.0–35.1**	25.5–32.4	**36.8** (30.0–40.1)	**35.7** (31.9–36.9)*

Note: See table 1 for measurements of *Nuchequula mannusella*. Data for holotypes (or syntypes for *N. blochii*) are in boldface.

with gray or lead coloration on the back (Valenciennes, in Cuvier and Valenciennes, 1835). A bright silver longitudinal band was described as separating the gray dorsal and silvery ventral areas. Valenciennes (in Cuvier and Valenciennes, 1835) noted that this species possesses a black blotch on the dorsal fin, but he did not comment on the presence of a nuchal spot. Although the two type specimens we have available (MNHN A-6757, 71.4 mm SL; MNHN A6759, 67.7 mm SL) are quite faded in preservative, they retain a dark brownish marking below the nuchal spine. The two syntypes are covered in guanine ventral to the midline, with some yellowish scales present on the chest and along the flank. The fins are a faint opaque yellow. No remnant of a blotch on the dorsal fin remains in either specimen.

DISTRIBUTION: From western India to Myanmar; Day (1875) had specimens from "Bombay, Malabar, Madras, Calcutta, and Akyab, and many young from the Sunderbunds [Sunderbans]."

REMARKS: Day (1875) confirmed the presence of a nuchal blotch in *N. blochii*, commenting that the species is "silvery with a dark brown blotch over the nape." Day (1875) does not mention whether he examined the syntypes of this species, but he does mention that he looked at specimens from Malabar, the type locality. Given that Day (1875) based his redescription of this species on topotypic material and that the features he presents are in agreement with both the original description of Valenciennes and the type series, we conclude that Day (1875) and Valenciennes (in Cuvier and Valenciennes, 1835) were describing the same species. The additional features that Day presents are most likely a consequence of examining fresher material than that available to Cuvier and Valenciennes at the time of their original description of *N. blochii*.

We initially identified individuals of the new species described here, *Nuchequula mannusella*, as *N. blochii* in the field. Only when we examined

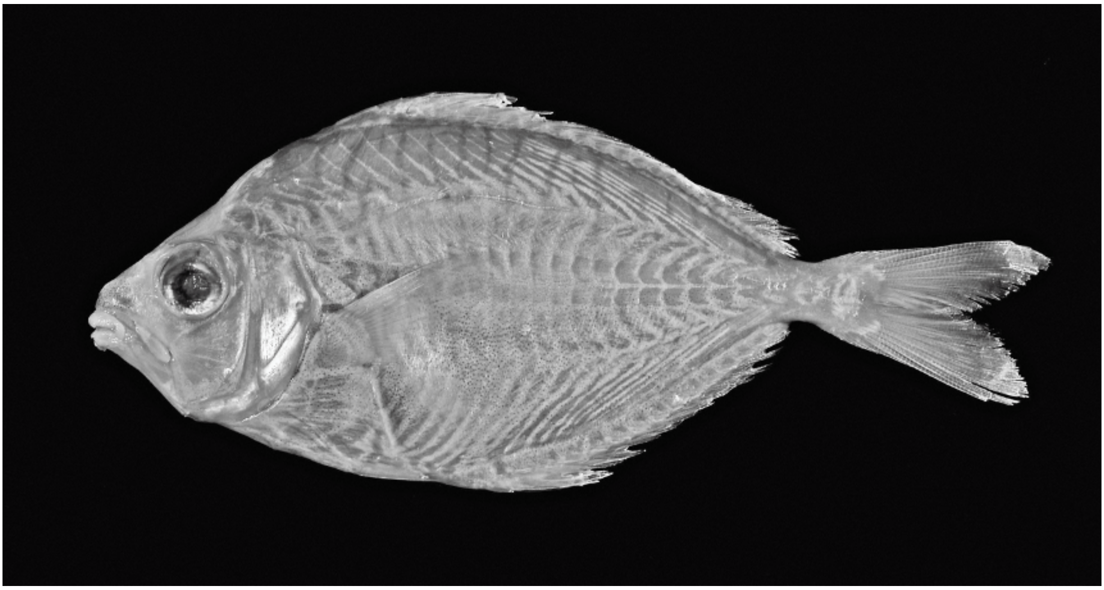

Fig. 8. *Nuchequula decora*, AMS I.22990002, 94.1 mm SL.

the type material and the original description of *N. blochii* did we recognize that our Taiwan material represented a novel species.

Another potentially novel species is what has been identified as *Leiognathus blochii* in Australia. Jones (1985) notes that her description of *N. blochii* from Australia "differs in some respects from accounts of *L. blochii* in the literature. Day (1875) and James (1975), for instance, describe *L. blochii* as having a distinct black blotch on the spinous dorsal fin, whereas in the Australian specimens the dorsal fin is colourless except for a yellow streak at midheight." Jones appears to have been unaware that in the original description of *Nuchequula blochii*, Valenciennes provided one of the few diagnostic characters useful for distinguishing *N. blochii*: the dorsal-fin pigmentation. It is unclear from Jones's (1985) description exactly which species she is referring to, and we have been unable to obtain any of the specimens she examined to corroborate our hypothesis. The main feature she uses to distinguish her Australian "*L. blochii*" from *N. decora* is the possession of scales on the chest in the former, the same feature used by Day (1875) to distinguish *N. blochii* from what he referred to as *Leiognathus brevirostris*.

We have observed that a mitten-shaped melanophore-free region is present posteroventrally from the pectoral-fin base in all species of *Nuchequula* except *N. blochii*. This pigment-free area can be observed only in specimens that lack guanine. Unfortunately, all specimens of *N. blochii* that we have for observation (which we restrict to syntypes) have guanine that obscures this ventral melanophore pattern (assuming that it is present in *N. blochii*). This feature is a synapomorphy of *Nuchequula*, as it has not been observed in other leiognathid species. We note, however, that other ponyfish species have been observed with differently shaped melanophore-free regions, which may prove useful for resolving relationships within the group.

Nuchequula decora (De Vis, 1884)
figures 6B, 8, tables 3–4

Equula decora: De Vis, 1884: 543.
Leiognathus decorus: Jones, 1985: 579–581, fig. 8.

Diagnosis: *Nuchequula decora* is distinguished from congeners by a nuchal spot that is U-shaped or irregularly shaped and concentrated (versus diffuse and rounded or triangular). A central (occasionally more anterior) portion of the nuchal spine associated with the nuchal spot is pigment-free, unlike other *Nuchequula* species, in which it is fully pigmented. In addition, *N. decora* is the only member of *Nuchequula* lacking dorsal-fin markings.

DESCRIPTION: Comparative features are presented in table 3; morphometric and meristic data are presented in table 4. The original description of *Nuchequula decora* by De Vis (1884) is not informative in terms of distinguishing the species from other leiognathids in that no diagnostic features are presented. Jones (1985), who examined type material and fresh material from the same general region (northern Australian waters) of the type series, describes *N. decora* as having "body depth between 43–55%, chest and suborbital naked … second dorsal spine approx. half body depth … gill rakers slightly less than half the length of gill lamellae." Our examination of material identified by Jones as "*Leiognathus decorus*" revealed that the mouth is terminal and directed ventrally when extended. (We base our redescription exclusively on material identified by Jones; see Remarks for a justification.) Teeth are villiform and in a narrow band of three to four poorly differentiated rows. Body depth ranges between 45% and 55% of SL. The length of the second dorsal-fin spine is 35–50% of the body depth; the length of the second anal-fin spine is about 30–40% of body depth. The length of the first dorsal-fin spine is about 12–15% of the second spine. The length of the first anal-fin spine is about 10–20% of the second. The dorsal- and anal-fin spines are weak and often are broken at the tips. In lateral view, a weak concavity is present on the head dorsal to the orbit. The caudal fin is deeply forked. Depth of the caudal peduncle is about 6–7% of SL. The lateral line is complete from the opercle to the posterior margin of the caudal peduncle and is parallel with the shape of the back. The lips are thin but somewhat fleshy. The dorsal- and pelvic-fin origins are located along the same vertical. The anal-fin origin is located on a vertical between the seventh and eighth dorsal-fin spines. There are 16 rakers on the lower limb of the first gill arch. These rakers are about one-quarter to one-half the length of the gill lamellae. Scales are absent on the chest and head but are present throughout much of the rest of the body, including the nape and caudal peduncle. The profile of the lower jaw in lateral view is slightly concave to straight. Two small postnasal spines are present dorsal to the orbit and posterior to the nasal pores; these spines do not protrude much from the body. The supraorbital ridge is very weakly serrated and is not rough to the touch.

Pigmentation pattern in life: We lack fresh material for examination and defer to Jones (1985) for a description of live coloration. Jones (1985) describes *Nuchequula decora* with "body silver, upper half with irregular dark brown wavy to zig-zag vertical lines; brown blotch across nape . . . outer half of spinous dorsal and anal fins yellow, colour continued along margins of rays, caudal fin with dusky yellow margin; other fins colourless."

Pigmentation in preservative: The body is silvery with guanine that becomes more concentrated ventral to the midline. Above the midline, the body is generally light brown. A U-shaped nuchal marking, or a nuchal spot with a small pigment-free region straddling the nuchal spine at its midpoint (or occasionally more anteriorly), is characteristic of this species. Pigmentation pattern on the dorsal flank consists of dark, wavy horizontal lines that are more strongly curved and more concentrated dorsal to the lateral line than ventrally. There is a concentration of melanophores dorsal to the upper lip and anterior to the orbit, as well as in the pectoral-fin axil. The dorsal fin in most preserved specimens is pigment-free, but in some specimens there is a light scattering of melanophores in the membranes of the fin and on the anterior edge of the second dorsal-fin spine.

DISTRIBUTION: Coastal waters surrounding northern Australia. Jones (1985) illustrates the Australian distribution as extending from north of Exmouth in Western Australia to north of Brisbane in Queensland.

REMARKS: In discussing the pigmentation pattern of *Nuchequula decora*, De Vis (1884) mentions "[t]hree dark lines, terminating very obscure bands, across the back, at the base of the soft dorsal and one on the edge of the caudal peduncle." It appears that De Vis was referring to the distinctive vertical bands on the upper flanks that are characteristic of this species. The fact that he mentions only four

Fig. 9. Holotype of *Nuchequula nuchalis*, RMNH 1287, 96.6 mm SL.

lines may indicate that he did not have access to fresh material (see Jones, 1985; Whitley, 1932), as these markings fade in preservation. The type series, a lectotype (QM I.1698) and two paralectotypes (QM I.4877), comprises all small specimens (24–40 mm SL; from fig. 8, Jones, 1985), and individuals of *N. decora* of this size range often lack the characteristic pigmentation pattern of the adults, even as fresh material (Jeff Johnson, QM, personal commun.).

Jones (1985) states in reference to the original description of *Equula decora* by De Vis (1884), "Although no mention is made of a nuchal blotch, this pigmentation often fades on preservation, leaving only the more persistent vertical bands across the back. The body proportions of the type-specimens are consistent with the species as described above." Half of the original six specimens examined by De Vis are lost. The remaining three specimens, all of which are small (24–40 mm SL; from Jones, 1985: fig. 8), have faded in preservative and lack pigmentation. Whitley (1932) commented, "[T]he scales are now rubbed off the types of *Equula decora* and it is impossible to observe whether the breast was naked or scaly … [T]he colours have now faded." Jones (1985) utilizes a number of measurements and other features to tie the type series and original description of De Vis to what she recognized as *Nuchequula decora*. We consider Jones's (1985) redescription as an accurate depiction of *Nuchequula decora* that is in agreement with the original description of De Vis (1884). Jones examined the type series as well as fresh material from the region of the type locality, which lends credibility to her redescription.

Nuchequula nuchalis
(Temminck & Schlegel, 1845)
figures 5B, 6C, 9, tables 3–4

Equula nuchalis: Temminck and Schlegel, 1845: 126, plate 67, fig. 1

Eubleekeria (Nuchequula) nuchalis: Whitley, 1932: 111

DIAGNOSIS: *Nuchequula nuchalis* is distinguished from congeners by the presence of two yellow-green horizontal lines extending from the operculum to the caudal fin. One stripe straddles the lateral line, and the other extends from near the dorsal margin of the operculum to the caudal peduncle.

DESCRIPTION: Comparative features are presented in table 3; morphometric and me-

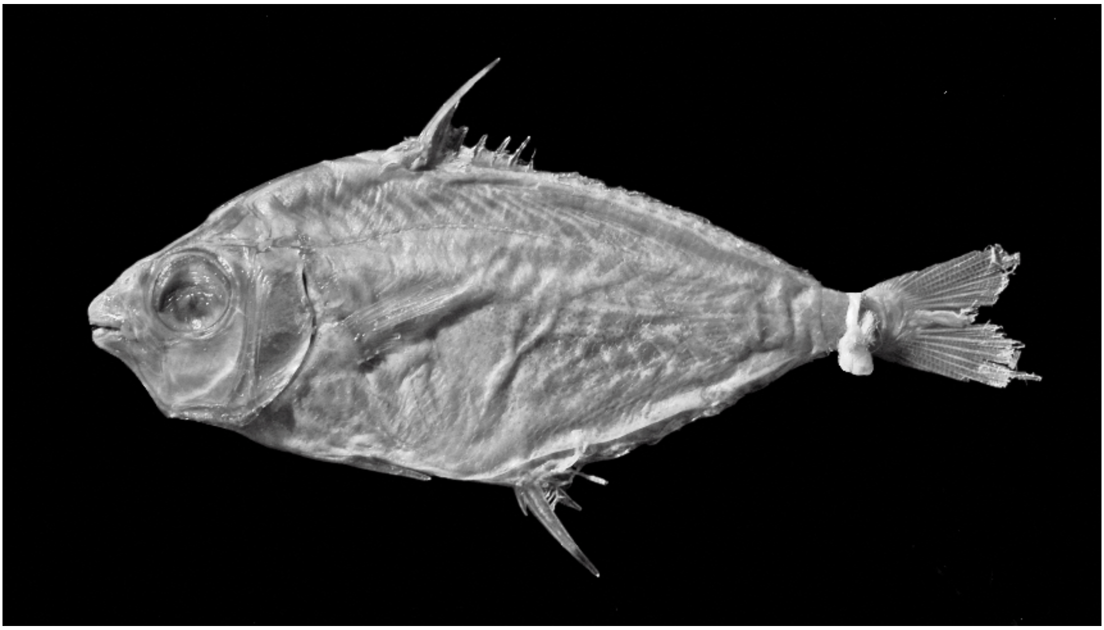

Fig. 10. Holotype of *Nuchequula pan*, CUMZ 2528, 2, 9, 1, 65.0 mm SL.

ristic data are presented in table 4. The original description by Temminck and Schlegel (1845) provides ample distinguishing features to permit clear identification of this species. Although only a single type specimen (which remains in excellent condition), collected off Japan, was deposited, it is clear from the description by Temminck and Schlegel (1845) that additional material was examined. Temminck and Schlegel (1845) described the species as having a blackish blotch on the nuchal area, with the spiny portion of the dorsal fin tinted black.

Our examination of individuals of *Nuchequula nuchalis* revealed that the mouth is terminal and directed ventrally when extended. The teeth are villiform and arrayed in a narrow band of three or four poorly differentiated rows. The body depth ranges between 40% and 50% of SL. The length of the second dorsal-fin spine is around 35–40% of body depth, whereas the length of the second anal-fin spine is about 20–30% of body depth. The length of the first dorsal-fin spine is about 12–15% of the second spine. The length of the first anal-fin spine is about 25–30% of the second spine. The dorsal- and anal-fin spines are robust. In lateral view, a weak concavity is present dorsal to the orbit. The caudal fin is deeply forked. The depth of the caudal peduncle is about 5–7% of SL. The lateral line is complete from the opercle to the posterior margin of the caudal peduncle and is parallel with the shape of the back. The lips are somewhat fleshy. The dorsal- and pelvic-fin origins are located along the same vertical. The anal-fin origin is located on the vertical from the eighth dorsal-fin spine. There are 16 rakers on the lower limb of the first gill arch. These rakers are about one-quarter to one-half the length of the gill lamellae. Scales are absent on the chest, head, and nape but present elsewhere on the flanks. The profile of the lower jaw in lateral view is slightly concave. Two postnasal spines are present dorsal to the orbit and posterior to the nasal pores. The supraorbital ridge is serrated.

Pigmentation pattern in life: The body is silvery, approaching white in the area posteroventral to the pectoral-fin base (see fig. 5B). There are two narrow, yellow-green stripes on the flank. One stripe straddles the lateral line, and another is near the midline, extending from near the dorsal margin of the opercle to the caudal peduncle. There is a mustard-yellow to light-yellow tint to all of the fins, particularly distally. There is more yellow on the edge of the ventral lobe of the caudal fin than there is on the dorsal lobe. There is a distinct black marking on the dorsal-fin membrane between the second and fifth spines. The second through fifth spines are silvery. The nuchal marking is black and triangular or rounded. Light yellow zigzagging lines are present on the dorsal flanks in life, but they rarely extend below the lateral line (Temminck and Schlegel, 1845).

Pigmentation in preservative: The body is silvery, with guanine covering most of the body. A slight golden-yellow tint remains in some areas, particularly where scales are intact. The area dorsal to the midline has a lower concentration of guanine than the region ventral to the midline, and the dorsal flank region is devoid of markings. A large, triangular (sometimes rounded) dark-brown marking is present in the nuchal region. The fins are tan, with some remnant silvery coloration retained on the second through fifth spines of the dorsal fin. The dorsal fin has a distinct black blotch on the membrane of the second through fifth spines. In specimens preserved with the guanine layer intact (including the holotype), the guanine layer appears quite deep and rich, and the specimens are highly reflective. Specimens without guanine are white to a yellowish off-white color throughout the body, and more yellowish on the head. There is a concentration of melanophores dorsal to the mouth and anterior to the orbit. There are scattered melanophores ventral to the midline, except for a mitten-shaped melanophore-free region posteroventral to the pectoral-fin base.

DISTRIBUTION: Coastal waters of Japan (Shikoku Island, Tokyo, and Nagasaki) and Taiwan.

Nuchequula pan (Wongratana, 1988)
figures 6D, 10, tables 3–4

Leiognathus pan: Wongratana 1988.

DIAGNOSIS: *Nuchequula pan* is distinguished from congeners by a series of four broken longitudinal lines on the dorsal flank (versus vertical zigzagging lines, vermiculations, or an absence of dorsal flank markings).

DESCRIPTION: Comparative features are presented in table 3; morphometric and meristic data are presented in table 4. *Nuchequula pan* has a terminal mouth that is directed ventrally when extended. The teeth are villiform and in a narrow band. The body is elongate. (Wongratana lists one paratype as having a body depth of 50% of SL, which is an error, given that the reported range he gives for types is 34.2–42.6% of SL, and our measurement of the same specimen, CUMZ 2528.2.9.3, found its maximum body depth to be 41%.) The length of the second dorsal-fin spine of the holotype and three paratypes we examined ranges from 47% to 54% of the body depth, whereas the length of the second anal-fin spine is 36–50% of body depth. The length of the first dorsal-fin spine is 14–16% of the second spine. The length of the first anal-fin spine is 20–30% of the second. The dorsal- and anal-fin spines are robust. In lateral view, a slight concavity is present above the orbit. The dorsal and ventral profiles are about equally convex. The caudal fin is deeply forked. The depth of the caudal peduncle is about 6–7% of SL. The lateral line is complete from the opercle to the posterior margin of the caudal peduncle. The lips are thin and not fleshy. The dorsal- and pelvic-fin origins are located along the same vertical. The anal-fin origin is located on the vertical from the eighth dorsal-fin spine. There are 15–17 rakers on the lower limb of the first gill arch. Scales are present on the chest. The profile of the lower jaw is slightly concave in lateral view. Two robust postnasal spines are present dorsal to the orbit and posterior to the nasal pores. The supraorbital ridge is weakly serrated. (We disagree with Wongratana's description of this ridge as "smooth.") The body width ranges from about 12% to 16% of SL.

Pigmentation pattern in life: Wongratana (1988) describes fresh material as "iridescent blue-green dorsally, silvery laterally, brilliant silvery white, washed with very pale orange ventrally from pectorals to above middle of anal-fin base … [U]pper half of body with four longitudinal rows of elongate, greenish blue spots, third row on lateral line, fourth below … prominent greenish-blue blotch across nape." The pigmentation pattern and coloration in life may also be diagnostic but should be verified with more recently collected material, as Wongratana described these specimens after having collected them more than a decade earlier.

Pigmentation in preservative: The material we examined has lost most of their pigmentation in preservation except nuchal and black dorsal-fin markings. This dorsal-fin marking is present on the edges of the second through fifth spines; unfortunately, the membrane is broken between these spines. According to Wongratana (1988), "Preserved specimens light brown on body and head; markings on back and sides obscure, blotch on nape diffuse. Snout and pectoral axil dusky. Inner surface of opercle dotted with dark [sic]. Breast dusky; lower sides conspicuously paler below pectoral fins, dusky posteriorly. Black blotch on spinous dorsal fin distinct." The reference to the pale area below the pectoral fins is what we refer to as the mitten-shaped, pigment-free area that is diagnostic of *Nuchequula*.

DISTRIBUTION: Currently known only from the type series, which was collected in the Gulf of Thailand. Additional specimens were reported from the Andaman Sea in the original description.

REMARKS: The relative length of the second and third dorsal-fin spines may be an additional diagnostic character for this species. In our examination of types, the third spines are about one-half to three-quarters the length of the second spines. If this difference in length can be confirmed in additional material, it would be diagnostic for *Nuchequula pan*, given that all other species of *Nuchequula* have second and third dorsal-fin spines of about equal length.

The prominent spinous dorsal-fin markings and horizontal lines on the flanks may suggest a close relationship between this species and *N. nuchalis*. These two species are the only members of *Nuchequula* that possesses horizontal markings on the flanks; however, in *N. nuchalis* these lines are not broken as they are in *N. pan* but continuous. In addition, the horizontal lines are more pronounced and are better retained in preservative in *N. pan* (Wongratana, 1988). The maximum size recorded for the species is that of the holotype at 65.0 mm SL, making it apparently the shortest *Nuchequula* species. Apart from the 10 specimens included in the type series, we were unable to locate any additional specimens of *N. pan* in museum collections.

FREQUENT MISIDENTIFICATIONS

Redescriptions of ponyfishes should be viewed with skepticism if no attempt is made to link these descriptions to the type specimens and/or original species descriptions. Several studies of this nature have contributed to the spread of misinformation in the literature regarding both the identity of and the features useful for distinguishing many species of ponyfishes. In Huang (1985), an illustration of a specimen resembling *Nuchequula decora* is labeled *Leiognathus rivulatus*, which is a much more elongate and very differently pigmented species than the more deep-bodied, nuchal-spotted specimen illustrated. Because this book is a guide, it is unfortunate that it inaccurately represents both the scientific name and the species illustrated. Another good example of the problem of not viewing type material or consulting original descriptions is provided by accounts of *Leiognathus brevirostris* (Valenciennes, in Cuvier and Valenciennes, 1835) in the literature, a species that has long been erroneously reported to be elongate and to possess a nuchal spot (Day, 1875; Kühlmorgen-Hille, 1974; Chen and Fang, 1999). More recently, several authors (e.g., Jones, 1985; Bauchot and Desoutter, 1989) have considered *L. brevirostris* a junior synonym of *Leiognathus bindus*. Our examination of a syntype of *Leiognathus brevirostris* (MNHN A-6763) agrees with this conclusion. *Leiognathus bindus* is a markedly deep-bodied species that does not conform well to redescriptions of *L. brevirostris* perpetuated in the literature. Although Valenciennes (in Cuvier and Valenciennes, 1835) based his description of *Equula bindus* exclusively on the informal description and illustration of "Bindoo Karah" by Russel (1803; i.e., no specimens were examined), he described *Equula brevirostris* on the basis of actual specimens. It appears that Day (1875) was the first erroneously to attribute a nuchal spot to *E. brevirostris*, doing so without examining the type material. Day correctly credits Cuvier and Valenciennes with the original description of *E. brevirostris*, but incorrectly cites page 84 in that text, which corresponds instead to the description of *E. blochii*. Day states that *E. brevirostris* has "a dark brown transverse blotch across the nape of the neck" and that "[t]there are two Indian *Equula*'s very similar, the one described above, *E. brevirostris*, which is destitute of scales on the breast and chest, but which is otherwise similar to the second or *E. blochii*." Without having examined the type series of *E. brevirostris*, it would be impossible for Day to justify these comments. (We presume that Day did not examine type material for this species, because for other species he is explicit if he or an aide examined type specimens; he did not make such a note for *E. brevirostris*.) The type specimens of *E. brevirostris* and *E. blochii* are very different in body shape. *Equula brevirostris* is deep-bodied (53% of SL), whereas *E. blochii* is elongate (39% of SL). Jones (1985) recognized this discrepancy and noted, "James (1975) states that *L. brevirostris* has a naked chest and teeth arranged in villiform bands, whereas the syntypes of the species have a fully scaled chest, and teeth arranged in a single row in each jaw … *Equula brevirostris* is recognized here as a junior synonym of *L. bindus* (Valenciennes)." Because it lacks a nuchal marking, *E. brevirostris* is not included within our concept of *Nuchequula*; however, we consider it likely that the photographed specimens with nuchal markings labeled *Leiognathus brevirostris* in Chen and Fang (1999) and Shen (1993) are *Nuchequula mannusella*.

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. *Gazza* n. sp. "Madagascar": AMNH 236138.

Leiognathus edentulus: ZMB 8756, holotype (dry skin; photograph and radiographs examined). *Leiognathus edwardsi*: USNM 55904, holotype. *Leiognathus equulus*: ZMUC P48219, lectotype (dry skin; photographs and radiographs examined); ZMUC P48220, paralectotype (dry skin, photograph and radiograph examined); AMNH 59535; AMNH 88039; AMNH 237139; CAS 57306; CAS-SU 35627; CAS-SU 38781; MNHN A-6723; UMMZ 191520; UMMZ 235029; UMMZ 238805 (in part); UMMZ 240133; UMMZ 240502; UMMZ 240503; UMMZ uncat. *Leiognathus robustus*: UMMZ 242144, holotype; AMNH 233607, 1 ex., paratype; UMMZ 240362, 1 ex, paratype; UMMZ 240360. *Leiognathus fasciatus*: AMNH 15520; AMNH 237140; CAS 1872; UMMZ 240504; UMMZ uncat.; USNM 191962; USNM 191966. *Leiognathus* n. sp. "Madagascar": AMNH 237141; AMNH 237142; AMNH 237143. *Leiognathus* n. sp. "Singapore": UMMZ 240361. *Leiognathus longispinis* (= *L. smithursti*): MNHN A-0579, holotype; AMNH 219296; AMS I.20907036; AMS I.22974001; AMS 22981001; AMS 23044001; USNM 324651. *Leiognathus* n. sp. "Sri Lanka": FRLM uncat.

"Leiognathus" daura: USNM 100291; USNM 373281. *"Leiognathus" dussumieri*: MNHN A-6721, syntype, 1 ex.; AMNH 234763. *"Leiognathus" jonesi*: UMMZ 240134; UMMZ 240505; UMMZ uncat. "*Leiognathus*" philippinus: ANSP 47486, holotype; ANSP 47487, paratypes, 4 ex.; UMMZ 240130. *"Leiognathus" splendens*: CAS 1485; CAS 38789; CAS 56438; CAS 56441; MNHN A-6724; UMMZ 191202; UMMZ uncat.; USNM 190258; USNM 190263.

Nuchequula blochii: MNHN A-6757, syntype, 1 ex.; MNHN A-6759, syntype, 1 ex. *Nuchequula decora*: AMNH 231297, AMS I.22990002; *Nuchequula mannusella*: ASIZP0059839; ASIZP0065686. *Nuchequula nuchalis*: RMNH 1287, holotype; AMNH 26819; AMNH 34861; AMNH 26819; AMNH 238766; CAS-SU 4757; UMMZ 240143. *Nuchequula pan*: CUMZ 2528.2.9.1, holotype; CUMZ 2528.2.9.2, paratype, 1 ex.; CUMZ 2528.2.9.3, paratype, 1 ex.; USNM 276536, paratype, 1 ex.

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; syntype of *Equula brevirostris*: MNHN A-6763. *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. *Photopectoralis sp.* "East China Sea": AMNH 237148.

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 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. *Photoplagios leuciscus*: BMNH 1858.4.21.243, holotype; AMNH 237149; AMS I.22967001; AMS I.22978004; AMS I.34365015; ANSP 27525, holotype of *Leiognathus vermiculatus*; UMMZ 240125; UMMZ uncat.; USNM 76609; USNM 191979; USNM 191991; USNM 307917; USNM 373280. *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 stercorarius*: USNM 55906, holotype; USNM 126395, cotype; ANSP 33289, paratype, 1 ex.; CAS 42171, paratype; CAS 17678; CAS-SU 20004, paratype, 1 ex.; UMMZ 240138; UMMZ uncat.; USNM 191996. *?Photoplagios (Leiognathus) oblonga*: MNHN A-6754, holotype. *?Photoplagios (Leiognathus) parviceps*: MNHN A-0580, syntype, 1 ex. *?Photoplagios sp.*: MNHN 1988-0327.

Secutor indicius: UMMZ 240127; UMMZ uncat. *Secutor insidiator*: CAS 29894; UMMZ uncat. *Secutor megalolepis*: UMMZ 240135. *Secutor ruconius*: CAS-SU 29895; UMMZ 225240; UMMZ uncat. *Secutor* n. sp. "Madagascar": AMNH 232550; AMNH 237150; AMNH 237151; AMNH 237152.

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