

Terateleotris, a New Gobioid Fish Genus from the Laos (Teleostei, Perciformes), with Comments on its Relationships

Koichi Shibukawa¹, Akihisa Iwata² and Sinthavong Viravong³

¹Department of Zoology, National Science Museum, 3–23–1 Hyakunin-cho, Shinjuku-ku, Tokyo, 169–0073 Japan.

E-mail: shibu@kahaku.go.jp

²Graduate School of Asian and African Area Studies, Kyoto University, 46 Shimoadachi-cho, Yoshida, Sakyo-ku, Kyoto, 606–8501 Japan.

E-mail: iwata@asafas.kyoto-u.ac.jp

³Living Aquatic Resources Research Center, National Agriculture and Forestry Research Institute, Ministry of Agriculture and Forestry, Lao P.D.R.

Abstract A new gobioid genus, *Terateleotris*, is described for the sleeper species, previously known as *Odontobutis aspro* Kottelat, 1998, from the Xe Banghai basin, Laos. This is the third known gobioid genus bearing a lateral-line canal extending onto body, and the only genus with typical sleeper-like appearance within those three. *T. aspro* is redescribed, based on six newly obtained specimens, including soft anatomy and osteology. *Terateleotris* is clearly nested within the basal gobioid assemblage that includes the rhyacichthyids and odontbutids, owing to the lack of several modifications in scales, cephalic sensory canals, axial skeleton and shoulder girdle, all of which are found in the more specialized gobioids (e.g., Gobiidae). We, however, failed to adequately classify it into any known supra-generic taxon, because such taxa have vaguely defined limits, particularly the *Odontobutidae*.

Key words: *Terateleotris*, new genus, Gobioidae, *Odontobutis aspro*, relationships

In a recent review of the freshwater fish fauna of the Nam Theun and Xe Bangfai basin, Laos, Kottelat (1998) described a new species of the odontobutid sleeper, *Odontobutis aspro* (Fig. 1), based on a single specimen collected from Xe Bangfai about 3 km upriver of Ban Pakphanang. This species resembled the other members of *Odontobutis* (*sensu* Iwata, 1994) in general appearance, but some features found in the photographs and illustration were heterogeneous to the other *Odontobutis* species, defined by Iwata *et al.* (1985) and Iwata (1994). Kottelat's account of the species was, however, too brief and incomplete to discern its affinity; he did not demonstrate any reason why it belonged in the family, much less the genus.

After the original description of *O. aspro* was published, the second author (AI) succeeded in capturing six specimens of this sleeper near the type locality. Examination of these specimens revealed that the species was similar to the odontobutid sleepers in general appearance. We, however, discovered several features that sug-

gested this species should not be assigned to *Odontobutis* nor to the Odontobutidae. The features included: lateral-line canal extending onto body; preopercular canal of cephalic sensory systems connected to oculoscapular canal; autogenous distal radial on first through fourth, fifth or sixth pterygiophores of spinous (=first) dorsal-fin; three epurals; penultimate branchiostegal ray lies between anterior and posterior ceratohyals. All of these features are regarded as plesiomorphous states that are not or rarely found in other gobioids. Further detailed analysis led us to the conclusion that this species should be assigned to a new gobioid genus.

Materials and Methods

Specimen lengths were expressed as standard length (SL). Measurements were made with calipers to the nearest 0.1 mm. The methods for measurements and counts followed Hubbs and Lagler (1958) and Akihito (1984), respectively, except for the following: all measurements to the snout tip were to the anteriormost point of the upper jaw; width and depth of head were measured at preopercular margin; width of nape was measured at dorsalmost edge of gill opening; body depth was measured at first dorsal-fin origin; pectoral- and caudal-fin lengths were represented by the length of the longest ray; pelvic-fin length was measured from the base of pelvic-fin spine to distal tip of the longest (=4th in the new genus) ray; counts of lateral-line scales included scales bearing tubed or grooved lateral line from just posterior to sensory canal pore L' to mid-point of caudal fin; gill rakers were counted the rakers on the outer surface of the first arch including all rudiments, and provided in the form of rakers on the upper + lower limbs; pseudobranchial filaments were counted including all rudiments. Where the meristic characters were countable on both sides, each is provided and separated by a slash (left side count given first). Counts and of dorsal- and anal-fin pterygiophores, vertebrae, intermuscular bones and epurals were taken from radiographs and a single specimen (LARREC-P1-6), cleared with trypsin and counter-stained for bone and cartilage, following the method of Potthoff (1984); other osteological characters were also noted from the cleared and stained specimen. The notation of the pattern of interdigitation of the dorsal-fin proximal pterygiophores between the neural spines ("P-V") follows Akihito (1984). The terminology of scale morphology follows Roberts (1993).

Cephalic sensory canals, pores and papillae were observed on specimens stained with suminol cyanine. The notation of cephalic sensory-papilla rows and sensory-canal pores follows Wongrat and Miller (1991) and Akihito (1984), respectively, except for that of an additional pore between K and L' ; the pore is located about midway along the longitudinal groove on lateral surface of posttemporal, and provisionally termed " K_2 " (the pore commonly referred as K is herein shown to be " K_1 "). Pore M is the dorsal terminal pore of the preopercular canal in the Akihito's (1984) system; three of the six examined specimens possess a continuous preopercular-ocu-

loscapular canal and lack pore M in both sides; although the canals are continuous, the smallest specimen (LARREC-P1-5) possesses a very minute pore, indicated as pore M (although not terminal), at about midway from oculoscapular/preopercular canal junction to pore N; a discontinuous, independent preopercular canal and typical pore M' are found in both sides of LARREC-P1-6 and right side of LARREC-P1-1. And also, in Akihito's system, pore H is the pore located at midpoint between pores G and I-J (when the oculoscapular canal uninterrupted between pore H and K); the pore herein shown as "pore H" is closed to the oculoscapular/preopercular canal junction, and may represent fused pores H and M owing to the canal connection (if so, the pore should be shown to be "HM"); we tentatively designated it as pore H, because it is located just posterior to (and not at the point of) the canal junction (see Fig. 5), and the occurrence of both pores "M" and H in the smallest specimen with connected preopercular canal to oculoscapular canal, is as noted above. Observations and illustrations of osteological features and cephalic sensory systems were made using a dissecting microscope with camera lucida attachment.

Sex was determined externally (see "Sexual dimorphism"), however, in certain specimens, verified by internal examination.

All specimens examined are deposited in the following institutions: Biological Laboratory, Imperial Household, Japan (BLIH); Living Aquatic Resources Research Center, National Agriculture and Forestry Research Institute, Ministry of Agriculture and Forestry, Lao P.D.R. (LARREC); National Science Museum, Tokyo (NSMT). The specimens of the new genus are listed at the top of the species account, and the other comparative materials cited in the text are listed at the end of the text. The comparative materials herein listed contain only the cited ones of rhyacichthyids and odontobutids, excluding *Odontobutis* species found in Iwata (1994).

In the present study we examined a number of odontobutid species for comparison, including several with ambiguous generic assignments, e.g., *Odontobutis aurarum* and *Phylipnus compressocephalus* (the latter assigned to *Percottus* by Hoesel and Gill, 1993). The generic assignment of the aforementioned taxa is reappraised by us. Accordingly, we tentatively use the original assignment of these taxa, but the generic names for them are in enclosed parentheses.

Terateleotris, New Genus

Type species. *Odontobutis aspro* Kottelat, 1998.

Diagnosis. The new genus, *Terateleotris*, is the third known gobioid genus possessing a lateral-line canal on the body, and the only genus with typical sleeper-like appearance among those three. It is also distinguished from other gobioid genera in having the following combination of characters: some rows of transforming cteni on head and body scales; right and left sides of gill membranes united medially, posterior margin entirely free from isthmus; gill membranes attached to isthmus at a ver-

tical through anterior part of eye (far forward from posteroventral margin of united gill membranes); autogenous distal radials on first through fourth, fifth or sixth pterygiophores of spinous (=first) dorsal-fin; single infraorbital bone (other than lacrymal); single lateral extrascapula; three epurals; gill rakers on outer surface of first arch stout, spinulose laminae; cephalic sensory-canal pores usually A', B, C, D (single), E, F, G, H, I, J, K₁, K₂, L', N, O, P and Q' (and, sometimes, pore M or M'); preopercular canal usually connected with oculoscapular canal (if discontinuous, dosalmost pore M' of preopercular canal present); mandibular and infraorbital canals undeveloped.

Comparisons. *Terateleotris* is superficially similar to *Odontobutis* (*sensu* Iwata, 1994), in the following characters: (1) general profile of head and body, e.g., slightly to well depressed head, strongly projecting lower jaw, moderately large mouth, and stout body; (2) widely separated pelvic fins, (3) some rows of transforming cteni on head and body scales (Fig. 2), (4) right and left gill membranes united medially, posterior margin entirely free from isthmus, (5) broad gill opening (attaching point of gill membranes to isthmus far forward from posteroventral edge of united gill membranes), (6) tongue with rounded anterior margin, (7) no vomerine teeth, (8) no spine-like projections at posterior margin of preopercle, (9) no serrated bony crest around orbit, (10) mesopterygoid overlaps metapterygoid posteriorly (Fig. 8), (11) gill rakers on outer surface of first arch stout, spinulose laminae (Fig. 9), (12) counts of fin rays, scale rows (excepting predorsal scales) and vertebrae, and (13) color pattern of head and body (dark gray-brown dorsally, becoming yellowish brown to pale ventrally; mottled with large black blotches). *Terateleotris* differs from *Odontobutis* in the following features: interorbital width narrower than eye diameter (vs. wider than eye diameter in *Odontobutis*); predorsal scales restricted to occipital and nuchal region (Fig. 3) (vs. predorsal scales extending just or far ahead from middle of interorbital region); lateral-line canals extend onto body (Figs. 5 and 6) (vs. no lateral-line canals on body); well developed sensory canals on head (Figs. 4 and 5) (vs. greatly reduced or absent); three epurals (Fig. 15) (vs. two); single infraorbital (Fig. 8A) (vs. none); single lateral extrascapula (Figs. 7 and 12) (vs. none); and autogenous distal radials on first dorsal-fin pterygiophore (Fig. 14A) (vs. none). No other gobioid genera possess both plural rows of transforming cteni on body scales and united gill membranes with entirely free posterior margins.

Etymology. The new genus name *Terateleotris* is derived from the Greek *teras*, meaning a marvel or a monster, and *Eleotris*, a genus of the eleotrid sleeper, in reference to its occurrence with remarkable character arrangements making the interrelationships of basal gobioids chaotic (see Discussion). Gender is feminine.

Terateleotris aspro (Kottelat, 1998)

(Figs. 1–15)

Odontobutis aspro Kottelat, 1998: 113, figs. 178 & 179 (Xe Bangfai about 3 km upriver of Ban Pakphanang, Laos; holotype ZRC 41811 [76.1 mm SL]).

Materials examined. LARREC-P1, 6 specimens (29.4–92.7 mm SL; largest one [LARREC-P1–6] cleared, stained and dissected), Xe Bangfai, Laos (17°22.3'N, 105°49.3'E), 7 Dec. 1999.

Diagnosis. As for genus.

Description. In the following description, counts of non-type specimens are given first, followed by those of the holotype in parentheses; the data of holotype were cited from Kottelat (1998). Dorsal-fin rays VIII-I, 9–10 (VIII-I, 9); anal-fin rays I, 7–8 (I, 7); pectoral-fin rays 17–18/17–18 (18); pelvic-fin rays I, 5/1, 5 (I, 5); segmented caudal-fin rays 8–9+8, including 6–8+6–8 (6+5) branched rays; dorsal unsegmented caudal-fin rays 8–10; ventral unsegmented caudal-fin rays 8; longitudinal scale rows 37–40/36–40 (37); lateral-line scales 30–32/30–31; scales with pit organs 31–32/31; transverse scale rows 12–14/11–13 (12); predorsal scales 17–20 (20); gill rakers 2+8; pseudobranchial filaments 15.

The following measurements are % of SL (based on five specimens, 55.0–92.7 mm SL); ranges are given first, followed by means in parentheses. Head length 32.8–35.5 (34.4); head width 20.0–21.9 (20.9); head depth 15.7–17.4 (16.5); width of nape 14.3–16.2 (15.5); snout length 10.0–10.9 (10.3); jaw length 13.7–14.5 (14.2); eye diameter 6.9–8.3 (7.4); fleshy interorbital width 2.1–4.2 (3.4); body depth 19.7–21.4 (20.4); body width 14.5–15.7 (15.2); length from snout to origin of first dorsal-fin 41.1–42.2 (41.6); length from snout to end of first dorsal-fin 58.6–59.6 (59.1); length from snout to origin of second dorsal-fin 59.6–61.5 (60.6); length from snout to terminus of second dorsal-fin 75.0–76.7 (75.8); length from snout to origin of anal fin 64.2–64.8 (64.5); length from snout to terminus of anal fin 74.5–76.0 (75.4); length from snout to base of pelvic-fin spine 31.3–34.1 (32.9); length from snout to anterior margin of anus 58.6–59.8 (58.9); caudal-peduncle length 24.0–25.9 (25.1); caudal-peduncle depth 9.4–10.5 (9.9); length of first dorsal-fin base 17.9–18.9 (18.5); length of second dorsal-fin base 15.3–17.6 (16.6); length of anal-fin base 10.9–13.9 (12.0); length of longest spine of first dorsal-fin 11.8–13.8 (12.7); length of spine of second dorsal-fin 8.6–11.7 (9.7); length of longest segmented ray of second dorsal-fin 13.8–16.3 (14.9); pectoral-fin length 22.1–25.5 (23.5); pelvic-fin length 18.9–21.9 (19.8); length of anal-fin spine 6.3–8.1 (7.3); length of fourth (=longest) segmented ray of pelvic fin 16.5–19.6 (17.8); length of fifth segmented ray of pelvic fin 14.3–16.6 (15.4); length of spine of anal fin 6.2–8.2 (7.3); length of longest segmented ray of anal fin 14.3–16.0 (15.4); caudal-fin length 21.7–24.6 (23.2).

Body stout, subcylindrical, compressed posteriorly. Head slightly depressed. Interorbital width narrower than eye diameter. Mouth oblique, forming an angle of

about 30 degrees with body axis. Lower jaw projected beyond upper jaw; posterior end of jaws below anterior margin of pupil. Anterior nasal opening a short tube with a minute triangular projection at posterior margin of its tip. Posterior nasal opening a pore, located at about approximate mid-point between anterior nasal opening and anterior margin of eye. Tongue nearly rectangular with rounded anterior margin, free from floor of mouth. Posteroventral margin of lower lip interrupted at symphysis. Mental flap on chin undeveloped. Gill membranes united medially, posterior margin entirely free from isthmus; gill membranes attach to isthmus at a vertical from anterior margin of pupil (far forward from posteroventral edge of united gill membranes). No fleshy projections on lateral wing of shoulder girdle. First dorsal-fin height subequal to second dorsal-fin; margin of first dorsal fin rounded, third or fourth spine longest; no filamentous dorsal-fin spines; first dorsal fin not continuous with second dorsal fin. Segmented rays of second dorsal fin progressively longer to fourth, fifth or sixth ray. All segmented rays of second dorsal and anal fins branched at least in adults and some subadults. Origin of anal fin on a vertical with base of third or fourth segmented ray of second-dorsal fin; segmented rays of anal fin progressively longer to fourth or fifth ray. Caudal fin nearly rounded. Pectoral fin rounded, ninth or tenth ray longest, not reaching to a vertical from anus; all pectoral-fin rays branched; no pectoral-fin rays free from fin membranes. Pelvic fins widely separated; no frenum and connecting membrane; all pelvic-fin segmented rays branched; fourth segmented pelvic-fin ray longest, not reaching to anus when appressed; fifth (=innermost) segmented pelvic-fin ray 84.7–87.1% of preceding ray.

Nape, body (excluding belly and anterior part of prepelvic region), operculum, dorsoposterior part of cheek and basal part of caudal fin covered by ctenoid scales with some rows of transforming cteni (those on caudal fin radically smaller than preceding ones); scales on most of pectoral-fin base (some ctenoid scales with transforming cteni on anterior region), belly and posterior two-thirds of prepelvic region cycloid; interspace between base of urogenital papilla and anal-fin origin covered by at least two cycloid scales; remaining part of head, body and fins naked; scales with sensory papillae and lateral-line tube as described below (Figs. 2, 5 and 6A).

Cephalic sensory systems (Figs. 4, 5 and 6A). — Oculoscapular canal with pores A', B, C, D (single), E, G, H, I, J, K₁, K₂ and L'; canal uninterrupted between pores A' and L'; right and left sides of canals close to each other on interorbital region; supraorbital pseudo-commissure (Takagi, 1988) undeveloped. Preopercular canal typically (five of six examined specimens, one of which bears disjunct preopercular canal in right side) joins to oculoscapular canal at just posterior to pore H (=intertemporal pore), as in generalized perciformes; preopercular canal usually with pores N, O, P, Q'; tiny pore M found in smallest specimen examined (LARREC-P1–5), and pore M' found in specimens with disjunct preopercular canal (LARREC-P1–1 [right side only] and 6). Infraorbital canal greatly reduced to very short tube restricted to posterior to eye, with terminal pore F' (Fig. 5). No mandibular canal and

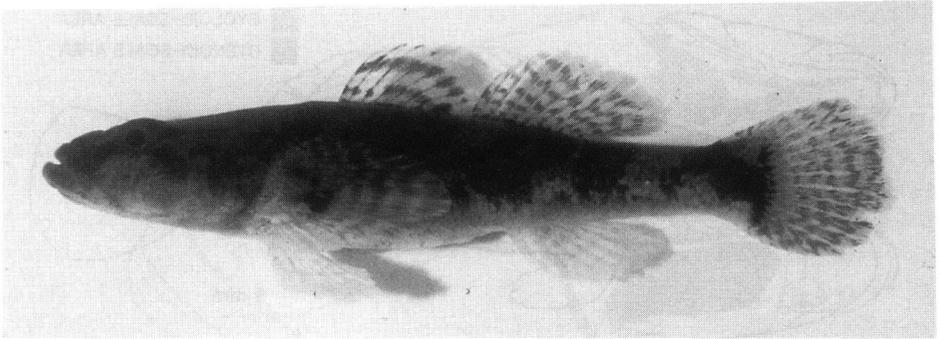


Fig. 1. *Terateleotris aspro* (Kottelat), LARREC-P1-1, male, 85.1 mm SL, Xe Banghai, Laos.

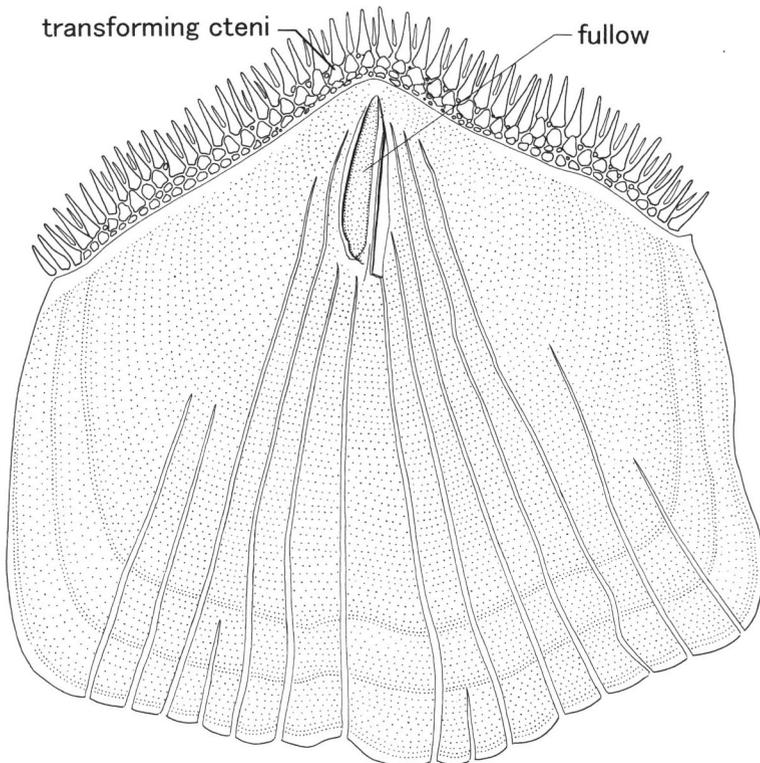


Fig. 2. Lateral-line scale at anteriormost part of caudal peduncle of *Terateleotris aspro* (LARREC-P1-6, 92.7 mm SL).

pores.

Sensory papillae on head not well developed, forming longitudinal rows (longitudinal sensory papilla pattern of Hoesé, 1982; 'longitudinal' type of Wongrat and

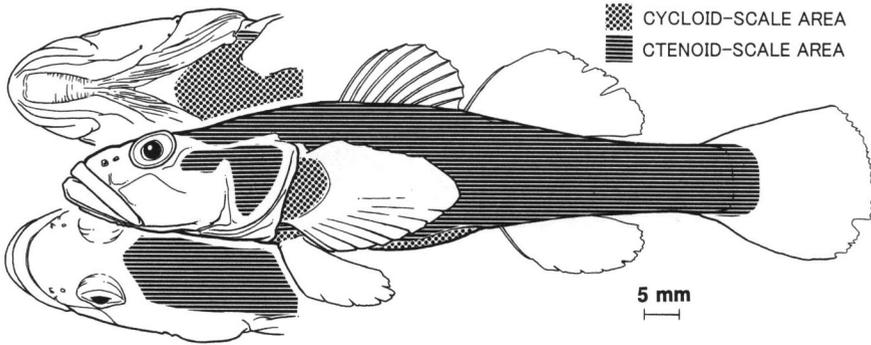


Fig. 3. Squamation of *Terateleotris aspro* (LARREC-P1-6, 92.7 mm SL). Some ctenoid scales with transforming cteni on anterior part of pectoral-fin base are omitted.

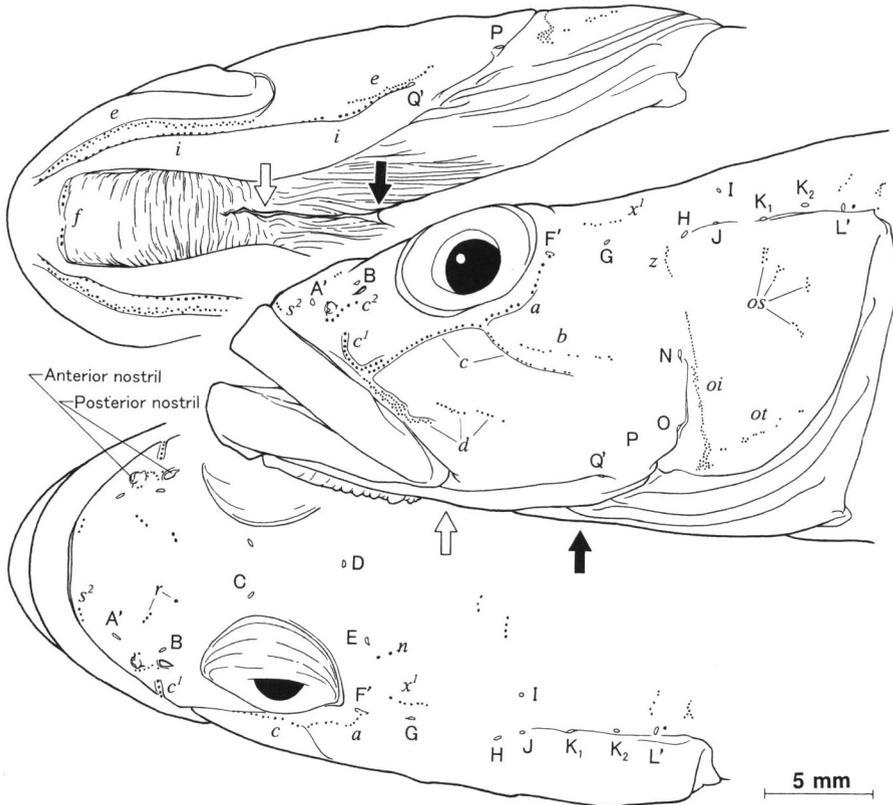


Fig. 4. Head of *Terateleotris aspro* (LARREC-P1-3, 89.8 mm SL), showing sensory canal pores (large capitals) and papilla rows (small capitals). Solid and open arrows indicate mid-posterior end of free margin of fused gill membranes and attaching point of gill membrane to isthmus, respectively.

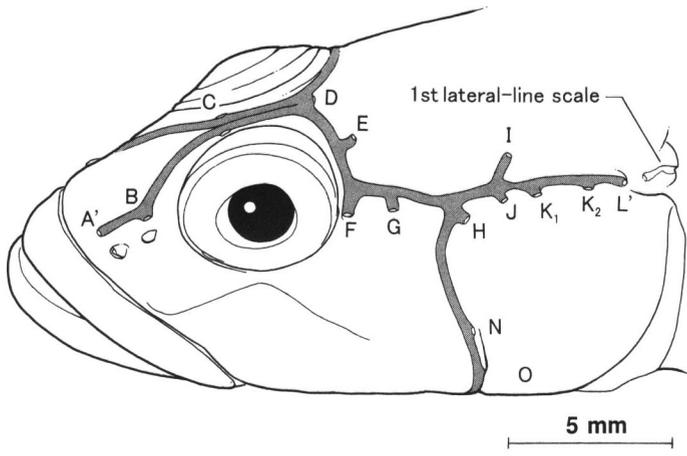


Fig. 5. Dorsolateral view of head of *Terateleotris aspro* (LARREC-P1-4, 55.0 mm SL), showing cephalic sensory canals (shaded area) and pores (large capitals).

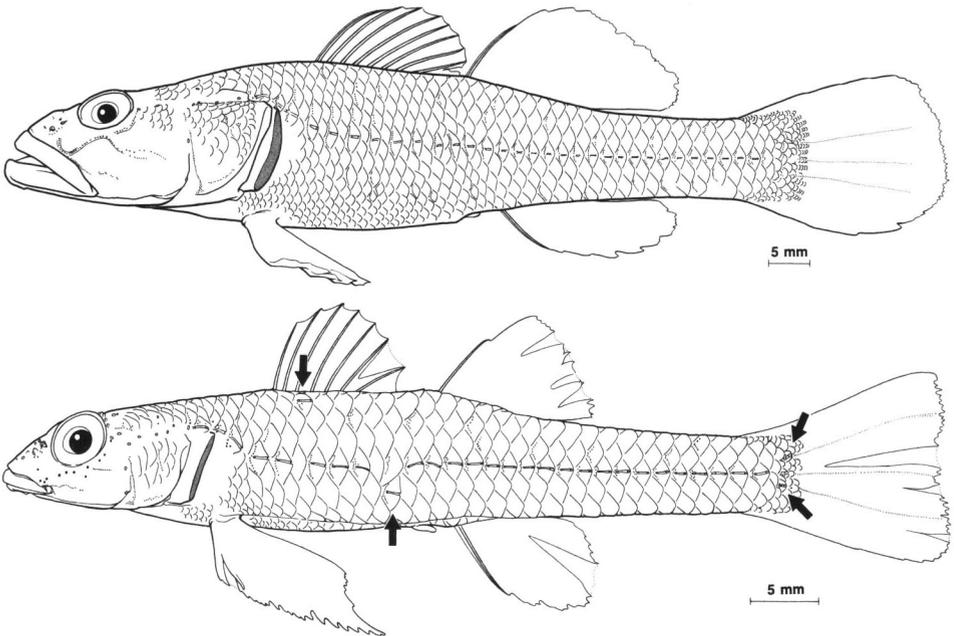


Fig. 6. Lateral-line canals and sensory papilla rows on head and body in two species of gobioid fish. A) *Terateleotris aspro* (LARREC-P1-1, 85.1 mm SL), B) *Protogobius attiti* (BLIH1997018, 52.3 mm SL). Arrows indicate accessory canals in *Protogobius*.

Miller, 1991). Four oblique or essentially longitudinal rows (*a*, *b*, *c* and *d*) ventral to eye; row *a* short, not extending below middle of eye; row *c* greatly risen about midway; dorsalmost point of row *c* close to anterior tip of row *a* (these two rows nearly connected in LARREC-P1-3 [Fig. 3], but the gap between them distinct in the other specimens [see Fig. 6A]); row *d* meets or very close to anteriormost of row *c* anterodorsally, interrupted about midway of own longitudinal portion. Rows *e* and *i* each form near uniserial row from pore Q' to chin, both interrupted medially. Row *n* comprises one or two sensory papillae. Three sensory papilla "rows" on operculum (*ot*, *os* and *oi*); row *ot* mostly uniserial transverse row with short multiple portion ventrally; rows *os* and *oi* forming aggregations in each. Row *s*³ forms short transverse row. Row *z* forms short transverse row or aggregation. Row *f* formed two short transverse sensory papilla rows set into shallow groove just behind chin.

Lateral-line systems on body (Figs. 2, 5 and 6A). All lateral-line components on body (both canals and grooves) epidermal, no pierced or true-tubed lateral-line scales; no trace or only shallow longitudinal furrow on those scales removed from epidermis (Fig. 2). Lateral-line canals or grooves found on scales at just behind cephalic sensory-canal pore L' and extending to middle portion of caudal-fin base (Figs. 5 and 6A); each lateral-line canal and groove on body situated at mid-lateral of exposed area of scale just posterior to short, uniserial transverse sensory papilla row. Occurrence of tubed or grooved lateral-line variable; at a minimum, lateral line on anterior most scales always tubed in adult (only four and three tubed scales on right and left sides of anterior part of body, respectively, in smallest specimen). In smallest specimen examined (LARREC-P1-5, 29.4 mm SL), lateral-line groove very shallow, often undeveloped especially on posterior part of body; in such undeveloped condition, one to three (usually two) sensory papillae forming longitudinal line just posterior transverse sensory papilla row. No accessory canals either dorsal or ventral to midrow lateral line on body.

Other than lateral-line canals or grooves, many small aggregations of sensory-papillae (most of them form uniserial short transverse lines) present on various parts of body, as shown in Fig. 6A. Caudal fin covered by some scales with transverse sensory papilla row basally, and bears three uniserial, radiating sensory papilla rows on fin membrane along middle caudal-fin rays (dorsalmost between fourth and fifth branched rays, medialmost one between seventh and eighth rays, and ventralmost between ninth and tenth rays [rays counted from dorsum to ventrum]).

Color in alcohol (Fig. 1).—Ground color of head and body dark gray brown dorsally, becoming pale ventrally; five diagonal broad black saddles on body, (following description goes anteriorly to posteriorly) first from posterior part of nape anteroventrally to dorsoposterior corner of operculum, second (broadest one) from posterior part of first dorsal-fin base to far posterior to pectoral-fin base, third from posterior part of second dorsal-fin base to center of body wall, fourth from slightly posterior to terminus of second dorsal-fin base to middle of anteriormost part of caudal pe-

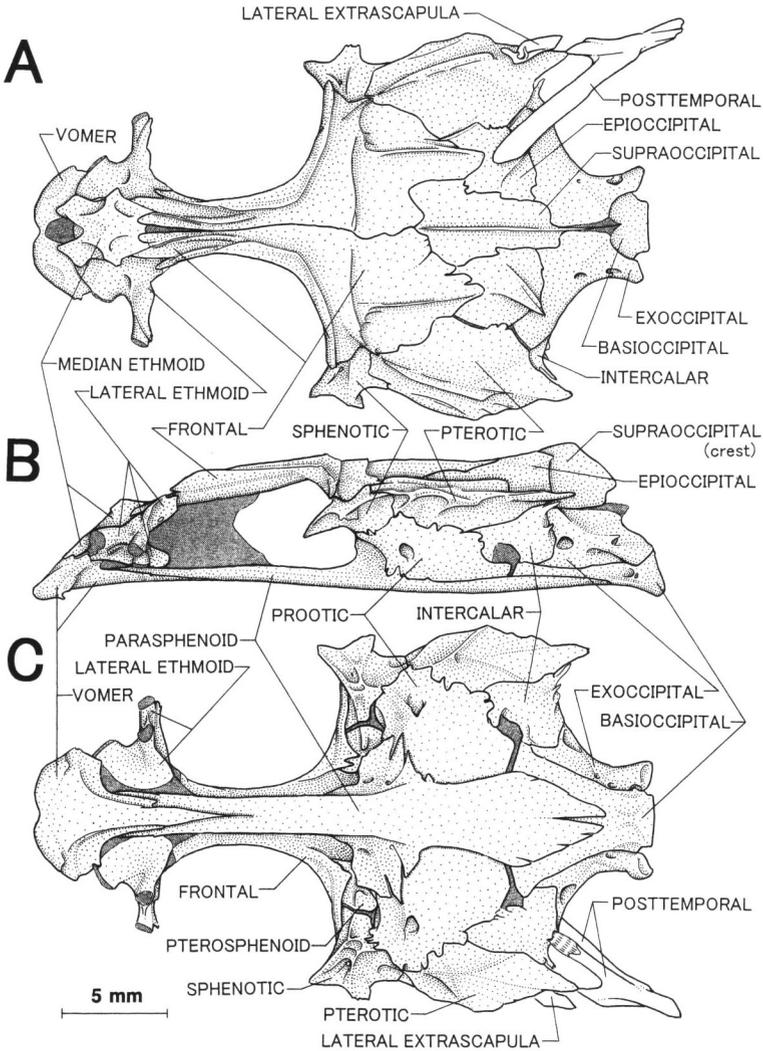


Fig. 7. Cranium of *Terateleotris aspro*, LARREC-P1-6, 92.7 mm SL, from dorsal (A), lateral (B) and ventral (C) views.

duncle, fifth from just beyond base of dorsal procurrent caudal-fin ray to center of caudal-peduncle wall; posteriormost black saddle continuous to T-shaped black blotch at base of caudal fin; two radiating black streaks from eye, one from anteroventral corner of eye to just behind middle of upper jaw, other from posteroventral corner of eye to middle of posterior part of cheek (usually divided into two part); one or two indistinct gray blotches on middle of cheek; gill membrane slightly to heavily blackish (vivid in larger specimens); genital papilla pale; three slightly curved

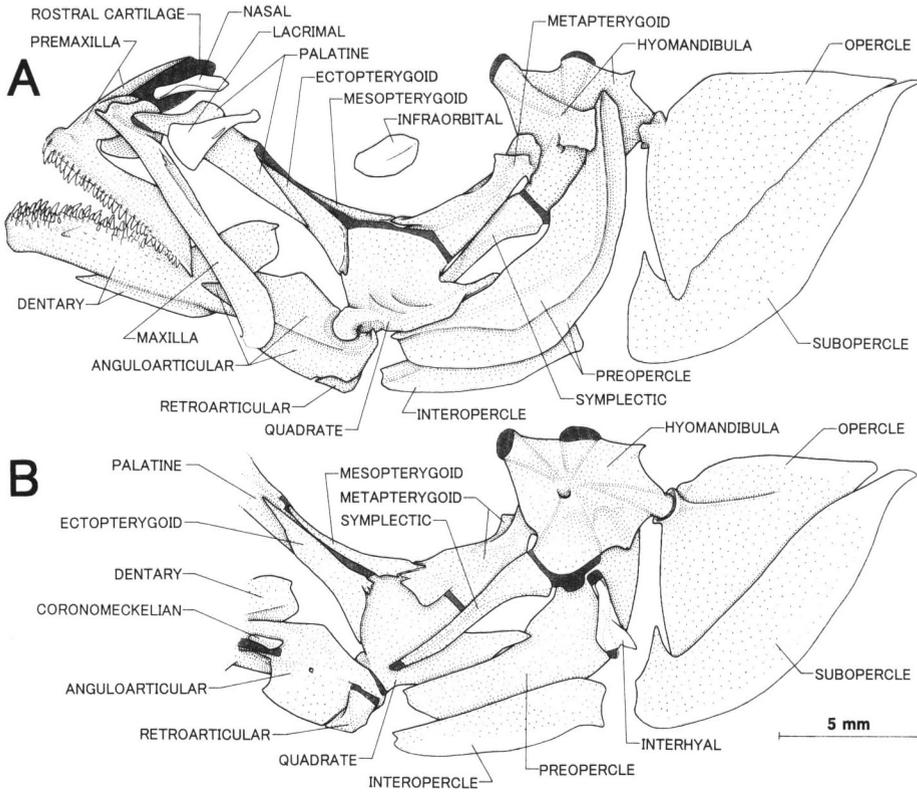


Fig. 8. Jaws, suspensorium, operculum and superficial bones (excepting lateral extrascapula) of *Terateleotris aspro*, LARREC-P1-6, 92.7 mm SL, from lateral (A) and medial (B) views.

longitudinal bars on first dorsal-fin, proximal one (=narrowest one) along base of fin, middle one from distal one fifths of first spine to base of eighth spine, distal one (=broadest one) from distal two thirds of first dorsal-fin to tip of eighth spine; two (in smallest specimen) to five (largest specimen) irregular, narrow diagonal (nearly longitudinal) bars on second dorsal-fin; anal fin pale (in smallest specimen) or bears some nearly longitudinal rows of indistinct gray spots (in others); conspicuous black spot about size of pupil on pectoral fin slightly behind pectoral-fin base; minute irregular-shaped black spot slightly above larger pectoral-fin spot described above; three (in smallest specimen) to seven (in largest specimen) indistinct, narrow transverse gray bars on pectoral fin; pelvic fin pale (in smallest specimen) or with minute scattered melanophores on fin membranes (in others); some to several indistinct V-shaped dusky marking on each caudal-fin rays except for anterior procurrent rays.

Color when fresh (based on color photographs of all examined specimens).— Similar to preserved coloration, except as noted here: ground color of head and body brown to grayish brown dorsally, whitish ventrally; all fin spines and rays brown to

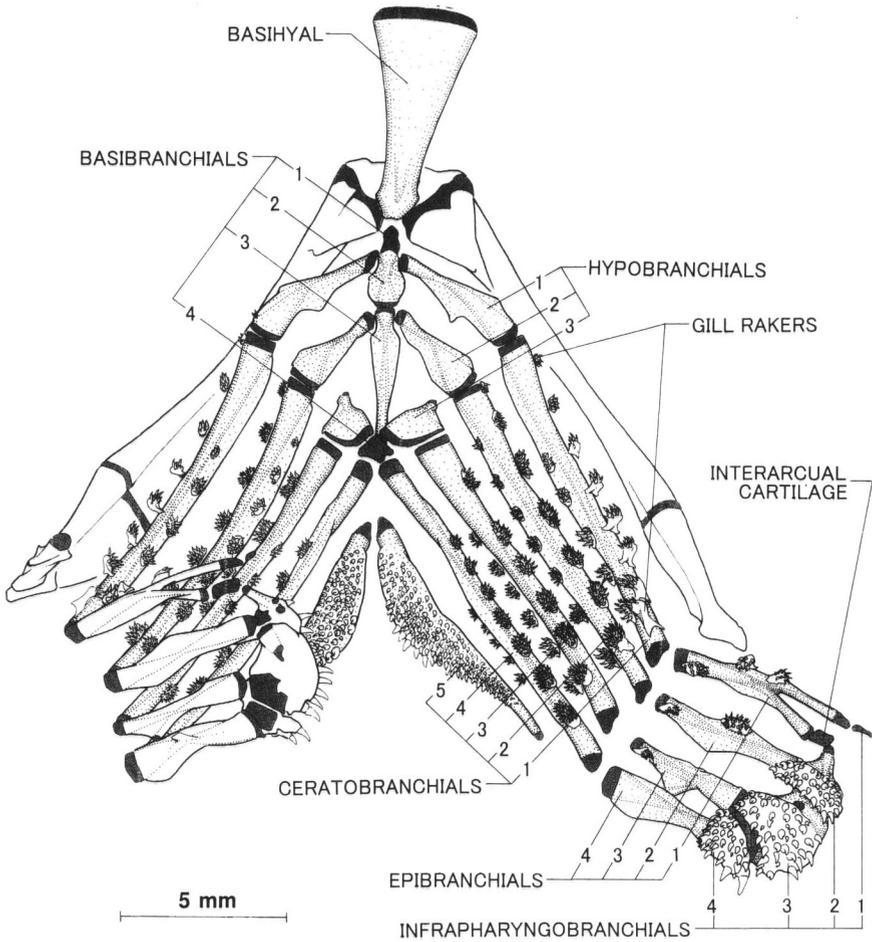


Fig. 9. Dorsal view of branchial arches of *Terateleotris aspro*, LARREC-P1-6, 92.7 mm SL (right-side dorsal elements removed and illustrated from ventral aspect).

yellowish brown, other than blackish markings (anal-fin spine and rays pale in smaller specimens).

Sexual dimorphism. — Male urogenital papilla slender, relatively simple; female urogenital papilla rounded, bulbous, with numerous tiny finger-like projections fringing distally. Although only a single mature female specimen was examined, we found certain differences in some measurements between males and female; for instance, in the female the interorbital width is distinctly narrower than that of males (2.1% in SL and 34.8% in eye diameter in female vs. 3.7–4.2% and 59.2–65.4%, respectively, in males).

Distribution and habitat. *Terateleotris aspro* is currently known only from the

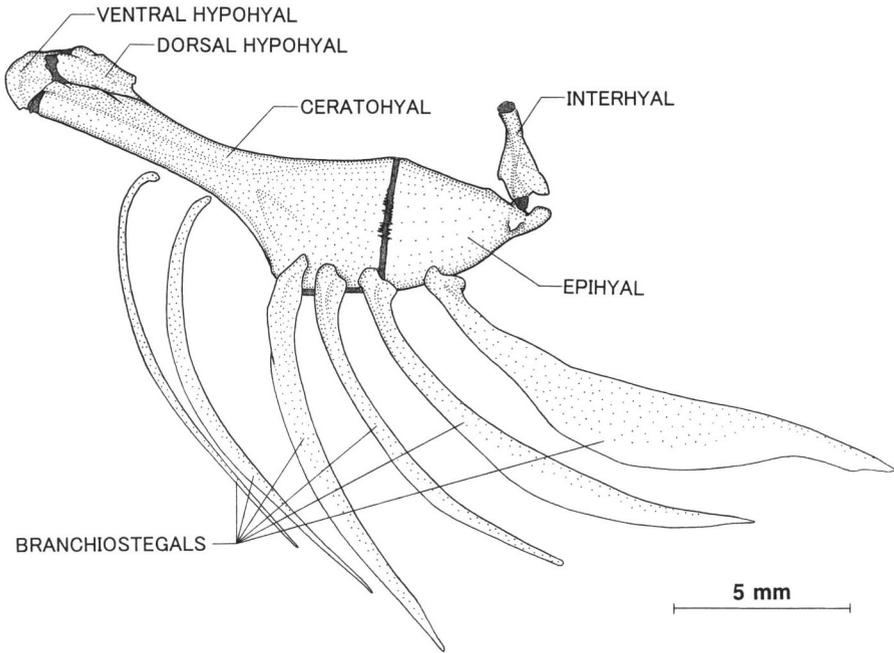


Fig. 10. Lateral view of left hyoid arch of *Terateleotris aspro*, LARREC-P1-6, 92.7 mm SL.

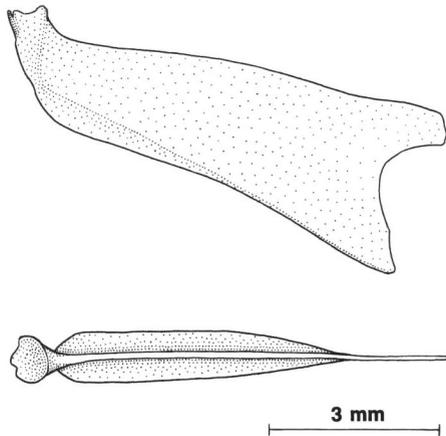


Fig. 11. Lateral (top) and dorsal (bottom) views of urohyal of *Terateleotris aspro*, LARREC-P1-6, 92.7 mm SL.

Xe Bangfai basin, Laos. Our specimens were captured from the gravelly-sandy bottom of a slow-flowing area just downstream of the exit of underground course of the river.

Osteology of *Terateleotris*

Cranium (Fig. 7).—*Terateleotris* possesses two gobioid specializations in the cranium, i.e., parietal and basisphenoid absent. The other selective features are: vomer edentate, indented anteriorly, well ossified excepting for dorsoanterior surface covered by narrow ethmoid cartilage medially; lateral ethmoid bears three condyles each with a cartilaginous tip (lateral one articulates with lacrimal, anterior and ventral ones articulate with palatine); frontals autogeneous, not fused medially; distinct T-shaped ridge on posterolateral surface of postorbital region (anterior transverse ridge receives anterior margin of epaxialis muscle); frontal crest undeveloped; epioccipital bears well developed posterlaterally-directed triangular projection (=“epiotic spine” of Gill and Hoese, 1993), attaching dorsal arm of posttemporal; supraoccipital with well developed mid-dorsal crest (=supraoccipital crest); basioccipital receives anterior end of Baudelot’s ligament that extends posteriorly to posterointernal surface of supracleithrum (passing through deep notch in dorsal end of cleithrum); intercalar well developed, large, posterior spinous part visible from dorsal view; ligament extending from ventral arm of posttemporal attaches to posterior surface of intercalar close to junction of intercalar with exoccipital; subtemporal fossa (Birdsong, 1975) slightly developed, encircled by prootic, intercalar and basiccipital; pterosphenoid well developed.

Jaws, suspensorium and superficial bones of head (Figs. 8 and 12A).—In these series, *Terateleotris* possesses a single gobioid specialization, i.e., distinct open space encircled by symplectic, quadrate and preopercle; but the space is relatively small for gobioids and similar in size and shape to that of *Rhyacichthys* (see Miller, 1973; Springer, 1983; Winterbottom, 1993). It further possesses two specializations shared with the other gobioids excepting the rhyacichthyids: mesopterygoid very narrow (absent in many specialized gobioids); dorsal end of interhyal fails to meet dorsal end of symplectic. On the contrary, *Terateleotris* shares a putative plesiomorphic feature, a single unroofed lateral extrascapula, with *Rhyacichthys*, *Protogobius* and, possibly, the odontobutids bearing this bone (e.g., “*Phylipnus*” *chalmersi* and “*P.*” *compressocephalus*); other gobioids possess two, three or no extrascapula (Akihito, 1971; Springer, 1983). The other selective features are: premaxilla bears well developed ascending, articular and postmaxillary processes; ascending process of premaxilla articulates with large, unpaired rostral cartilage; palatine edentate, L-shaped (namely, ethmoid process undeveloped), articulates with anterior condyle of lateral ethmoid at articulation facet dorsomedially; coronomeckelian bone well developed; mesopterygoid slightly overlaps metapterygoid posteriorly, quadrate ventrally; dorsoanterior lamina of metapterygoid well developed, broad (similar in width to [or slightly broader than] symplectic, as in odontobutids [see Hoese and Gill, 1993, fig. 4A; Iwata, 1994]), overlapping quadrate anteriorly; posterior condyle (for opercle) of hyomandibular well developed, moderately long; symplectic process (Miller, 1973) of

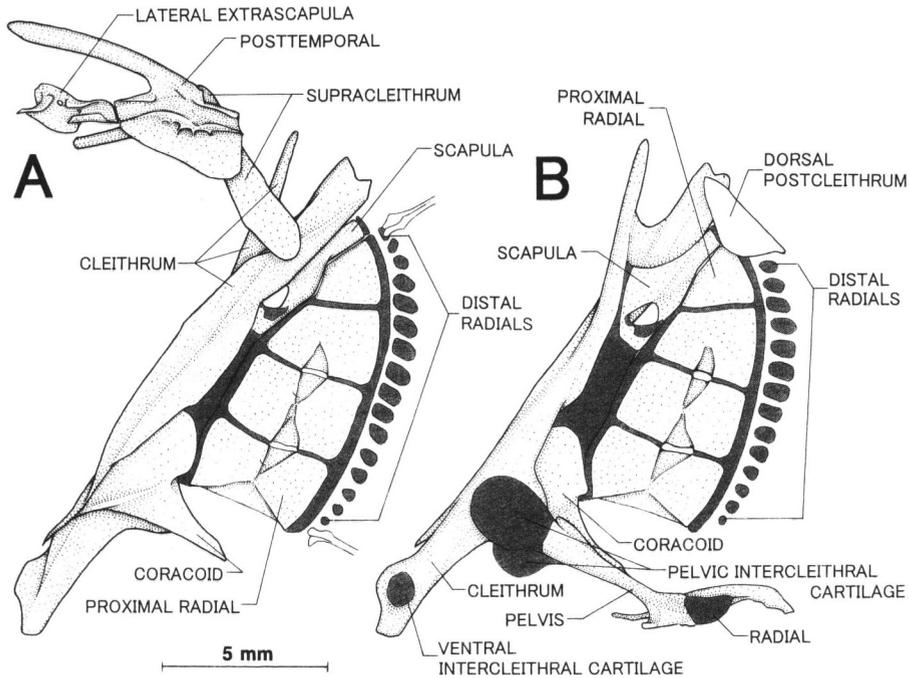


Fig. 12. Pectoral and pelvic girdles of *Terateleotris aspro*, LARREC-P1-6, 92.7 mm SL. Lateral view of left pectoral girdle (A); lateral view of pelvic girdle and medial view of right pectoral girdle (B).

preopercle undeveloped; bony preopercular canal support (Hoese and Gill, 1993) extends most of length of preopercle; near rectangular, unroofed nasal bone; lacrymal and single ovoid infraorbital bone; single, circular scleral ossification in eye.

Hyoid and branchial arches (Figs. 7–10).—In these series, *Terateleotris* possesses a single gobioid specialization, i.e., basibranchial 1 cartilaginous (Springer, 1983). The other selective features are: basibranchial 2 ossified, synchondrally joins basibranchial 1 anteriorly, ossified basibranchial 3 posteriorly; basibranchial 4 cartilaginous; tiny cartilaginous infrapharyngobranchial 1; infrapharyngobranchials 2, 3 and 4 toothed; interarcual cartilage well developed, but not so elongate; gill rakers on outer surface of first gill arch form short, stout spinulose laminae, slightly larger than those on inner rows; basihyal simple, narrow triangular shape; urohyal with well developed transverse shelf ventrally; six branchiostegal rays; penultimate (=5th) branchiostegal ray articulates anterior/posterior ceratohyal junction.

Paired fins and girdles (Figs. 11 and 12).—*Terateleotris* possesses following six gobioid specializations; pectoral-fin ray articulates with uppermost pectoral radial rather than scapula; scapula and coracoid small in size and joined by cartilage, so that middle pectoral radial(s) appears to reach, or closely approaches, posterior margin of

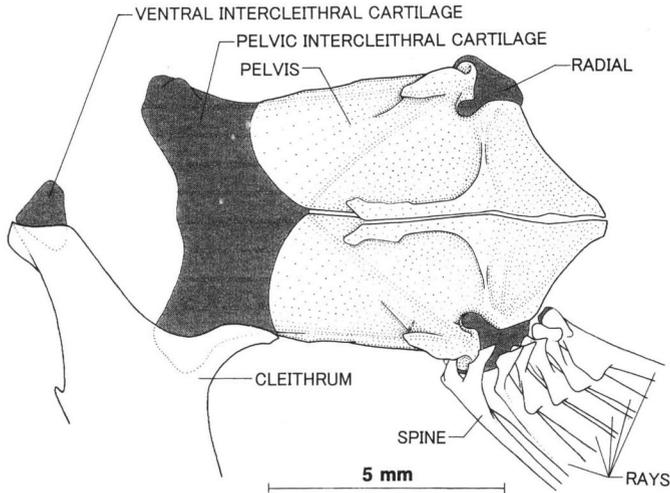


Fig. 13. Ventral view of pelvic girdle of *Terateleotris aspro*, LARREC-P1-6, 92.7 mm SL.

cleithrum; pelvic intercleithral cartilage; ventral intercleithral cartilage; pelvic articular process of cleithrum; and cleithral notch (see Springer, 1983; Johnson and Brothers, 1993; Winterbottom, 1993). The other selective features are: single dorsal postcleithrum (lower postcleithrum absent); scapula well ossified (ossification enclosing scapula foramen) and well developed, extends dorsally to exclude contact between uppermost proximal radial of pectoral fin and cleithrum, with cartilaginous cap distally; four pectoral radials; pelvis articulates with cleithrum via pelvic intercleithral cartilage.

Vertebrae and unpaired fins (Figs. 13–15). — *Terateleotris* possesses following nine gobioid specializations: no supraneurals; no distal radial on last dorsal- and anal-fin pterygiophores; proximal tip of parhypural separated by small gap from ural centrum (parhypural is very close to urostyle in figured specimen [LARREC-P1-6], but not so in the other specimens examined [especially the smaller specimens], judging from soft-x ray negatives); first centrum not shorter than succeeding centra; all neural and haemal spines fused to relevant centrum; hypurals 1 and 2 fused to one another; hypurals 3 and 4 fused with urostyle; uroneurals absent; single supranumerary spine (sometimes segmented ray in other gobioids) on first anal-fin pterygiophore embraces autogenous distal radial. Within the gobioids, *Terateleotris* shares the ossified, autogenous distal radials on first dorsal-fin pterygiophores only with *Rhyacichthys* (Mooi and Johnson, 1997; pers. obs.) and *Protogobius* (pers. obs.); in *Terateleotris*, this radial is found on first through fourth or fifth (or, possibly, sixth) pterygiophores of the fin. Other selective features are: 13+18=31 vertebrae; P-V 3/I II II I I I/10 (four specimens), 3/II I II I I I/10 (1 specimen, LARREC-P1-5) or 3/I II II I I I/9 10 (1 specimen, LARREC-P1-6); middle radial of first pterygiophore of sec-

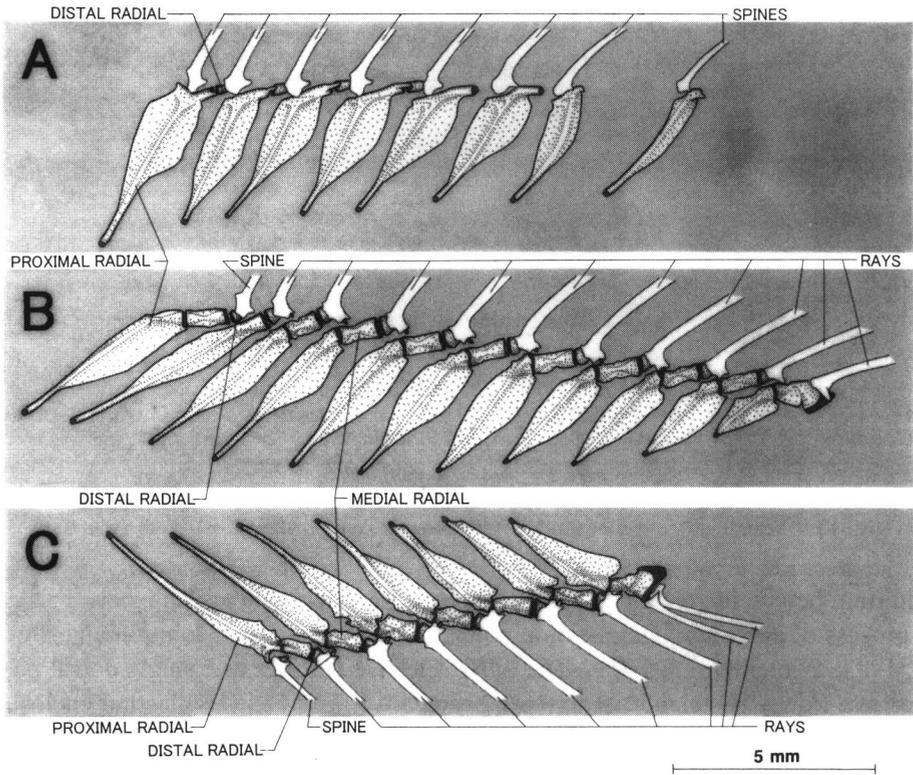


Fig. 14. Lateral view of dorsal and anal fins and fin supports of *Terateleotris aspro*, LARREC-P1-6, 92.7 mm SL. A) first dorsal-fin; B) second dorsal-fin (ultimate dorsal-fin pterygiophore abnormally supports single ray); C) anal fin (first pterygiophore abnormally bears middle radial).

ond dorsal-fin present; second pterygiophore of second dorsal fin lacks middle radial; two or three anal pterygiophores anterior to first haemal spine; pleural ribs on third to twelfth vertebrae; epineural ribs on first to twelfth vertebrae; each epineural not fused to relevant pleural; three epurals, including posterior two with cartilaginous caps distally; dorsal and ventral procurrent cartilage small, restricted posterior to neural and haemal spines of preural centra 2, respectively; neural spine of preural centra 1 very short, blunt; procurrent spur undeveloped. The figured specimen (LARREC-P1-6) has the ultimate dorsal-fin pterygiophore supporting a single ray (Fig. 14B) and the middle radial in first anal-fin pterygiophore (Fig. 14C). These conditions are, however, regarded as abnormal, because the other five specimens have the ultimate dorsal pterygiophore supporting two ray elements (counted as a single ray) and no middle radial in first anal pterygiophore, as in the other typical gobioids.

Remarks. The single (dorsal) postcleithrum (ventral postcleithrum absent) has

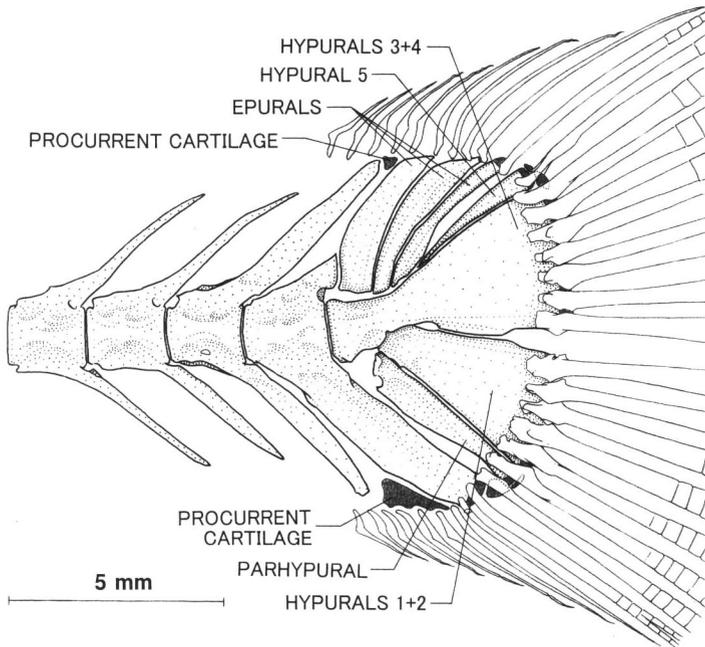


Fig. 15. Lateral view of caudal skeleton of *Terateleotris aspro*, LARREC-P1-6, 92.7 mm SL.

been considered as putative apomorphy shared by *Rhyacichthys* and two odontobutid genera (*Odontobutis* and *Perccottus* — note: Akihito, 1986, reported the same condition in the remaining odontobutid genus *Micropercops*) by Winterbottom (1993). Namely, Winterbottom (1993) hypothesized that the presence of two postcleithra was the primitive condition among the gobioids. Similarly, as in other basal gobioids (i.e., *Rhyacichthys*, *Protogobius* and the odontobutids), *Terateleotris* also possesses a single dorsal postcleithrum. The other “more specialized” gobioids have both dorsal and ventral, only ventral, or no postcleithra (see Akihito, 1969). Following Winterbottom’s (1993) hypothesis, the single dorsal postcleithrum condition has occurred more than twice during gobioid radiation, because the monophyly of the basal gobioid assemblage, at least including *Rhyacichthys* and the odontobutids, is rejected, judging from the cladograms reconstructed using both morphological (Hoese and Gill, 1993) and molecular data (Akihito, 2000). The phylogenetic direction of this feature within the Gobioidae is in need of further analysis.

The *autogenous distal radial on spinous dorsal-fin pterygiophore* occurs in various other perciform families, and is recognized as the unspecialized perciform condition (e.g., Johnson, 1980; Smith-Vaniz and Johnson, 1984; Mooi, 1993; Springer, 1993); it has not been known from the gobioids until recently. For example, Birdsong *et al.* (1988), who surveyed that the arrangement of first dorsal-fin pterygiophores of approximately 200 gobioid genera, stated that the spinous dorsal-fin pterygiophores of

all gobioids was composed of a single element via the loss or fusion of the medial and distal segments. Johnson and Patterson (1993) listed the gobioids as one of the percomorph assemblages with loss or reduction of the distal radial on spinous dorsal-fin pterygiophores. The occurrence of this radial in gobioid fishes was first introduced by Mooi and Johnson (1997). They noted that the distal radials of the spinous dorsal-fin were primitively present in gobioids (e.g., *Rhyacichthys* and some eleotrids). We have found distal radials in the spinous dorsal-fin of *Rhyacichthys*, *Protogobius* and *Terateleotris*. However, as the presence of this radial is considered primitive within the Gobiioidei (Mooi and Johnson, 1997), it is of little value in resolving relationships among *Terateleotris* and *Rhyacichthys/Protogobius*.

Discussion

Although the new genus *Terateleotris* shows several primitive features of gobioids, the assignment of the genus to the Gobiioidei is clearly warranted. As described above, we confirm that *T. aspro* possesses almost all of the gobioid specializations discussed by several recent authors (e.g., Birdsong, 1975; Springer, 1983; Winterbottom, 1993; Hoese and Gill, 1993; Johnson and Brothers, 1993). Brothers (1984) and Johnson and Brothers (1993) indicated that the sagitta with elongate primordium is a gobioid autapomorphy, but we did not examine this otolith in *Terateleotris*. Also, we did not investigate whether the sperm duct glands, suggested as an autapomorphy of gobioids by Miller (1986a, 1992), were present in *Terateleotris*.

Judging from available evidence, *Terateleotris* appears to be nested within the basal gobioid assemblage that includes *Rhyacichthys*, *Protogobius*, and the odontobutids. *Terateleotris* does not have close relationships with the other "more specialized" gobioids (=gobiids *sensu* Hoese and Gill, 1993), owing to lacking all gobiid apomorphies (i.e., anterior expansion of procurrent cartilage, scapula reduced in size [so that radial extends dorsally past scapula], loss of middle radial of first pterygiophore of second dorsal fin, and loss of transforming cteni on scales) discussed by Hoese and Gill (1993).

Among basal gobioids, the Rhyacichthyidae is considered the most primitive extant gobioid family and the sister group to all other gobioid families (Miller, 1973; Hoese, 1976, 1984; Springer, 1983; Birdsong *et al.*, 1988; Winterbottom, 1993; Hoese and Gill, 1993). This family was believed to comprise a single genus *Rhyacichthys*, currently known by only two species (Dingerkus and Séret, 1992), which possesses a number of plesiomorphous features not found in the other gobioids (see Springer, 1983; Hoese and Gill, 1993).

Relationships among the Rhyacichthyidae, Odontobutidae and *Protogobius* have not been well elucidated. The Odontobutidae was erected by Hoese and Gill (1993), based on three East Asian genera previously assigned to the Eleotrididae (=Eleotridae), i.e., *Micropercops*, *Odontobutis* and *Perccottus*. According to Hoese and Gill

(1993), the odontobutids share five derived features with the gobiids (*sensu* Hoese and Gill, 1993 = gobioids excluding rhyacichthyids + odontobutids) (i.e., penultimate branchiostegal ray attaches to anterior ceratohyal, loss of lateral line extending onto body, loss of mandibular canal, loss of infraorbital canal, and interhyal well separated from symplectic), but lack four gobiid specializations (i.e., anterior expansion of dorsal procurrent caudal cartilage, scapula reduced in size [so that pectoral radial extends dorsally past scapula], loss of middle radial of first pterygiophore of second dorsal fin, and loss of transforming cteni on body scales). The monophyly of the family, however, has been not established. As noted by Hoese and Gill (1993), no unique specializations shared by the three odontobutid genera have been discovered.

Protogobius was recently described by Watson and Pöllabauer (1998) as a new genus based on their new species, *Protogobius attiti*, discovered from the small streams in New Caledonia. Like the rhyacichthyids, this species possesses a lateral-line canal extending onto body (a feature previously known only from *Rhyacichthys* within the Gobioidae), and the loss or reduction of it had been believed as the one of synapomorphies for the other gobioids. Watson and Pöllabauer (1998), however, did not classify their new genus into any higher taxa within the Gobioidae, because some other features apparently indicated closer affinity with more derived gobioids rather than with *Rhyacichthys*. Watson and Pöllabauer (1998) concluded, "Until complete survey of osteology and mtDNA analysis is completed, *Protogobius* remains unassigned."

Akihito *et al.* (2000) subsequently attempted to verify the interrelationships of almost all major gobioid groups, including *Protogobius*, based on molecular data. Their reconstructed phylogenetic tree (unrooted) contained various useful suggestions in the gobioid classification. For example, it showed: (1) *Protogobius* and *Rhyacichthys* formed a single cluster, as the ratios of nucleotide substitutions for *Rhyacichthys* and *Protogobius* did not appear to be much different from the ratios found as intrageneric variation in *Eleotris* (Eleotridae) or *Tridentiger* (Gobiidae); (2) *Odontobutis* and *Micropercops* did not form a single cluster (i.e., the Odontobutidae was a non-monophyletic unit). Akihito *et al.* (2000) identified six major lineages (not all in agreement with currently recognized groupings based on morphology), and implied that these lineages had diverged almost at the same time or in extremely short period of times. However, because of very small bootstrap values between any pair of those clusters in their analysis, they did not provide any new concepts of gobioid classification.

Additionally, Akihito *et al.* (2000) provided new information on the morphological aspects of *Protogobius*. These included: scapula extends dorsally between uppermost proximal radial of pectoral fin and cleithrum, 3/II II II I 0/9 P-V pattern, 11-12+16-17=28 vertebrae, presence of infraorbital, endopterygoid, upper postcleithrum, supratemporal (=extrascapular), interneural gap between two dorsal fins, complete bony preopercular canal support, transforming cteni on scales, three epu-

rals, and absence of lower postcleithrum. All these features agree with *Rhyacichthys*, but most of them appear to be primitive or of uncertain affinity within the Gobioidae (see also above Remarks).

In this study, we examined a single paratype (BLIH1997006; already cleared, stained and dissected) and three non-type species of *Protogobius attiti* housed in BLIH (BLIH 1997017, 1997018 and 1997019). We discovered the following two unusual features of lateral line on body: (1) short accessory lateral-line canals dorsal and ventral to the lateral line; (2) lateral line on body discontinuous due to shifting of one or two lateral-line scales to lower scale row (Fig. 6B). Accessory canals on caudal-fin base, reported in *Rhyacichthys aspro* by Springer (1983), was reported as absent in *P. attiti* by Watson and Pöllabauer (1998). We confirmed the presence of accessory lateral-lines in two adult specimens of *P. attiti* (absent in smallest specimen); those of *Protogobius* are, when present, formed by only a single canal in each. Springer (1983) noted that accessory lateral-line canals were present in various other perciform fishes, and he putatively regarded it as primitive for gobioids. The other accessory canal on body we found, however, has not been reported within the Gobioidae. This canal is found in a single scale near the first dorsal-fin base. We also confirmed the presence of an accessory canal near the first dorsal-fin base in *Rhyacichthys*. The only other gobioid genus with lateral-line canals on body, *Terateleotris*, does not exhibit the same lateral-line condition; *Terateleotris* possesses only a single, uninterrupted lateral-line row on mid-lateral body, as illustrated in Fig. 6A. *Terateleotris*, however, possesses a sensory-papilla row arrangement on the body that is similar to *Protogobius*. The scales where accessory canals are found in *Protogobius* possess only sensory-papilla rows in *Terateleotris*. The other “more specialized” gobioids possess no lateral-line canals on body, but their sensory-papilla row arrangements are essentially similar to *Terateleotris* and *Protogobius*, excluding extremely specialized ones (note: the sensory papillae on body of gobioids are easily rubbed off along with loss of scales, and, if present, are usually difficult to discern without staining with suminol cyanine, except in some genera that possess well developed, raised sensory papillae [e.g., *Callogobius*, *Tomiyamichthys*, *Flabelligobius*, *Mangarinus* and *Taenioides*]). We do not know of other fishes that possess the same lateral-line condition as *Protogobius* and *Rhyacichthys* (i.e., lateral-line interrupted at midpoint of body with a single dorsal and two caudal accessory canals), but the condition might be the reductive condition found in the fishes with multiple lateral lines on body. Owing to our lack of knowledge concerning the sister group to the Gobioidae, we cannot say at this time whether the presence of accessory canals in *Rhyacichthys* and *Protogobius* is primitive within the suborder.

Within the Gobioidae, *Terateleotris* shares several unusual features with *Rhyacichthys* and/or *Protogobius*, as follows: lateral-line canal extends onto body; three epurals; free distal radials on first dorsal-fin pterygiophores; penultimate branchiostegal ray articulates at anterior/posterior ceratohyal junction (with *Rhyacichthys*); rela-

tively small open space enclosed by symplectic, quadrate and preopercle (at least with *Rhyacichthys*; the condition in *Protogobius* is difficult to ascertain); and, typically, connection exists between preopercular and oculoscapular canals (with *Rhyacichthys*). All of these features are, however, regarded as plesiomorphic within gobioid fishes. Consequently, there is no evidence to suggest that *Terateleotris* belongs within the Rhyacichthyidae.

Terateleotris and *Protogobius* share two specialized cephalic sensory-canal features (i.e., reduction of infraorbital and mandibular canals); this condition is shared with most of the other gobioids except *Rhyacichthys*. The possession of a well-developed infraorbital canal has been also reported in two East-Asian gobiine genera, *Lophiogobius* and *Siphonogobius*, but the occurrence in those gobiines and *Rhyacichthys* are considered as examples of convergence (Iwata and Jeon, 1995; Shibukawa and Iwata, 1998). Hoese and Gill (1993) recognized such canal reduction as synapomorphies for the gobioids minus *Rhyacichthys*. Within the Gobioidae, the development of cephalic sensory canals is quite variable; variation in presence, absence or state of development is often found even within a genus, e.g., odontobutid *Odontobutis* (Iwata *et al.*, 1985), eleotrid *Bostrychus* and *Oxyeleotris* (Akihito, 1986), xenisthmid *Xenisthmus* (Akihito *et al.*, 2000), gobiid *Callogobius* (Akihito and Meguro, 1977; McKinney and Lachner, 1978, 1984), *Eviota* (Lachner and Karnella, 1980), *Gobiopsis* (Lachner and McKinney, 1978, 1979), *Gymnogobius* (Akihito *et al.*, 2000), *Hetereleotris* (Akihito and Meguro, 1981; Hoese, 1986a), *Knipowitschia* (Miller, 1986b), *Myersina* (Akihito and Meguro, 1983), *Sueviota* (Winterbottom and Hoese, 1988), *Stonogobiops* (Hoese and Randall, 1982; Iwata and Hirata, 1994; Akihito *et al.*, 2000), *Tomiyamichthys* (Iwata *et al.*, 2000), *Vanderhorstia* (Akihito *et al.*, 2000) and *Vanneaugobius* (Van Tassell *et al.*, 1988), and microdesmid *Parioglossus* (Rennis and Hoese, 1985) and *Ptereleotris* (Randall and Hoese, 1985). Due to intra-generic variation in *Bostrychus* and *Oxyeleotris*, Akihito (1986) opined that the reduction in canals had often occurred independently during gobioid evolution. We believe that the reduction of sensory canals exhibited by *Protogobius* and *Terateleotris* (as well as other gobioids) does not indicate a close relationship based on other character distributions noted above.

Terateleotris shares a single specialization (i.e., dorsal end of interhyal fails to meet dorsal end of symplectic) with the gobioids exclusive of *Rhyacichthys* and *Protogobius*. This feature, which has been considered as a synapomorphy of the gobioids excluding the Rhyacichthyidae by recent authors (Springer, 1983; Winterbottom, 1993; Hoese and Gill, 1993; Johnson and Brothers, 1993), also supports the hypothesis that *Terateleotris* does not belong within the Rhyacichthyidae.

The placement of *Terateleotris* within a currently recognized gobioid family is problematic, because the genus lacks at least three specializations shared by the odontobutids and other specialized gobioids (=Gobiidae of Hoese and Gill, 1993), i.e., lateral-line canal not extend onto body, penultimate branchiostegal ray articulates

with posterior ceratohyal, and fewer than two epurals (excepting the odontobutids "*Phylipnus*" *compressocephalus* and *Micropercops swinhonis*, which exhibit three epurals in some specimens). Alternatively, because *Terateleotris* shares some apparent specializations with certain genera of the Odontobutidae, some might conclude that it should be assigned to the Odontobutidae. For example, as noted in the section on "Comparisons" above, the united gill membrane with a free rear fold from isthmus is also found in all known *Odontobutis* species (*sensu* Iwata, 1994). The feature appears to be very rare within the Gobioidae, and does not occur in other gobioids, except for the eleotrid *Talasseleotris* (Hoese and Larson, 1987) and some gobiine gobiids (*sensu* Pezold, 1993) such as *Myersina* (Akihito and Meguro, 1978, 1983; Hoese and Lubbock, 1982), *Stonogobiops* (Hoese and Randall, 1982; Iwata and Hirata, 1997), *Paratrimma* (Hoese and Brothers, 1976), *Psammogobius* (Hoese, 1986b), a species of *Glossogobius* (i.e., *G. biocellatus*—note: Hoese, 1983, suggested this species appeared to be related with *Psammogobius*) (Akihito and Meguro, 1975, 1978; Hoese, 1983), *Phyllogobius* (Larson, 1986, 1990), and some *Vanderhorstia* species (Akihito *et al.*, 1993, 2000). (We do not know the state of this character in *Myersina larsonae* as the character was not addressed in the original description by Allen, 1999). This specialized gill-membrane condition found in *Terateleotris*/*Odontobutis* and the gobiines specified above is likely homoplastic, owing to the wide phylogenetic divergence of the above taxa. Furthermore, *Terateleotris* shares the short, stout spinulous gill rakers on outer surface of first gill arch with *Odontobutis* (*sensu* Iwata, 1994) and *Perccottus glehni* (the condition in the latter two was illustrated by Iwata, 1994). This feature is also very rare within the gobioids, but a similar condition was also described and illustrated in a few species of the eleotrid genus *Eleotris* (i.e., *E. oxycephala* and, possibly, *E. amblyopsis*) (Akihito, 1967; Springer, 1983, fig. 12). In the Gobioidae, ossified gill rakers on the outer surface of first arch are usually slender, blade- or weakly spine-like (sometimes greatly reduced into small round structures) with or without accessory spines, when present. Both *Rhyacichthys* and *Protogobius* possess slender blade-like gill rakers without spines (Miller, 1973; Iwata, 1994; Watson and Pollabauer, 1998; pers. obs.), and thus we regard the gill-raker condition found in *Terateleotris* and two odontobutid genera as derived. Lastly, as far as we know, the suspensorial feature, i.e., mesopterygoid joins and slightly overlaps metapterygoid, is known only in *Odontobutis* and *Terateleotris* amongst the gobioids. In his phylogenetic analysis of *Odontobutis* using the odontobutid *Micropercops* and *Perccottus* and rhyacichthyid *Rhyacichthys* as outgroups, Iwata (1994) considered this feature as one of synapomorphies of *Odontobutis*. This evidence suggests that at least some odontobutids, e.g., *Odontobutis* (=type genus of the Odontobutidae) and *Perccottus*, are closely related to *Terateleotris*.

As noted above, the intra- and inter-familial relationships of the Odontobutidae are still unresolved. Before proposing an appropriate supra-generic assignment for *Terateleotris*, further detailed analysis of the basal gobioid assemblage, especially the

odontobutids *sensu* Hoese and Gill, 1993, is needed. Re-definition and re-organization of the “Odontobutidae” will help resolve this problem and KS and AI are now beginning this task.

Cited comparative materials.

Rhyacichthyidae. *Protogobius attiti*: BLIH1997006, 1 specimen (paratype of *P. attiti*; cleared, stained and dissected), 55.2 mm SL (male), rivièrè Fausse Yaté about 200 m upstream from bridge, southeastern South Province, New Caledonia, 10 Nov. 1997; BLIH1997017, 1 specimen (male), 60.4 mm SL, same collecting locality with BLIH1997006, 11 Nov. 1997; BLIH1997018, 1 specimen (female), 52.3 mm, same collecting data with BLIH1997017; BLIH1997019, 1 specimen (immature young), 33.8 mm SL, same collecting data with BLIH1997017. *Rhyacichthys aspro*: BLIH1987526, 1 specimen, 64.7 mm SL, Omija-gawa River, Iriomote-jima Island, Ryukyu Islands, Japan, 4 Oct. 1987; BLIH1989043, 1 specimen, 118.9 mm SL, Omija-gawa River, Iriomote-jima Island, Ryukyu Islands, Japan, 19 Aug. 1989; BLIH1990184, 1 specimen (cleared, stained and dissected), 84.5 mm SL, Yonara-gawa River, Iriomote-jima Island, Ryukyu Islands, Japan, 30 Sept. 1990; BLIH1997065, 2 specimens, 129.8–131.3 mm SL, Urauchi-gawa River, Iriomote-jima Island, Ryukyu Islands, Japan, 14 Nov. 1997; NSMT-P21408, 1 specimen (female), 106.6 mm SL, Omija-gawa River, Iriomote-jima Island, Ryukyu Islands, Japan, 9 May 1982; NSMT-P33970, 1 specimen (stained and partly dissected), 154.4 mm SL, Nakama-gawa River, Iriomote-jima Island, Ryukyu Islands, Japan, 18 July 1980.

Odontobutidae (all examined materials of *Odontobutis* are not included here, but appeared in Iwata, 1994). “*Odontobutis*” *aurarmus*: BLIH1990130, 4 specimens (paratypes; one [24.2 mm SL] of which cleared and stained), 24.2–44.5 mm SL, Kud Thing marsh, Buengkarn Nongkhai, Thailand. *Perccottus glehni*: BLIH1992253-1, 1 specimen (cleared, stained and dissected), 62.9 mm SL, China, 18 Aug. 1992; NSMT-P56061, 83 specimens, 15.3–136.8 mm SL, Pelis Island, Far East region of Russia, 26 Aug. 1994. “*Phylipnus*” *compressocephalus*: NSMT-P61460, 3 specimens, probably China (purchased at aquarium shop in Japan), 76.8–79.1 mm SL. “*Phylipnus*” *chalmersi*: BLIH1983440, 1 specimen, Hainan Island, China, 7 Apr. 1983.

Acknowledgements

We are grateful to Thongly Xayachack (Faculty of Agriculture, National University of Laos), Soukkongseng Saignaleuth and Souksompong Prixar (Faculty of Forestry, National University of Laos), and Xaypladeth Choulamany and Kaviphone Phouthavong (LARREC) for many considerations that made it possible to conduct research in Laos, and offer special thanks to Edward O. Murdy (National Science Foundation, U.S.A.) and Keiichi Matsuura (NSMT) for their critical reading of this manu-

script. We also wish to thank the following persons: Kazuo Ando (Center for South-east Asian Studies, Kyoto University), Shinya Takeda and Kouichi Ohnari (Graduate School of Asian and African Area Studies, Kyoto University) and Yuka Kiguchi (Mekong Watch) for helping field survey; Katsuichi Sakamoto, Yuji Ikeda and Kayo Sugiyama (BLIH) for helping examination of comparative specimens housed in BLIH; Kiyoshi Fujita and Hiroshi Kohno (Laboratory of Ichthyology, Tokyo University of Fisheries) for kindly providing the working space to the first author. This study was partly supported by the Japan Ministry of Education, Science and Culture Grand in Aid for COE project (#10CE2001), “Making Regions: Proto-Areas, Transformations and New Formations in Asia and Africa,” International Scientific Research (#10041071), project “Transmigration and transformation of eco-system and resource use,” and Toyota Foundation (#99B3-103), “Transformation of eco-system and indigenous knowledge on natural resources management in Xe Ban Hiang basin, Laos — succession of indigenous culture and conservation of environment —”.

References

- Akihito, Prince, 1967. On four species of the gobiid fishes of the genus *Eleotris* found in Japan. *Japan. J. Ichthyol.*, **14**: 135–166.
- Akihito, Prince, 1971. On the supratemporals of gobiid fishes. *Japan. J. Ichthyol.*, **18**: 57–64.
- Akihito, Prince, 1984. Suborder Gobioidae. In: H. Masuda, K. Amaoka, C. Araga, T. Uyeno and T. Yoshino (eds.): *The Fishes of the Japanese Archipelago*. English text. Tokai Univ. Press, Tokyo. xxii+473 pp.
- Akihito, Prince, 1986. Some morphological characters considered to be important in gobiid phylogeny. In: T. Uyeno, R. Arai, T. Taniuchi & K. Matsuura (eds.): *Indo-Pacific Fish Biology: Proceedings of the Second International Conference on Indo-Pacific Fishes*. Ichthyological Society of Japan, Tokyo.
- Akihito, A. Iwata, K. Sakamoto & Y. Ikeda, 1993. Gobioidae. In: T. Nakabo (ed.): *Fishes of Japan with Pictorial Keys to the Species*. Tokai Univ. Press, Tokyo. xxxiv+1478 pp. (In Japanese.)
- Akihito, A. Iwata, T. Kobayashi, K. Ieko, T. Imanishi, H. Ono, Y. Umehara, C. Hamamatsu, K. Sugiyama, Y. Ikeda, K. Sakamoto, F. Fumihito, S. Ohno & T. Gojobori, 2000. Evolutionary aspects of Gobioid fishes (Teleostei: Perciformes) based upon a phylogenetic analysis of Mitochondrial Cytocrome *b* genes. *Gene*, **259**: 5–15.
- Akihito, Prince & K. Meguro, 1975. Description of a new gobiid fish, *Glossogobius aureus*, with notes on related species of the genus. *Japan. J. Ichthyol.*, **22**: 127–142.
- Akihito, Prince & K. Meguro, 1977. Five species of the genus *Callogobius* found in Japan and their relationships. *Japan. J. Ichthyol.*, **24**: 113–127. (In Japanese with English abstract.)
- Akihito, Prince & K. Meguro, 1978. First record of the goby *Myersina macrostoma* from Japan. *Japan. J. Ichthyol.*, **24**: 295–299. (In Japanese with English abstract.)
- Akihito, Prince & K. Meguro, 1981. A gobiid fish belonging to the genus *Heteroleotris* collected in Japan. *Japan. J. Ichthyol.*, **28**: 329–339. (In Japanese with English abstract.)
- Akihito, Prince & K. Meguro, 1983. *Myersina nigrivirgata*, a new species of goby from Okinawa Prefecture in Japan. *Japan. J. Ichthyol.*, **29**: 343–348.
- Akihito, K. Sakamoto, Y. Ikeda & A. Iwata, 2000. Gobioidae. In: T. Nakabo (ed.): *Fishes of Japan with Pictorial Keys to the Species*, second edition. Tokai Univ. Press, Tokyo. 1748 pp. (In Japanese.)

- Allen, G. R., 1999. *Myersina larsonae*, a new species of goby (Pisces: Gobiidae) from North-western Australia. *Revue fr. Aquariol.*, **26**: 49–51.
- Birdsong, R. S., 1975. The osteology of *Microgobius signatus* Poey (Pisces: Gobiidae), with comments on other gobiid fishes. *Bull. Florida State Mus. Biol. Sci.*, **19**: 134–186.
- Birdsong, R. S., E. O. Murdy & F. L. Pezold, 1988. A study of the vertebral column and median fin osteology in gobioid fishes with comments on gobioid relationships. *Bull. Mar. Sci.*, **42**: 174–214.
- Brothers, E. B., 1984. Otolith studies. In: H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr. and S. L. Richardson (eds.): *Ontogeny and Systematics of Fishes Based on an International Symposium Dedicated to the Memory of Elbert Halvor Ahlstrom*. Am. Soc. Ichthyol. Herpetol. Spec. Publ. 1.
- Dingerkus, G. & B. Séret, 1992. *Rhyacichthys guilberti*, a new species of loach goby from northeastern New Caledonia (Teleostei: Rhyacichthyidae). *Tropical Fish Hobbyist*, **1992**: 174–176.
- Fowler, H. W., 1962. A synopsis of the fishes of China. Part X. The Gobioid fishes (concluded). *Quart. J. Taiwan Mus.*, **15**: 1–77.
- Hoese, D. F., 1976. Higher classification of gobioid fishes. *Rev. Trav. Inst. Peches Marit.*, **40**: 605.
- Hoese, D. F., 1983. Sensory papilla patterns of the cheek lateralis system in the gobiid fishes *Acentrogobius* and *Glossogobius*, and their significance for the classification of Gobioid fishes. *Rec. Aust. Mus.*, **35**: 223–229.
- Hoese, D. F., 1986a. Descriptions of two new species of *Heteroleotris* (Pisces: Gobiidae) from the western Indian Ocean, with discussion of related species. *Special Publ. J.L.B. Smith Inst. Ichthyol.*, **41**: 1–25.
- Hoese, D. F. 1986b. Family No. 240: Gobiidae. In: Smith, M. M. and P. C. Heemstra (eds.): *Smith's sea fishes*. Springer-Verlag.
- Hoese, D. F. & E. B. Brothers, 1976. *Paratrimma*, a new genus of gobiid fish and two new species. *Copeia*, **1976**: 494–497.
- Hoese, D. F. & A. C. Gill, 1993. Phylogenetic relationships of eleotridid fishes (Perciformes: Gobioidei). *Bull. Mar. Sci.*, **52**: 415–440.
- Hoese, D. F. & H. K. Larson, 1987. New Australian fishes. Part II. A new genus and species of eleotridid (Gobioidei) from southern Australia with a discussion of relationships. *Mem. Mus. Victoria*, **48**: 43–50.
- Hoese, D. F. and J. E. Randall. Revision of the gobioid fish genus *Stonogobiops*. *Indo-Pacific fishes*, (1): 1–18.
- Hubbs, C. L. & K. F. Lagler, 1958. *Fishes of the Great Lakes Region*. vii+213 pp., 44 pls. Cranbrook Inst. Sci., Bloomfield Hills, Michigan.
- Iwata, A., 1994. Systematics and speciation of the fishes of the genus *Odontobutis* (Gobioidei: Odontobutidae). 253 pp. Unpublished Ph.D dissertation, Tokyo University of Fisheries.
- Iwata, A. & T. Hirata, 1994. A new gobiid fish, *Stonogobiops pentafasciatus*, from Kashiwajima Island, Kochi Prefecture, Japan. *Japan. J. Ichthyol.*, **41**: 189–193.
- Iwata, A. and S.-R. Jeon. 1995. Description of the cephalic sensory canals of *Lophiogobius ocellicauda* (Perciformes: Gobiidae). *Japan. J. Ichthyol.*, **42**: 329–333.
- Iwata, A., S.-R. Jeon, N. Mizuno & K. C. Choi, 1985. A revision of the eleotrid goby genus *Odontobutis* in Japan, Korea and China. *Japan. J. Ichthyol.*, **31**: 373–388.
- Iwata, A., N. Ohnishi & T. Hirata, 2000. *Tomiyamichthys alleni*: a new species of Gobiidae from Japan and Indonesia. *Copeia*, 2000: 771–776.
- Johnson, G. D., 1980. Limits and relationships of the Lutjanidae and associated families. *Bull. Scripps Inst. Oceanogr. Univ. Calif.*, **24**: 1–114.
- Johnson, G. D. & E. B. Brothers, 1993. *Schindleria*: a pedomorphic goby (Teleostei: Gobioidei). *Bull. Mar. Sci.*, **52**: 441–471.

- Johnson, G. D. & C. Patterson, O. 1993. Percormorph phylogeny: a survey of Acanthomorphs and a new proposal. *Bull. Mar. Sci.*, **52**: 554–626.
- Kottelat, M., 1998. Fishes of the Nam Theun and Xe Bangfai basin, Laos, with description of twenty-two new species (Teleostei: Cyprinidae, Balitoridae, Cobitidae, Cobiidae and Odontobutidae). *Ichthyol. Explor. Freshwaters*, **9**: 1–128.
- Koumans, F. P., 1953. Gobioidae. In: Weber, M. & L. F. de Beaufort (eds.): The Fishes of the Indo-Australian Archipelago X. 423 pp. E. J. Brill, Leiden.
- Lachner, E. A. & S. J. Karnella, 1980. Fishes of the Indo-Pacific genus *Eviota* with descriptions of eight new species (Teleostei: Gobiidae). *Smithson. Contr. Zool.*, **315**: 1–127.
- Lachner, E. A. & J. F. McKinney, 1978. A revision of the Indo-Pacific fish genus *Gobiopsis* with description of four new species (Pisces: Gobiidae). *Smithson. Contr. Zool.*, **262**: 1–52.
- Lachner, E. A. & J. F. McKinney, 1979. Two new gobiid fishes of the genus *Gobiopsis* and a redescription of *Feia nympha* Smith. *Smithson. Contr. Zool.*, **262**: 1–52.
- Larson, H. K., 1986. *Phyllogobius*, a new generic name for *Cottogobius platycephalus* Smith (Pisces: Gobiidae), and a redescription of the species. *Beagle, Occ. Pap. N. T. Mus. Arts and Sci.*, **3**: 131–136.
- Larson, H. K., 1990. A revision of the commensal gobiid fish genera *Pleurosicya* and *Luposicya* (Gobiidae), with descriptions of eight new species of *Pleurosicya* and discussion of related genera. *Beagle, Rec. N. T. Mus. Arts and Sci.*, **7**: 1–53.
- McKinney, J. F. & E. A. Lachner, 1978. Two new species of *Callogobius* from Indo-Pacific waters (Teleostei: Gobiidae). *Proc. Biol. Soc. Wash.*, **91**: 203–215.
- McKinney, J. F. & E. A. Lachner, 1984. *Callogobius crassus*, a new fish from Indo-Pacific region (Teleostei: Gobiidae). *Proc. Biol. Soc. Wash.*, **97**: 627–631.
- Miller, P. J. 1973. The osteology and adaptive features of *Rhyacichthys aspro* (Teleostei: Gobioidei) and the classification of gobioid fishes. *J. Zool., Lond.*, (171): 397–434.
- Miller, P. J., 1986 a. Reproductive biology and systematic problems in gobioid fishes. In: T. Uyeno, R. Arai, T. Taniuchi and K. Matsuura (eds.): Indo-Pacific fish biology: Proceedings of the Second International Conference on Indo-Pacific Fishes. Ichthyological Society of Japan, Tokyo.
- Miller, P. J., 1986 b. Gobiidae. In: P. J. P. Whitehead, M.-L. Bauchot, J.-C. Hureau, J. Nielsen and E. Tortonese (eds.): Fishes of the North-eastern Atlantic and the Mediterranean. UNESCO, Paris. 1473 pp.
- Miller, P. J., 1992. The sperm duct gland: a visceral synapomorphy for gobioid fishes. *Copeia*, **1992**: 253–256.
- Mooi, R. D., 1993. Phylogeny of the Plesiopidae (Pisces: Perciformes) with evidence for the inclusion of the Acanthoclinidae. *Bull. Mar. Sci.*, **52**: 284–326.
- Mooi, R. D. & G. D. Johnson, 1997. Dismantling the Trachinoidei: evidence of a scorpaenoid relationship for the Champsodontidae. *Ichthyol. Res.*, **44**: 143–176.
- Potthoff, T., 1984. Clearing and staining techniques. In: H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr. & S. L. Richardson (eds.): Ontogeny and Systematics of Fishes Based on an International Symposium Dedicated to the Memory of Elbert Halvor Ahlstrom. Am. Soc. Ichthyol. Herpetol. Spec. Publ. 1.
- Randall, J. E. & D. F. Hoese, 1985. Revision of the Indo-Pacific dartfishes, genus *Ptereleotris* (Perciformes: Gobioidei). *Indo-Pacific Fishes*, (7): 1–36.
- Rennis, D. S. & D. F. Hoese, 1985. A review of the genus *Parioglossus*, with descriptions of six new species (Pisces: Gobioidei). *Rec. Aust. Mus.*, **36**: 169–201.
- Shibukawa, K. & A. Iwata, 1998. *Siphonogobius nue*, a new genus and species of gobioid fish from Japan. *Ichthyol. Res.*, **45**: 141–150.
- Smith-Vaniz, W. F. & G. D. Johnson, 1990. Two new species of Acanthoclininae (Pisces: Plesiopidae)

- with a synopsis and phylogeny of the family. *Proc. Acad. Nat. Sci. Philad.*, **142**: 211–260.
- Springer, V. G., 1983. *Tyson belos*, new genus and species of Western Pacific fish (Gobiidae, Xenisthmiinae), with discussions of gobioid osteology and classification. *Smithon. Contr. Zool.*, (390). iii+40 pp.
- Springer, V. G., 1993. Definition of the suborder Blennioidei and its included families (Pisces: Perciformes). *Bull. Mar. Sci.*, **52**: 472–495.
- Takagi, K., 1988. Cephalic sensory canal system of the gobioid fishes of Japan: comparative morphology with special reference to phylogenetic significance. *J. Tokyo Univ. Fish.*, **75**: 499–568.
- Van Tassell, J. L., P. J. Miller & A. Brito, 1988. A revision of *Vanneaugobius* (Teleostei: Gobiidae), with description of a new species. *J. Nat. Hist.*, **22**: 545–567.
- Vidthayanon, C., 1995. *Odontobutis aurarmus*, a new species of odontobutid goby from wetlands of the Mekong basin, Thailand. *Ichthyol. Explor. Freshwaters*, **6**: 235–242.
- Watson, R. E. & C. Pöllabauer, 1998. A new genus and species of the freshwater goby from New Caledonia with a complete lateral-line (Pisces: Teleostei: Gobioidi). *Senckenbergiana biologica*, **77**: 147–153.
- Winterbottom, R., 1993. Search for the gobioid sister group (Actinopterygii: Percomorpha). *Bull. Mar. Sci.*, **52**: 395–414.
- Winterbottom, R. & D. F. Hoese, 1988. A new genus and four new species of fishes from the Indo-West Pacific (Pisces: Perciformes; Gobiidae), with comments on relationships. *Roy. Ontario Mus., Life Sci. Occ. Pap.*, **37**: 1–17.
- Wongrat, P. & P. J. Miller, 1991. The innervation of head neuromast rows in eleotridine gobies (Teleostei: Gobioidi). *J. Zool., Lond.*, **225**: 27–42.

