A revision of the gobiid fish genus *Odontamblyopus* (Gobiidae: Amblyopinae)

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Abstract The Indo-West Pacific gobiid genus *Odontamblyopus* Bleeker is defined and revised. *Odontamblyopus* is unique within the Amblyopinae in having free and silklike pectoral-fin rays. *Odontamblyopus* comprises four species: *O. lacepedii*, distributed from southern China to Taiwan, Korea, and Japan; *O. roseus*, distributed along the west coast of India; *O. rubicundus*, ranging from the east coast of India to Myanmar; and *O. tenuis*, known only from Pakistan and Myanmar. A key to species is provided. Figures and descriptions of each species are also given. *Odontamblyopus* has often been confused with *Taenioides*; the two genera are compared and characters to distinguish them are provided. The phylogeny and biogeography of *Odontamblyopus* are discussed.

Key words *Odontamblyopus* · Amblyopinae · Gobiidae · Taxonomic revision · Relationships

Gobies of the subfamily Amblyopinae are inshore, mud-dwelling fishes of the Indo-West Pacific region. Members of this subfamily are commonly referred to as "eel gobies" or "worm gobies" because of their elongate bodies with a continuous dorsal fin. The subfamily is not speciose, likely comprising fewer than 30 species in 12–13 genera.

The Amblyopodini was established by Bleeker (1874). This taxon comprised a new genus (*Odontamblyopus*) and four other genera including *Taenioides*. Since Bleeker erected *Odontamblyopus*, the genus has been considered monotypic by many authors including, most recently, Koumans (1953), Fowler (1972), Lindberg and Krasyukova (1989), and Kottelat et al. (1993). Norman (1966) is the only recent author who listed *Odontamblyopus* as having "two or more" species. In their survey of character distributions of constituent members of the *Taenioides* group of the Amblyopinae, Birdsong et al. (1988: 196) assigned all specimens of *Odontamblyopus* to *O. rubicundus*. The variation in vertebral counts caused the authors to speculate, however, that *Odontamblyopus* may be more speciose. That statement was the impetus for this study.

Odontamblyopus has been confused, or synonymized, with *Taenioides* by some authors including Jordan and Snyder (1901), Weber (1913), Hora (1924), Tomiyama (1936), and Akihito et al. (1984). Other authors (Bleeker, 1874; Koumans, 1931; Norman, 1966) have distinguished *Odontamblyopus* from *Taenioides* based on the presence or absence of chin barbels. Although all *Taenioides* do possess four or more chin barbels, some *Odontamblyopus*, especially juveniles, do so as well. This character was probably most responsible for the confusion regarding the proper identification of *Odontamblyopus* and *Taenioides*.

The objectives of this study are (1) to revise and define *Odontamblyopus* using putative derived characters, (2) to provide characters for recognizing the included species, (3) to list synonyms for all valid forms, and (4) to provide and analyze distributional and ecological data.

Materials and Methods

All measurements are straight-line distances made with dial calipers and recorded to the nearest 0.1 mm. All fish lengths given are standard lengths (SL) except where noted as total length (TL). Methods of measurements and counts follow Murdy (1989) except as follows.

In amblyopines, the spinous elements of the dorsal and anal fins are soft and flexible. Additionally, the spinous (first) and soft (second) dorsal fins are connected by membrane; the anteriormost ray (or spine) associated with two pterygiophores was determined as the first element of the "second dorsal fin" as in other gobiids, following Akihito et al. (1984). In *Odontamblyopus*, the first element of the second dorsal and anal fins is formed variably by a spine, or a branched or unbranched ray; such variation is intraspecific rather than interspecific within the genus.

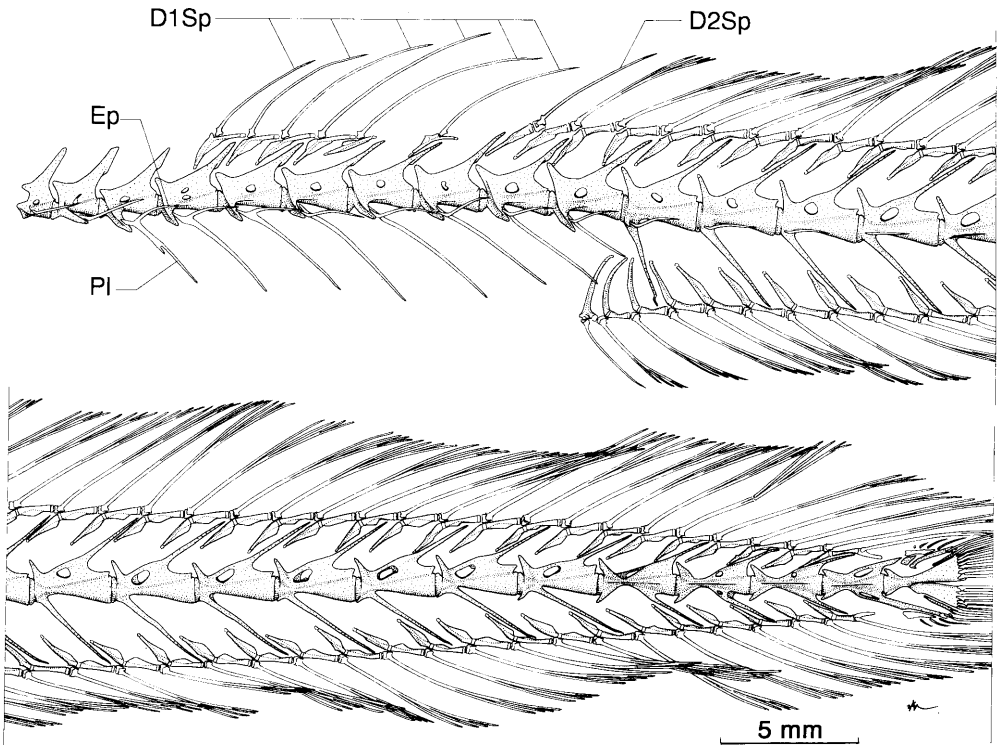

Fig. 1. Vertebrae and median fin elements of *Odontamblyopus tenuis*, NSMT-P 57164, male, 107.9-mm SL. *D1Sp*, first dorsal-fin spine; *D2Sp*, second dorsal-fin spine; *Ep*, epineural rib; *Pl*, pleural rib

In contrast to many other gobiids, the ultimate dorsal- and anal-fin pterygiophores of amblyopines support only a single ray (Fig. 1), whereas two rays are typical among other gobiids. We consider this character state in amblyopines to be derived. In those gobiids whose ultimate dorsal- and anal-fin pterygiophores support two rays, the common practice is to count these two rays as a single element. Because the ultimate dorsal- and anal-fin pterygiophores of *Odontamblyopus* only support a single ray, it was counted as such. Unsegmented caudal-fin rays are distinctively shorter (forming rudiments anteriorly) than segmented rays, and were counted from radiographs and specimens cleared and stained. Clearing and staining was done following the method of Potthoff (1984) or, in some instances, Dingerkus and Uhler (1977).

The vertebral count is separated into precaudal and caudal counts, the latter including the urostylar complex; caudal vertebrae possess a distinct hemal spine that is lacking in precaudal vertebrae. Counts of axial skeletal features (i.e., vertebrae, pleural and epineural ribs, pterygiophores, and epurals) were taken from radiographs and cleared and stained material. The methods of Birdsong et al. (1988) were used in describing the relationship between the spinous dorsal fin pterygiophores and the underlying vertebrae. Cephalic sensory papillae were observed on specimens stained with suminol cyanine.

Institutional abbreviations are as listed in Leviton et al. (1985), except for BLIH (Biological Laboratory, Imperial Household, Japan). All specimens examined are listed in the material examined section and grouped by major geographic areas. The total number of specimens and size range follow each catalog number. Data referring to type specimens, including those pertaining to synonyms, are listed by specific name and type category.

Odontamblyopus Bleeker, 1874

(Japanese name: Warasubo-zoku)

Odontamblyopus Bleeker, 1874: 330 (type species, *Gobioides rubicundus* Hamilton-Buchanan, 1822, by monotypy and original designation).

Sericagobioides Herre, 1927: 335 (type species, *Sericagobioides lighti* Herre, 1927, by monotypy and original designation).

Nudagobioides Shaw, 1929: 1 (type species, *Nudagobioides nankaii* Shaw, 1929, by monotypy and original designation).

Included species. *Odontamblyopus* comprises four species: *O. lacepedii*, *O. roseus*, *O. rubicundus*, and *O. tenuis*.

Diagnosis. *Odontamblyopus* is unique within the Amblyopinae in having the pectoral-fin rays free and silklike. Furthermore, *Odontamblyopus* differs from other amblyopines in having the following combination of characters: almost all pectoral-fin rays simple and unbranched; two posteriorly directed symphyseal canine teeth in lower jaw; teeth on outermost row of both jaws fanglike and much larger than those on inner rows; pectoral fin similar in size and length to pelvic fin; dermal

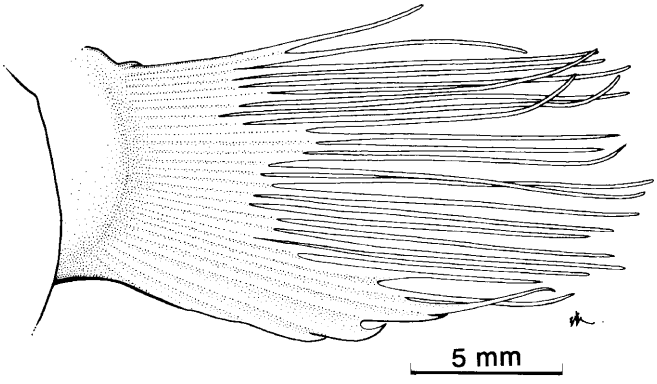

Fig. 2. Lateral view of the pectoral-fin rays of *Odontamblyopus lacepedii*, NSMT-P 47141, male, 147 mm SL

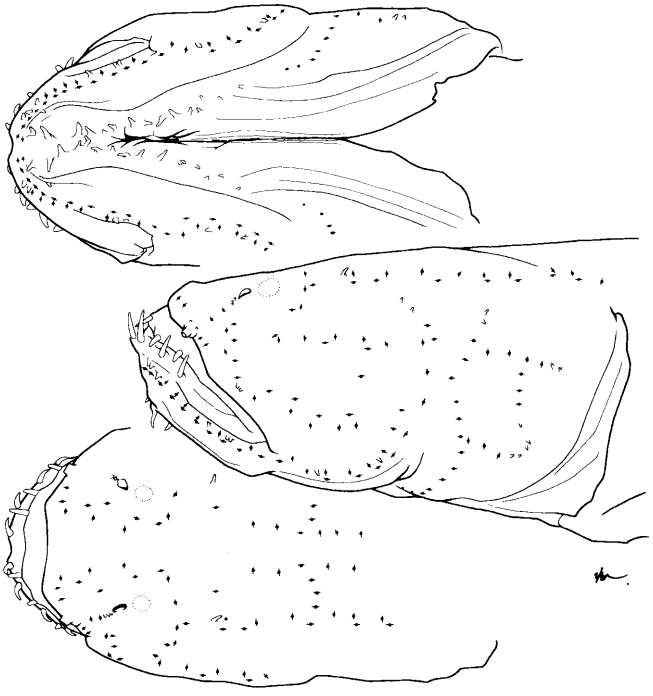

Fig. 3. Ventral (*top*), lateral (*middle*), and dorsal (*bottom*) views of the head of *Odontamblyopus tenuis*, NSMT-P 57164, male, 107.9 mm SL. Sensory papillae, barbels, and fanglike teeth are visible in all views

folds on head and body lacking; small, embedded cycloid scales on head and body; single interneural gap between pterygiophores of spinous and soft dorsal fins; well-developed pleural ribs on 3rd to 10th precaudal vertebrae; no forked proximal or medial radials of dorsal- or anal-fin pterygiophores; and 8 + 7 branched caudal-fin rays.

Description. Total dorsal-fin elements 40–54; first dorsal fin with six flexible spines; first element of second dorsal fin spinous or segmented, and simple or branched, all others segmented and branched rays; dorsal-fin base long and broadly joined with caudal fin. Total anal-fin elements 32–45, first element typically spinous, all other elements segmented and branched; anal-fin height less than second dorsal-fin height; anal-fin membrane broadly joined with caudal fin. Pectoral fin with 20–65 rays, rounded posteriorly, slightly shorter to approximately equal in length to pelvic fin; all pectoral-fin rays segmented, occasionally one or more ventralmost rays branched, all others unbranched; distal membranous connection lacking so that rays are free and silklike (Fig. 2). Pelvic-fin rays I, 5; frenum present; basal membrane uniting fins present throughout length of innermost rays. Caudal fin with 17 segmented rays including 8 + 7 branched rays and a dorsal and ventral simple ray; unsegmented procurrent rays 2–4, dorsally and ventrally.

Scales cycloid, embedded, nonimbricated, and difficult to discern without magnification; present on body and head, largest posteriorly.

Typically, two lateral rows of teeth in each jaw, more than two rows anteriorly; outer-row teeth much larger and more pointed than those of inner rows; lower-jaw teeth longer than upper-jaw teeth; 6–18 fanglike teeth in outer row of upper jaw, typically interlocking with those of lower jaw; numerous conical teeth on inner rows of upper jaw; 6–12 fanglike teeth in outer row of lower jaw; numerous conical teeth in inner rows of lower jaw. Two stout caninoid teeth internal to symphysis of lower jaw. No palatine nor vomerine teeth present.

Tongue thick, tip rounded, free from floor of mouth [in contrast to Hoese (1984), who stated amblyopines have the tongue fused to floor of mouth]. Gape wide, mouth oblique; maxilla extending posteriorly to vertical below anterior half of eye; posteriorly, near tip of maxilla, upper lip expanded into large fold that joins similar fold of lower lip at rictus, fold completely covers posterior part of jaws even when agape. Adults of most species, except *O. tenuis*, typically lack barbels on underside of head. In *O. tenuis*, small barbels (10–20 in number) extend posteriorly in two rows starting near lower jaw (Fig. 3). For other *Odontamblyopus* that possess barbels, the barbels are small and few in number (2–8).

Eye rudimentary, but distinct, covered by skin, slightly larger than length of posterior nostril. Posterior nostril located immediately anterolateral to eye; anterior nostril at tip of small flap that slightly overhangs upper jaw.

Cephalic sensory canals and pores absent. Sensory papillae present on head, but not found on dermal folds (Fig. 3). Sensory papillae rows also present on body, but difficult to observe without use of a stain such as suminol cyanine.

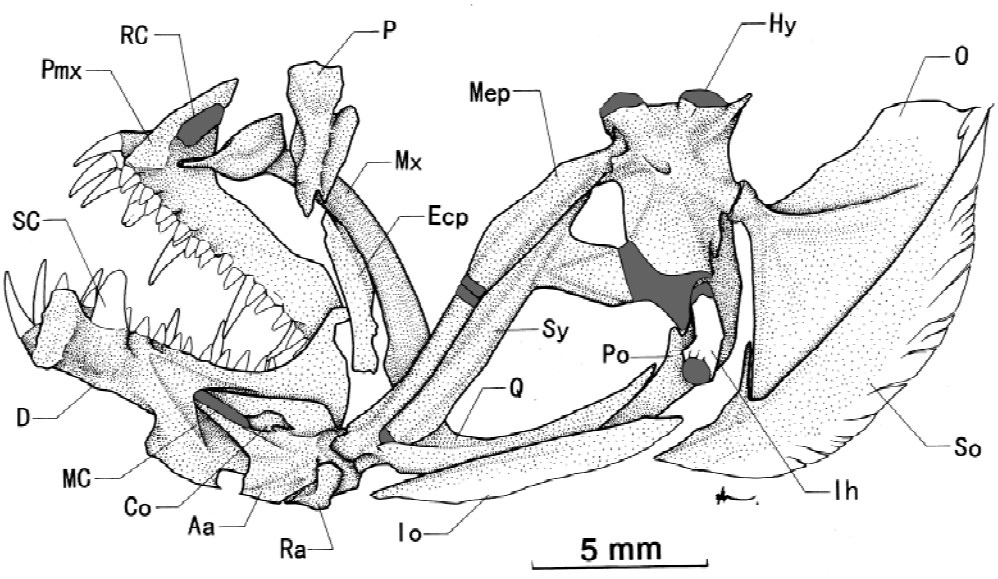

Fig. 4. Internal view of the jaws, suspensorium, and opercular bones of *Odontamblyopus lacepedii*, MTUF 25841, male, 210 mm SL. *Aa*, anguloarticular; *Co*, coronomeckelian; *D*, dentary; *Ecp*, ectopterygoid; *Hy*, hyomandibula; *Ih*, interhyal; *Io*, interopercle; *MC*, Meckel's cartilage; *Mep*, metapterygoid; *Mx*, maxilla; *O*, opercle; *P*, palatine; *Pmx*, premaxilla; *Po*, preopercle; *Q*, quadrate; *Ra*, retro-articular; *RC*, rostral cartilage; *SC*, symphyseal canine tooth; *So*, subopercle; *Sy*, symplectic

Gill rakers short, blunt, and not ossified; gill opening narrow, extending only the length of pectoral-fin base or slightly more ventrally. Small pseudobranchial filaments present, but secondary gill lamellae reduced.

Osteology. Spinous dorsal-fin pterygiophore formula 3-12210. Precaudal vertebrae 10, caudal vertebrae 17, or 20–24. Pterygiophore of the second soft dorsal-fin ray (posteriormost pterygiophore inserting in 8th interneural space) lacks a medial radial. Two or three anal-fin pterygiophores anterior to first hemal spine. Epurals 2. Basihyal spatulate. Symplectic with a posteriorly directed arm that cartilaginously joins the hyomandibula; this arm creates a prominent gap between dorsal aspect of symplectic and the hyomandibula (Fig. 4). Dorsoposterior tip of metapterygoid in contact with inner surface of hyomandibula (Fig. 4). Infrapharyngobranchials 2–4 present. Atlas with well developed parapophyses, in contact with first epineural rib. Epineurals present from 1st precaudal vertebra to 3rd caudal vertebra in *O. lacepedii*; 3rd or 5th caudal vertebra in *O. rubicundus*; 5th in *O. tenuis*; and 10th in *O. roseus*. Well-developed pleural ribs on 3rd to 10th precaudal vertebrae. Numerous minute, circular cavities on lateral surface of opercle and subopercle. All medial and proximal radials of anal- and dorsal-fin pterygiophores simple and not forked.

Comparisons with *Taenioides*

Because of their similarities in size and shape, *Odontamblyopus* has been most often confused with *Taenioides*. However, *Taenioides* is easily distinguished from *Odontamblyopus* as follows: pectoral fins much reduced in comparison to pelvic fins, typically only 40%–50% of pelvic-fin length (vs pectoral-fin length typically 80%–100% of pelvic-fin length in *Odontamblyopus*); almost all pectoral-fin rays branched (vs almost all rays simple); symphyseal canine teeth on lower jaw absent (vs present); head and body naked (vs covered by small, embedded cycloid scales); dermal folds on head well developed (vs not developed); proximal radial of second anal-fin pterygiophore forked (vs not forked); and pleural ribs absent (vs long, well-developed and diagonally oriented).

Key to the species of *Odontamblyopus*

1a. Pectoral-fin rays more than 45, typically 55–60; chin with numerous small barbels. (Pakistan, Myanmar) . . . . . *O. tenuis*

1b. Pectoral-fin rays fewer than 35, typically 25–30; chin with only a few barbels or totally lacking barbels 2

2a. In preservative, distal margins of dorsal and anal fins tinged chocolate-brown; dorsal surface of skull bony; epineurals present from 1st precaudal vertebra to 10th caudal vertebra (west coast of India) . . . . . *O. roseus*

2b. In preservative, distal margins of dorsal and anal fins the same color as rest of fin but not chocolate-brown; dorsal surface of skull covered by adductor mandibulae muscle; epineurals present from 1st precaudal vertebra to 3rd or 5th caudal vertebra. 3

3a. Caudal fin very long, standard length typically less than 80% of total length; total dorsal-fin elements 40–47; anal-fin elements 33–40; caudal vertebrae 17; 3 anal-fin pterygiophores preceding first

hemal spine (east coast of India, Bangladesh, Myanmar) . . . . . *O. rubicundus*

3b. Caudal fin long, standard length more than 80% of total length; total dorsal-fin elements 44–55; anal-fin elements 36–45; caudal vertebrae 20–24; 2 (rarely 3) anal-fin pterygiophores preceding first hemal spine (China, Hong Kong, Taiwan, Korea, Japan) . . . . . *O. lacepedii*

Odontamblyopus tenuis (Day, 1876)

(Figs. 1–6, Table 1)

Gobioides tenuis Day, 1876: 319, pl. 69, Fig. 3 (type locality, Sind, Pakistan).

Material examined (26 specimens from 1 locality; size range 55–128). Myanmar, Hlaing River 16°53′41″N, 96°05′28″E: AMS I 39089-001, 6:55–93; NSMT-P 57164, 8:82–128; NTM S.14865-001, 6:70–92; USNM 356396, 6:77–108.

Diagnosis. Easily distinguished from congeners by its high number of pectoral-fin rays, 46–65 (mean = 59.5), the highest in the genus; extremely elongate body, HL/SL 0.078–0.130 (mean = 0.114); and narrow head, HW/SL 0.040–0.059 (mean = 0.054). Barbels present on underside of chin.

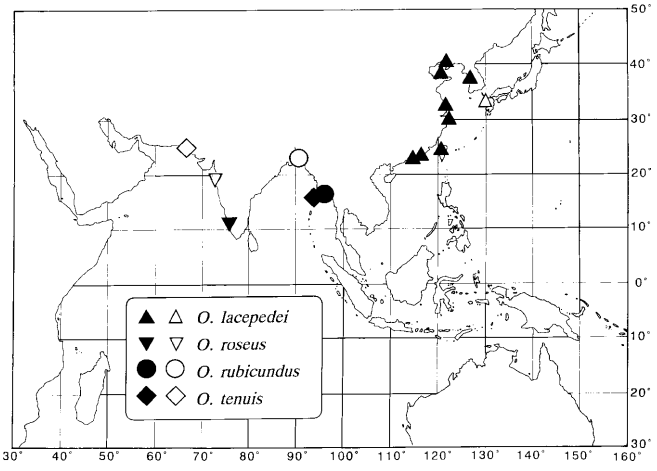

Fig. 5. Geographic distributions of the four species of *Odontamblyopus*. *Open symbols* represent location of type specimens; *closed symbols* may indicate more than one collection or specimen

Description. As for genus except as follows. Total elements in dorsal fin 40–42 (mean = 40.4); total elements in anal fin 32–35 (mean = 33.2); fanglike upper-jaw teeth 5–10 (mean = 7.2); fanglike lower-jaw teeth 7–12 (mean = 8.3); anal-fin pterygiophores preceding the first hemal spine (AP) 3–4 (mean = 3.08); vertebral count 10 + 17; SL/TL 0.739–0.817 (mean = 0.779); pectoral-fin length (PEL)/SL 0.084–0.094 (mean = 0.091); PEC/SL 0.084–0.119 (mean = 0.102); pelvic-fin length (PEL)/HL 0.710–1.08 (mean = 0.822); PEC/PEL 0.978–1.26 (mean = 1.12); PEC/HL 0.746–1.08 (mean = 0.912).

Coloration. No fresh specimens were available to us. Based on the original description, this species has a "general roseate tinge, fins colourless except the caudal which is dark with a light outer edge." In preserved material, dorsum of head and body dark brown to gray, remainder of head and body uniformly pale or pale brown; faint black melanophores on caudal-fin rays and on proximal part of dorsal-fin rays and occasionally on dorsal spines; pectoral, pelvic, and anal fins nearly translucent; fanglike teeth on outer rows of both jaws often reddish-brown in larger specimens.

Distribution. Pakistan and Myanmar.

Ecology. We have no information on the ecology of this species.

Remarks. Day (1876) based his description on a single specimen (7.25 in. in length) collected from Sind, Pakistan; the holotype (ZSI 2071) is lost according to Eschmeyer (1998). We see no need to designate a neotype as this species was easily identifiable based on characters provided in Day's description.

All our specimens were obtained by Carl J. Ferraris, Jr., on October 31, 1997, from a fish market along the Hlaing River, southern Myanmar. According to Dr. Ferraris, the specimens were collected by tiger-mouth net. It is assumed the specimens were obtained in the river near the market. The only other record known to us is that of the type.

Nguyên (1991) reported an unidentified species of *Odontamblyopus* from Vietnam and stated that the

Fig. 6. *Odontamblyopus tenuis*, NSMT-P 57164, 98.0 mm SL, 120.9 mm TL, Hlaing River, Myanmar

Table 1. Selected meristic counts for species of *Odontamblyopus*

	Dorsal-fin rays (total elements)														
	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54
O. lacepedii					1	2	1	3		3	2	3	3		2
O. roseus				1		1		3	1						
O. rubicundus	3			3	3	5		1							
O. tenuis	19	4	3												

	Anal-fin rays (total elements)													
	32	33	34	35	36	37	38	39	40	41	42	43	44	45
O. lacepedii					1	2	1	1	1	3	3	3	3	2
O. roseus					1		1	1	2		1			
O. rubicundus		2		3	4	5			1					
O. tenuis	4	16	4	2										

	Pectoral-fin rays																								
	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42		
O. lacepedii					1	3		1	1		2		1	1											
O. roseus	1	1					1	1	2																
O. rubicundus						1	2	1	4	2	4	2	1	1											
O. tenuis																									

	Pectoral-fin rays (continued)																								
	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65		
O. lacepedii																									
O. roseus																									
O. rubicundus																									
O. tenuis				2										2	4	4	8	10	15	4	1	1	1		

	Upper-jaw teeth (outer row)														Lower-jaw teeth (outer row)								
	5	6	7	8	9	10	11	12	13	14	15	16	17	18	6	7	8	9	10	11	12		
O. lacepedii			2				1	1	1								2	1	1	1			
O. roseus									1				1	1			1	1	1				
O. rubicundus		3	4	1	1										1	1	6	1					
O. tenuis	2	5	10	6	2	1										6	12	˜5	2		1		

species possessed: VI, 39–42 dorsal-fin rays; 37–41 anal-fin rays; 43–50 pectoral-fin rays; 10 + 19 (18, 20) vertebrae. Although the high pectoral-fin ray count and the general appearance indicated in Nguyên's figure of this species are similar to those of *O. tenuis*, the other meristics are not in accord. As Nguyên's specimens were not available to us, we were unable to ascertain the identity of this species.

Odontamblyopus roseus (Valenciennes, 1837)

(Figs. 5, 7, Table 1)

Amblyopus roseus Valenciennes in Cuvier & Valenciennes, 1837: 164 (type locality, Bombay [Mumbai], India)

Material examined (11 specimens from 2 localities; size range 86–134). India, Bombay (Mumbai): MNHN A. 1447, lectotype of *Amblyopus roseus* Valenciennes, 107; MNHN 2000-300, paralectotypes of *Amblyopus roseus* Valenciennes, 2: 92–97; CAS 29610, 2:86–87; USNM 346544, 4:75–102. Kerala: CAS 29747, 1:134; USNM 346545, 1:111.

Diagnosis. In preservative, distal margins of dorsal and anal fins tinged chocolate-brown. Top of skull bony, adductor mandibulae complex not originating from frontal bone as in congeners. Vertebral count 10 + 22. Epineurals present from 1st precaudal vertebrae to 10th caudal vertebrae.

Description. As for genus except as follows. Total elements in dorsal fin 43–49 (mean = 46.3); total elements in anal fin 36–42 (mean = 39.2); pectoral-fin rays 20–28

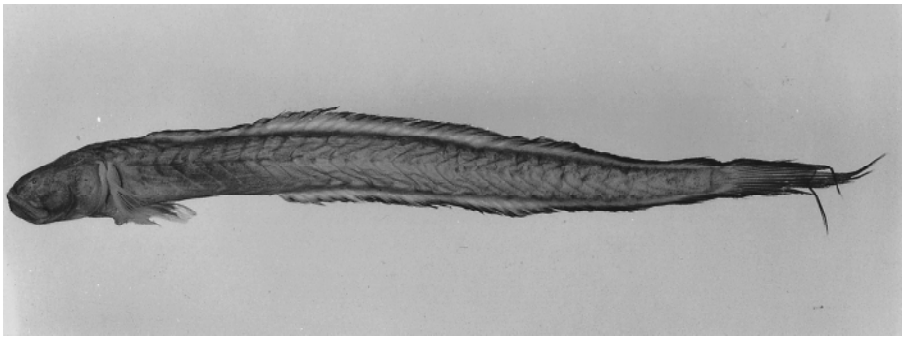

Fig. 7. *Odontamblyopus roseus*, CAS 29747, 134 mm SL, 171 mm TL, female, Cochin, India

Fig. 8. *Odontamblyopus rubicundus*, USNM 302348, 114 mm SL, 143 mm TL, Bangladesh

(mean = 25); upper-jaw teeth (outer row) 13–18 (mean = 16); lower-jaw teeth (outer row) 8–10 (mean = 9); AP 2 (mean = 2); SL/TL 0.783–0.812 (mean = 0.802); HL/SL 0.144–0.182 (mean = 0.168); PEL/SL 0.124–0.151 (mean = 0.141); PEC/SL 0.120–0.158 (mean = 0.139); HW/SL 0.072–0.080 (mean = 0.077); PEL/HL 0.804–0.865 (mean = 0.841); PEC/PEL 0.915–1.05 (mean = 0.988); PEC/HL 0.777–0.889 (mean = 0.829). Several short barbels present on underside of chin in one adult specimen (CAS 29747).

Coloration. No fresh material was available for this study. In preserved specimens, distal margins of dorsal and anal fins are tinged chocolate-brown; much of distal portion of caudal fin is chocolate-brown; body tannish. Body with a general roseate tinge according to Valenciennes (1837).

Distribution. Pakistan and west coast of India. Specimens have only been examined from two localities, Bombay (Mumbai) and Cochin, India.

Ecology. We have no information on the ecology of this species.

Remarks. Day (1876) speculated this species may be synonymous with his *Gobioides tenuis* (described above as *O. tenuis*). However, the high number of pectoral-fin rays, along with other character distributions, clearly separates *O. tenuis* from *O. roseus*. The unique condition of cheek musculature and numerous epineurals distinguishes this species from congeners. Cheek musculature is not only unique with the genus but also within the Amblyopinae; it is a putative autapomorphy for this species. The presence of epineurals from the 1st precaudal to the 10th caudal vertebra, although similar to the condition found in most other amblyopines, is not shared with the three congeners of *O. roseus* (i.e., *O. lacepedii*, *O. rubicundus*, and *O. tenuis*).

From the syntypic series of *O. roseus*, we hereby designate MNHN A. 1447 as lectotype (107 mm SL, 127 mm TL) with MNHN 2000-300 comprising two paralectotypes (92 and 97 mm SL, 116 and 121 mm TL).

Odontamblyopus rubicundus (Hamilton-Buchanan, 1822)

(Figs. 5, 8, 9, see Table 1)

Gobioides rubicundus Hamilton-Buchanan, 1822: 37, pl. 5, fig. 9 (type locality, estuaries of the Ganges River)

Amblyopus mayenna Valenciennes *in* Cuvier and Valenciennes, 1837: 163 (type locality, Rangoon, Burma [Myanmar])

Amblyopus taenia Günther, 1861: 135 (type locality, East Indies)

Taenioides rubicundus Tomiyama, 1936: 102 (new combination)

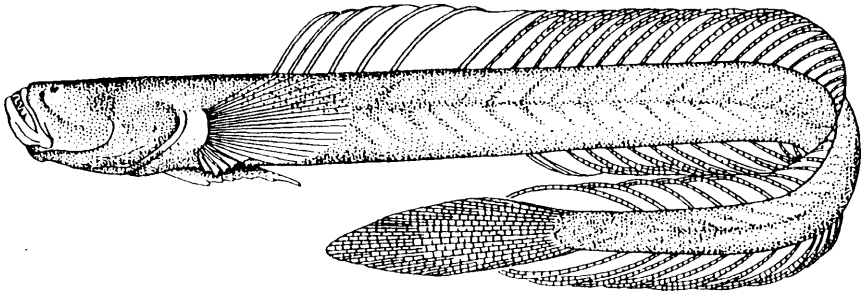

Fig. 9. *Odontamblyopus rubicundus*. (From Koumans, 1953)

Material examined (15 specimens from seven localities; size range 48–209). Myanmar, Rangoon (Yangon): MNHN A. 1466, syntypes of *Amblyopus mayenna* Valenciennes, 3 specimens: 75–81; ANSP 77022, 4:89–113; CAS 140242, 1:48; India, Ganges: MNHN A. 1467, syntype of *Amblyopus mayenna* Valenciennes, 54. Uttarbhag: CAS 134772, 1:88. Pulta: CAS 134773, 2:156–172. Bombay(?): ANSP 85791, 1:105; Bangladesh: USNM 302348, 1:114; "East Indies": BMNH 1860.3.13.968, holotype of *Amblyopus taenia* Günther, 209.

Diagnosis. Caudal fin very long, standard length typically less than 80% of total length [SL/TL 0.749–0.824 (mean = 0.784)]; total dorsal-fin elements 40–47; anal-fin elements 33–40; caudal vertebrae 17; 3 anal-fin pterygiophores preceding first hemal spine.

Description. As for genus except as follows. Total elements in dorsal fin 40–47 (mean = 43.5); total elements in anal fin 33–40 (mean = 36.0); pectoral-fin rays 25–33 (mean = 28.9); upper-jaw teeth (outer row) 6–9 (mean = 7.0); lower-jaw teeth (outer row) 6–9 (mean = 7.8); HL/SL 0.136–0.237 (mean = 0.181); PEL/SL 0.096–0.191 (mean = 0.136); PEC/SL 0.097–0.229 (mean = 0.131); HW/SL 0.085–0.133 (mean = 0.101); PEL/HL 0.711–0.810 (mean = 0.755); PEC/PEL 0.812–1.20 (mean = 0.952); PEC/HL 0.628–0.965 (mean = 0.719). Eight small barbels present on the underside of chin of one adult specimen examined (USNM 302348) and small barbels occasionally observed on juveniles.

Coloration. No fresh material was available for this study. Based on the original description, this species is "dirty brown above, and red below." Koumans (1941, 1953) described the color of this fish as ". . . green to red above, red to whitish below. Fins green to red. Caudal fin violet posteriorly." Based on a color slide transparency in Kottelat et al. (1993) (photographed by Hans Horsthemke and provided by Maurice Kottelat) of a specimen collected from the Hooghly River near Calcutta, India, and photographed in an aquarium, the body and median fins are silvery-white and the caudal fin, dark brown to black. Curiously, in this photo, the pectoral-fin rays are spread in a circular pattern at a right angle to the body.

In preserved specimens, dorsum of head and body, occasionally, septum of myomeres dark brown; dorsal-fin rays brown to gray; caudal fin dark brown to black with narrow pale streaks dorsally and ventrally; all other fins pale.

Distribution. East coast of India eastward to Myanmar.

Ecology. Found in estuaries (Hamilton-Buchanan, 1822).

Remarks. According to Eschmeyer (1998), no type specimens of *O. rubicundus* are known. We see no need to designate a neotype as this species was easily identifiable based on the figure and characters provided in Hamilton-Buchanan's description.

Based on available specimens, this species has a much more restricted distribution than has been reported. Excepting for Günther's specimen of *Amblyopus taenia* from the "East Indies" and ANSP 85791 (see following), our examined material ranges only from the east coast of India to Myanmar. In addition to India, Koumans (1953) reported this species from Singapore, Sumatra, Java, Borneo, Ambon, and Malaya. Kottelat et al. (1993) followed Koumans (1953) in reporting *O. rubicundus* from western Indonesia. We, unfortunately, cannot say anything further about the origin of Günther's specimen of *Amblyopus taenia* other than that Koumans (1953) contended that *A. taenia* came from India.

The Bombay (Mumbai) locality for ANSP 85791 (catalogued as *Amblyopus buchanani*) is possibly erroneous. According to E.B. Böhlke (in manuscript), the specimen was donated by the Bombay Natural History Society to Henry Fowler of ANSP in 1925; it is possible that the specimen was not collected from Bombay, only sent from there. Consequently, we have not included this lot on our distribution map (see Fig. 5).

Odontamblyopus lacepedii (Temminck and Schlegel, 1845)

(Japanese name: Warasubo)

(Figs. 5, 10–12; Table 1)

Amblyopus lacepedii Temminck and Schlegel, 1845: 146, pl. 75, fig. 2 (based on Burger figure; figured fish collected from Omura, Japan)

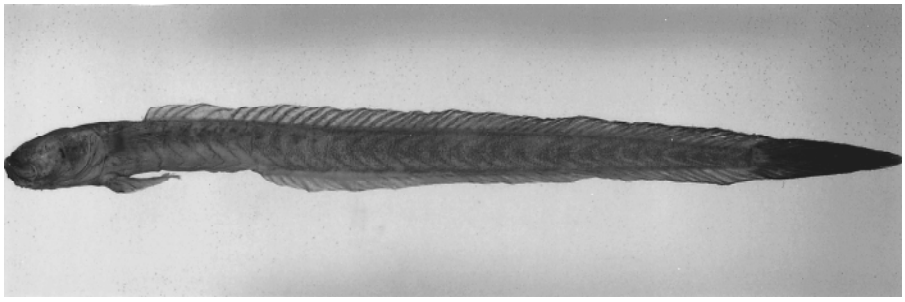

Fig. 10. *Odontamblyopus lacepedii*, NSMT-P 47141, 147 mm SL, 181 mm TL, Ariake Sea, Kyushu, Japan

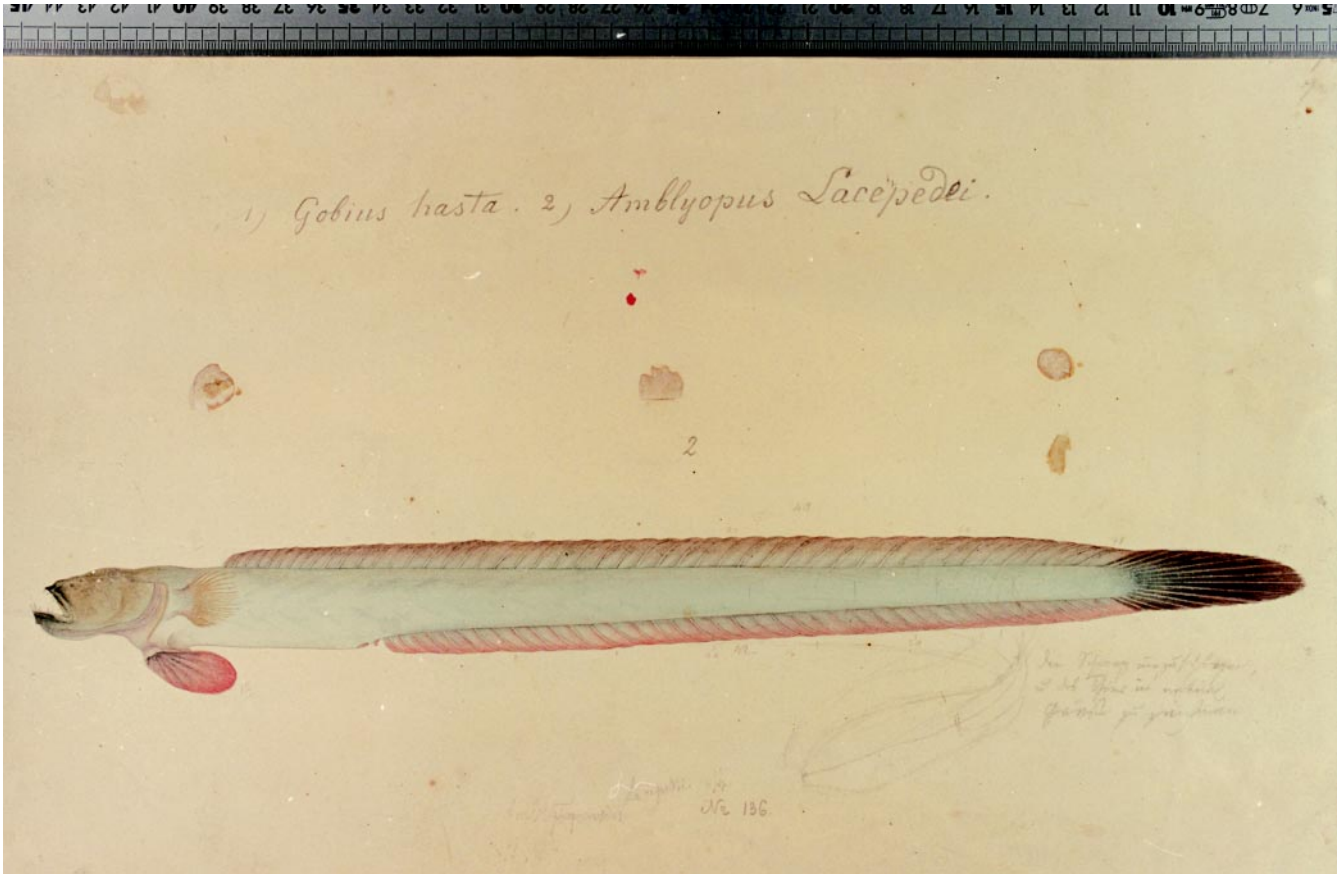

Fig. 11. Photograph of the original Japanese drawing in Burger's collection on which Temminck and Schlegel (1845) based their description of *Odontamblyopus lacepedii* (Photograph courtesy of Martien van Oijen of the Naturalis National Museum of Natural History, Leiden)

Amblyopus sieboldi Steindachner, 1867: 119 (type locality, mouth of Amur River, Russia)
Gobioides petersenii Steindachner, 1893: 235 (type locality, Swatow [Shantou], China)
Taenioides abbotti Jordan and Starks, 1907: 524, fig. 4 (type locality, Port Arthur [Lüshun], China)
Taenioides petschiliensis Rendahl, 1924: 31 (type locality, Chihli, Pei-Tai-Ho, China)
Sericagobioides lighti Herre, 1927: 335, pl. 26, fig. 2 (type locality, Amoy, China)
Nudagobioides nankaii Shaw, 1929: 1, figs. 1, 2 (type locality, Nankai, China)
Taenioides limboonkengi Wu, 1931: 51, fig. 9 (type locality, Foochow [Fuzhou], China)

Material examined (36 specimens from 13 localities; size range 69–303). Taiwan: ASIZP 056794, 1:189; Taiwan or Southern China (?); HUMZ 1861, 1:180; China, Hong Kong: BLIH 1975131, 1:140; CAS 160944, 1:210; CAS 161280, 1:180; China, Shantou: NMW 31085, holotype of *Gobioides petersenii*

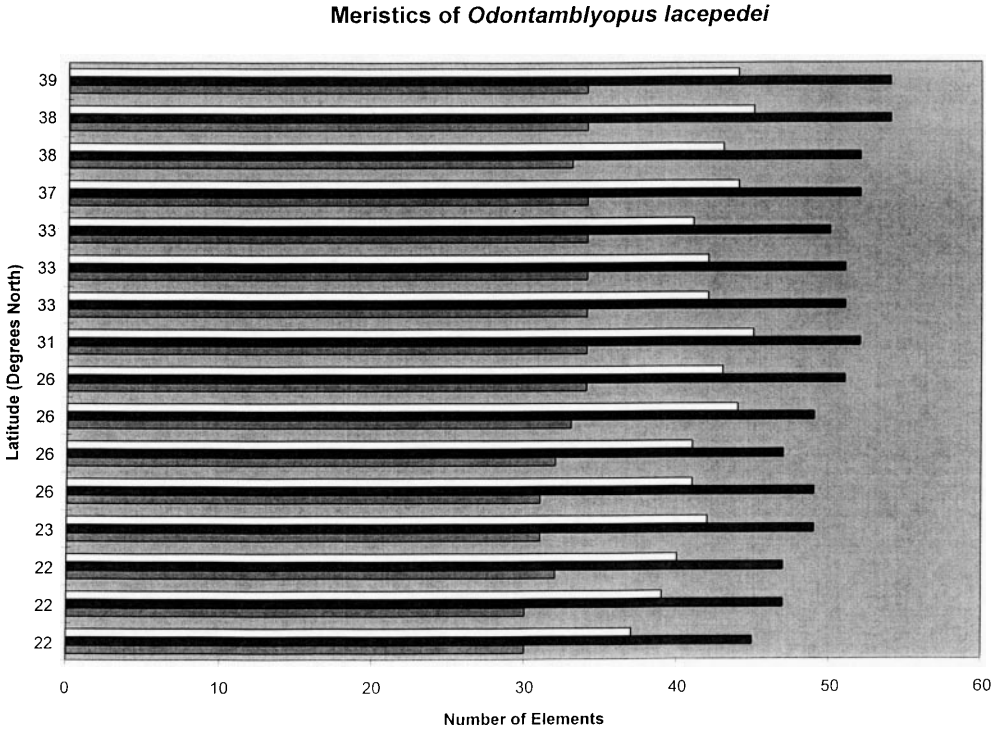

Fig. 12. Meristics and latitudinal distribution of *Odontamblyopus lacepedii*. *White bars*, anal fin; *black bars*, dorsal fin; *gray bars*, vertebrae

Steindachner, 69. China, Fuzhou: MNHN 1941-186, 1:116; MNHN 1941-187, 1:79; USNM 86380, 1:140; USNM 86955, 2:111–114; USNM 130431, 2:133–168; China, Woosung: USNM 85845, 1:114; China, Shanghai: USNM 86025, 1:95; USNM 130393, 2:91–102; China, Chihli: ANSP 124239, 2:180–210; NHRM 28372, syntypes of *Taenioides petschiliensis* Rendahl, 2:184–206; China, Lüshun: USNM 55634, holotype of *Taenioides abbotti* Jordan and Starks, 70; Japan, Saga Prefecture: MNHN 1987-1218, 2:150–163; MTUF 25841, 2:210–211; Nagasaki Prefecture: HUMZ 64834, 1:303; NSMT-P 47141, 7:146–242; Korea, Inchon: BLIH 1995031, 1:121; Russia(?), Amur River: NMW 76854, syntype of *Amblyopus sieboldi* Steindachner, 181.

Diagnosis. Caudal fin long, standard length more than 80% of total length [SL/TL 0.808–0.850 (mean = 0.825)]; total dorsal-fin elements 44–55; anal-fin elements 36–45; caudal vertebrae 20–24; 2 (rarely 3); anal-fin pterygiophores preceding first hemal spine.

Description. As for genus except as follows. Total elements in dorsal fin 44–54 (mean = 49.3); total elements in anal fin 36–45 (mean = 41.4); pectoral-fin rays 24–33 (mean = 27.9); upper-jaw teeth (outer row) 7–13 (mean = 10.0); lower-jaw teeth (outer row) 8–11 (mean = 9.2); HL/SL 0.108–0.157 (mean = 0.132); PEL/SL 0.087–0.121 (mean = 0.105); PEC/SL 0.082–0.132 (mean = 0.101); HW/SL 0.064–0.107 (mean = 0.079); PEL/HL 0.665–1.08 (mean = 0.810); PEC/PEL 0.775–1.36 (mean = 0.981); PEC/HL 0.597–1.22 (mean = 0.788). Several short barbels present on underside of chin in one adult specimen (CAS 160944).

Coloration. No fresh material was available for this study. Based on a color photograph in Akihito et al. (1984), this species has a bluish-gray body and head; the caudal fin is blackish-red whereas the anal and pelvic fins are blood-red. A similar color description of the head and body was noted by Shaw (1929) for his new genus and species. Temminck and Schlegel (1845) described the ventral fins as red. Dotsu (1957) described this fish as red.

Distribution. Known from western and southwestern Korea, southern Japan (Ariake and Yatsushiro Sounds, west coast of Kyushu, only), China, Hong Kong, and Taiwan.

Ecology. A marine and brackish-water goby that creates elaborate burrows in mud. Its burrows are tunnel shaped, vertical, and extend to depths of 50–90 cm into the substrate; four to nine other smaller tunnels radiate from the primary tunnel and connect to the outside (Dotsu, 1957). According to Dotsu (1957), this species eats a variety of foods including bivalves, crustaceans, cephalopods, and small fishes.

Remarks. This species exhibits variation in vertebral counts that indicate a trend toward increasing numbers of vertebrae and associated fin rays with increasing latitude (Fig. 12); this phenomenon is well known in fishes and, within gobiids, has been reported in *Acanthogobius hasta* from this same region (Shibukawa, 1997).

A radiograph of the syntype of *Amblyopus sieboldi* was examined by us. Additionally, Helen Larson exam-

ined this same specimen (NMW 76854) and provided her notes to us. Combining Larson's evaluation and data with our radiographic data (pectoral and pelvic fins approximately equal in length, two symphyseal canine teeth, pectoral-fin rays 31 and 33, total dorsal-fin elements 54, total anal-fin elements 44, vertebrae 10 + 24), we provisionally place this species in synonymy of *O. lacepedii*. We are concerned, however, about the locality of the type material (Amur River, Russia); no other conspecifics have been collected or reported this far north (54°N). In fact, only a few species of gobies are found north of 50° (Birdsong et al., 1988). Because Lindberg and Krasyukova (1989) did not mention *A. sieboldi* in their book that includes fishes in the Sea of Okhotsk, we assume the locality for *A. sieboldi* is in error. In the same paper in which Steindachner describes *A. sieboldi* (Steindachner, 1867), he also describes new species from China; possibly *A. sieboldi* came from China as well.

As type material for *Sericagobioides lighti* was destroyed during World War II, synonymy was based on the original description and figure. For his new genus and species, Herre (1927) described features of *Odontamblyopus* (i.e, symphyseal canines, no chin barbels, no sensory ridges on head, and pectoral-fin length being equal to or greater than head length) whereas the total number of vertebrae (30) as well as the ranges for the total number of dorsal and anal fin elements (46–54 and 39–45, respectively) were consistent with *O. lacepedii*. The accompanying figure also helped confirm the synonymy. Herre speculated that *Amblyopus taenia* Günther might belong to his new genus.

The type specimen of *Nudagobioides nankaii* was not examined by us; presumably, it resides at the Museum of Nakai University, China (Eschmeyer, 1998). Synonymy was based on the original description and figures. The description clearly stated distinctive features of *Odontamblyopus* (i.e, symphyseal canines, no chin barbels, and PEC/PEL = 1.1) whereas the meristics for dorsal, anal, and pectoral fins (51, 43, and 33, respectively) were consistent with *O. lacepedii*. The figures accompanying the description also served to confirm the synonymy.

Type material for *Taenioides limboonkengi* may exist, but its whereabouts are unknown (Eschmeyer, 1998). We based synonymy on the original description that indicates the presence of two symphyseal canine teeth and no chin barbels, and the figure that shows the pectoral and pelvic fins of approximately equal size and length as well as the absence of dermal folds on the head.

Whether type material of *Amblyopus lacepedii* exists is unknown, but it undoubtedly is lost. The species name is based on a Japanese plate in the Burger collection (Boeseman, 1947); a photograph of that plate is reproduced here as Fig. 11. According to Boeseman (1947), Burger's plate was based on a specimen (not saved) collected near Omura, Japan. According to Prof. Toru Takita (personal communication), *O. lacepedii* is not found anywhere in Omura Sound. Therefore, it is likely that the Burger specimen was obtained from a market in or around Omura, but the specimen probably originated from somewhere in the Ariake Sound.

Based on Burger's plate, Temminck and Schlegel (1845) rendered their own figure (Boeseman, 1947). The Temminck and Schlegel figure is easily recognizable and cannot be confused with another species; therefore, the designation of a neotype is not warranted at this time.

Phylogenetic and Biogeographic Discussion

We have attempted, but failed, to produce a well-supported species-level cladogram for *Odontamblyopus*. This failure can be attributed to the lack of a generic level cladogram for amblyopines and, concomitantly, the lack of a defensible sister group for both the Amblyopinae and *Odontamblyopus*. We can certainly speculate that a plausible sister group for the Amblyopinae is the Oxudercinae, based on similarities in jaw structure as outlined in Harrison (1989) and Murdy (1989). Likewise, we can speculate that because of overall similarity *Taenioides* is a more likely candidate as sister group to *Odontamblyopus* than any other member of the Taenioides group. However, until a synapomorphy of the Taenioides group (Birdsong et al., 1988) is elucidated and extensive study is done on generic relationships of the Amblyopinae, a species-level cladogram for *Odontamblyopus* will be a quest of limited reward.

Similarly, we are unable to propose a well-defended vicariance scenario to explain the distribution of *Odontamblyopus* species. Vicariance scenarios should, of course, follow an hypothesis of interrelationships; for reasons stated earlier, this was not possible. We also believe we are seriously hampered by having only a limited number of collection sites. For one species, *O. tenuis*, we have only a single collection site outside of the type locality. Because *Odontamblyopus* is found in burrows in silty mud habitats, collecting this fish is a daunting task. The degree of difficulty in collecting *Odontamblyopus* helps explain its relative paucity in museum collections. We believe *Odontamblyopus* is more widely distributed than the literature and collections indicate. Consequently, the biogeographic discussion that follows is largely descriptive rather than theoretical. A vicariance scenario must await more complete data.

The four species of *Odontamblyopus* are confined to the Laurasian Plate and are distributed from the west coast of India and Pakistan eastward to Sarawak and Hong Kong and then northward to southern Korea and southern Japan. Based on museum records and verifiable published information, the genus has a broad hiatus in distribution from Myanmar to southern China (approximately 96°E to approximately 112°E). This hiatus may be more apparent than real because suitable habitat for *Odontamblyopus* appears plentiful in Malaysia, Thailand, and elsewhere. Springer and Williams (1994) noted that many marine organisms with essentially continuous Indo-Pacific distributions are missing from the Gulf of Thailand and the southwestern South China Sea.

Odontamblyopus may have once been distributed coastally from near the mouth of the Arabian Gulf to the Korean peninsula and southern Japan. However, the collision of the Indian subcontinent with mainland Asia 60 million years ago (Klootwijk et al., 1986) may have been a vicariant event that isolated eastern and western populations of *Odontamblyopus*. Such a scenario has been hypothesized for other marine taxa (Hocutt, 1987; Springer, 1988; Murdy, 1989) and accounts for the presence and distribution of *O. rubicundus* (east coast of India to Myanmar) and *O. roseus* (west coast of India). However, the putative presence of *O. tenuis* in Pakistan in conjunction with its verifiable presence in Myanmar requires a different hypothesis. The most parsimonious explanation is that *O. tenuis* existed before the collision of India with Asia (60 mya) and that the Pakistan and Myanmar populations of *O. tenuis* have maintained their identity, separately, since that vicariant event. We note that the congrogadin, *Halidesmus thomseni*, has a somewhat similar disjunct distribution (Winterbottom, 1985).

Odontamblyopus lacepedii, found in China, Hong Kong, Taiwan, Korea, and Japan, shows a general trend toward increasing vertebrae and median fin elements with increasing latitude (see Fig. 12). Thus, we have elected to recognize only a single, wide-ranging species with variable meristics. Based on our sample, caudal vertebral numbers for *O. lacepedii* range from 20 to 24. A synonym of *O. lacepedii* could probably be attached to each of these character states, and we acknowledge that other taxonomists might choose to do so. It is also acknowledged that periods of relative isolation have also occurred in the region that may have facilitated speciation. For instance, as recently as 20 000 years ago, sea levels were 130 m lower than present and Japan was joined to mainland Asia (Myers, 1989).

Without fossil evidence, we have no way of knowing if the *Odontamblyopus* in the region at that time possessed the same number of caudal vertebrae. With subsequent rising sea levels, populations of *Odontamblyopus* in the north may have become reproductively isolated from those to the south. However, has this period of potential separation been sufficient to genetically isolate 24-caudal vertebrae *Odontamblyopus* from 20-caudal vertebrae *Odontamblyopus*? Or is the variability in vertebral counts more directly a response to the fish's development in waters of different temperatures, for instance, between Hong Kong (about 22°N) and Lüshun (about 39°N)? Clearly, this is a question that merits further study. For now, we believe there is greater heuristic value in recognizing only a single, variable species in the region.

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