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Some Morphological Characters Considered to be Important in Gobiid Phylogeny

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Abstract The sensory canals, infraorbital bone, endopterygoid, upper and lower postcleithra, branchiostegal rays, scapula, and the urohyal are considered to be important in gobiid phylogeny. The degree of specialization of these characters was determined by comparing with characters of some generalized perciforms. On the basis of these characters, the species having the largest number of unspecialized characters in gobiids were examined.

Bostrychus sinensis, *Oxyeleotris herwerdenii*, and *Oxyeleotris marmorata* can be considered to represent a basic form closest to the ancestral form of gobiids from which all the specialization of the other gobiids can be deduced. *Rhyacichthys aspro* was also compared with them, but is not considered to represent the form closest to the ancestral form of gobiids because it has some specialized characters in addition to its unspecialized characters.

The suborder Gobioidae, which includes the families Rhyacichthyidae and Gobiidae, belongs to the order Perciformes, but there are no fishes among the perciforms which seem to be closely related to the gobioids, as Miller (1973) and Springer (1983) remarked. The phylogeny of the gobiids is considered here by comparing some morphological characters of gobiids with those of some generalized perciforms.

The gobiids have many specialized characters, including the development of the pelvic fins into a sucking disc. Among them the degeneration of the sensory canals and bones is noticeable when compared with those of generalized perciforms, and a gradual loss of sensory canals and bones is also seen. The comparison of these characters of various gobiids with those of generalized perciforms is described and discussed from the viewpoint of specialization of these characters.

In conducting this study I have referred to Takagi (unpublished), Miller (1973), Birdsong (1975), Wongrat (unpublished), and Springer (1983), in addition to my previous works (Prince Akihito, 1969, 1971; Prince Akihito *et al.*, 1984). However, the results of this study are sometimes different from those of the above papers.

The classification of gobiids has been variously discussed (Takagi, unpublished; Miller, 1973; Birdsong, 1975; Springer, 1983). The family Gobiidae here designated includes the subfamily Eleotridinae with six branchiostegal rays and the Gobiinae with five branchiostegal rays.

The generalized perciforms referred to here have been selected on the basis of the remarks by Gosline (1966).

Materials

Rhyacichthyidae

Rhyacichthys aspro, LICPP (Laboratory of Ichthyology, the Crown Prince's Palace) 1978104 (1); LICPP 1982002 (1).

Gobiidae

Eleotridinae. *Bostrychus sinensis*, LICPP 1968431 (3); YCM (Yokosuka City Museum)-P 8462 (5); URM (Department of Marine Sciences, University of the Ryukyus)-P 4864 (1). *Bostrychus strigogenys**, AMNH (American Museum of Natural History) 13652, type; AMS (Australian Museum) I A 7251–52 (2). *Bostrychus zonatus**, ZMA (Zoölogisch Museum, Universiteit van Amsterdam) 111.764 (12), syntypes; NTM (Northern Territory Museum of Arts and Sciences) S 10791–001 (3). *Butis amboinensis*, LICPP 1981082 (9); LICPP 1981107 (1); URM-P 3166 (1). *Butis butis*, LICPP 1966119 (1); LICPP 1967279 (2); LICPP 1968426 (1); LICPP 1977005 (2). *Butis melanostigma*, LICPP 1963198 (3); LICPP 1966092 (9); LICPP 1968427 (1). *Eleotris oxycephala*, LICPP 1978062 (5). *Gobiomorphus australis*, LICPP 1976055 (3); LICPP 1980129 (1). *Gobiomorphus breviceps*, LICPP 1966091 (1). *Gobiomorphus cotidianus*, LICPP 1969190 (1). *Gobiomorphus hubbsi*, LICPP 1962037 (1). *Gobiomorphus huttoni*, LICPP 1972241–1 (1). *Gobiomorus dormitor*, LICPP 1972380 (2). *Gobiomorus maculatus*, LICPP 28 (1). *Grahamichthys radiatus*, LICPP 1969188 (2). *Grahamichthys* sp., LICPP 1984183 (10). *Hypseleotris aurea*, C56–241 (AMS) (2). *Hypseleotris compressa*, LICPP 1973072 (4); LICPP 1973073 (1). *Hypseleotris cyprinoides*, LICPP 1980118 (10). *Hypseleotris galii*, LICPP 16 (1). *Hypseleotris klunzingeri*, LICPP 25 (1). *Incara multisquamatus*, ROM (Royal Ontario Museum) 39293 (4); ROM 39294 (2); ROM 39295 (4); AMSI 22717–001 (1); AMSI 22717–002 (9); LICPP 1981208 (4). *Micropercops swinhonis*, LICPP 1959004 (4); LICPP 1973065 (1); LICPP 1973066 (4). *Odontobutis obscura obscura*, LICPP 1964168 (1). *Ophieleotris aporos**, MNHN (Muséum National d'Histoire Naturelle, Paris) A. 5178, Syntypes of *Eleotris aporos*. *Ophiocara porocephala*, YCM-P 8432 (6); YCM-P 8517 (6); YCM-P 8554 (2); YCM-P 8595 (4); YCM-P 8732 (5); YCM-P 8746 (2); URM-P 4848 (1). *Oxyeleotris* (= *Boroda*) *albooculata**, SU (Stanford University Collection, California Academy of Sciences) 26204 (12). *Oxyeleotris aruensis**, ZMA 110.973 (2), syntypes of *Eleotris (Oxyeleotris) aruensis*; AMS IA 7254 (19). *Oxyeleotris fimbriata*, ZMA 111.814, holotype of *Eleotris fimbriatus*; BM(NH) (British Museum (Natural History)) 1913–12–9: 179 (1); USNM (United States National Museum, Smithsonian Institution) 217288 (4); USNM 217289 (3); USNM 217290 (1). *Oxyeleotris* (= *Bunaka*) *herwerdenii**, ZMA 112.932 (1); ZMA 112.934 (2); ZMA 112.935 (1); ZMA 112.936 (1); ZMA 112.937 (1); ZMA 112.938 (5), syntypes of *Eleotris herwerdenii*. *Oxyeleotris heterodon**, ZMA 112.014 (7), syntypes of *Eleotris (Oxyeleotris) heterodon*. *Oxyeleotris lineolata**, NMW (Naturhistorisches Museum, Wien) 77249, holotype of *Eleotris lineolatus*; LICPP 13 (3). *Oxyeleotris marmorata*, LICPP 1970197 (10); LICPP 1977071 (4). *Oxyeleotris urophthalmoides**, RMNH (Rijksmuseum van Natuurlijke Historie, Leiden) 6206 (3), syntypes of *Eleotris urophthalmoides*; BM(NH) 1894–1–19: 32 (1); BM(NH) 1894–1–20: 8 (1); BM(NH) 1938–12–1: 168 (1). *Oxyeleotris urophthalmus**, RMNH 6205 (5), syntypes of *Eleotris urophthalmus*; BM(NH) 1859–7–1: 64–66 (6), syntypes of *Eleotris siamensis*. *Perccottus glehnii*, LICPP 31 (2). *Philypnodon grandiceps*, LICPP 1974038 (2). *Prionobutis koilomatodon*, LICPP 1963199 (3); LICPP 1971213 (2). *Xenisthmus clarus*, LICPP 10 (2); URM-P 3154 (1); URM-P 3510 (2).

Gobiinae. *Acanthogobius flavimanus*, LICPP 1963080 (3). *Awaous ocellaris*, LICPP 1963159 (3). *Awaous* sp., LICPP 1944001 (2). *Bathygobius cocosensis*, LICPP 1971194 (4).

Bathygobius cotticeps, LICPP 1967191 (8); URM-P 5531 (1). *Bathygobius cyclopterus*, LICPP 1968204 (6); URM-P 5512 (1). *Bathygobius fuscus*, LICPP 1980079 (2). *Chaenogobius castaneus*, LICPP 1984139 (5). *Glossogobius olivaceus*, LICPP 1977046 (5). *Sicyopterus japonicus*, LICPP 1968136 (3); LICPP 1969246 (2). *Stonogobiops xanthorhinica*, YCM-P 9249 (1). *Stonogobiops* sp., URM-P 4945 (1). *Tridentiger barbatus*, LICPP 1976033 (6); URM-P 5402 (1). *Tridentiger nudicervicus*, LICPP 1948003 (11); LICPP 1983013 (1); LICPP 1983048 (8). *Tridentiger obscurus*, LICPP 1985013 (5). *Tridentiger trigonocephalus*, LICPP 1969084 (5).

The generalized perciforms

- Apogonidae: *Apogon amboinensis*, collected in Japan.
 Centrarchidae: *Ambloplites rupestris*, collected in U.S.A.
 Centropomidae: *Lates japonicus*, collected in Japan.
 Kuhliidae: *Kuhlia mugil*, collected in Japan.
 Percichthyidae: *Lateolabrax japonicus*, collected in Japan.
 Percidae: *Perca fluviatilis*, collected in Finland.
 Scorpiidae: *Microcanthus strigatus*, collected in Japan.

Species whose infraorbital bone was examined only by radiography are indicated with an asterisk.

Sensory Canals

There are various differences in the sensory canals of the gobiids, from none to the most developed state found in the species such as *Bostrychus sinensis* shown in Fig. 1. *B. sinensis* has the oculoscapular canals extending from before the nasal bones to behind the posttemporal bones, and has 11 pores on each canal and a single pore on a canal connecting the right and left canals. The supratemporal bones are attached to the canal between pores H and K. The preopercular canal is not continuous with the oculoscapular canal, and does not extend to the lower jaw. It has 5 pores. But when compared with generalized perciforms, even the sensory canals of *B. sinensis* are much reduced. The sensory canals of *B. sinensis* differ from those of generalized perciforms in that *B. sinensis* has neither infraorbital canals nor body lateral line canals and has a reduced supratemporal canal at the tip of which pore I opens, and the isolated preopercular canal is confined to the posterior part of the preopercle.

Those gobiids with the least loss of sensory canals are listed in Table 1. Some of them differ from *B. sinensis* in the canal pores, such as in having pore D paired without a canal connecting the right and left canals, in having a small additional pore on the canal between pores K and L, or in lacking pore G. The sensory canals of the species of the genus *Butis* and *Prionobutis koilomatodon* are different from those of the others in that they are covered by a thin membrane and the canal pores are not at the end of branch canals, but open directly onto the main canals.

Gobiids generally have pores in a definite position in the canals, and various differences of canals and pores can be expressed as the loss of a certain part of the canals or of a certain pore as shown in Table 2.

In both the Eleotridinae and the Gobiinae some species with complete loss of sensory canals are found. However, there is a difference between them in the degree of the most developed canals as shown in Fig. 2. Those species with the most developed canals in the Gobiinae differ from those in the Eleotridinae in that the former lack the oculoscapular canal between pores H and K and part of the preopercular canal below pore O. The supratemporal bones are also lost with this part of the oculoscapular canal. The lack of this part of the canal

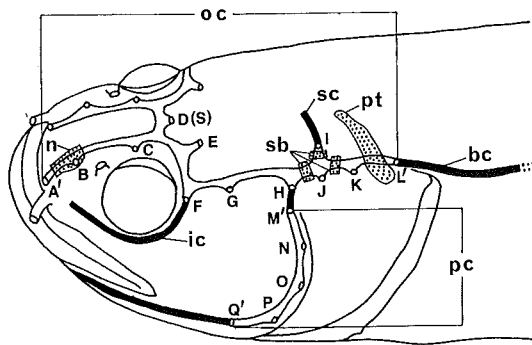


Fig. 1. Sensory canals of *Bostrychus sinensis* showing the reduction from the state found in *Lateolabrax japonicus*, which is shown in black. A to Q indicate sensory canal pores. Letters with a prime mark such as A' indicate a terminal pore. (S), single pore; bc, body lateral line canal; ic, infraorbital canal; oc, oculoscapular canal; pc, preopercular canal; sc, supra-temporal canal; n, nasal (stippled portion); pt, posttemporal (stippled portion); sb, supratemporal bones (stippled portions).

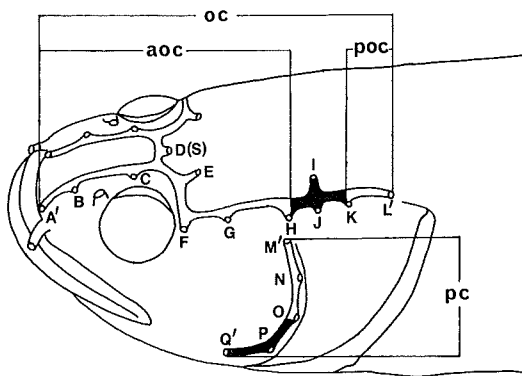


Fig. 2. Comparison between the least loss of sensory canals found in the Eleotridinae (white portions with black portions) and that found in the Gobiinae (white portions only). aoc, anterior oculoscapular canal; poc, posterior oculoscapular canal.

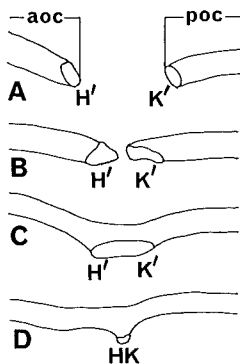


Fig. 3. Various relations between the anterior and posterior oculoscapular canals. A, *Tridentiger obscurus*, anterior and posterior oculoscapular canals separated; B, *Bathygobius fuscus*, anterior and posterior oculoscapular canals very close; C, *Tridentiger nudicervicus*, anterior and posterior oculoscapular canals nearly united; D, *Bathygobius cyclopterus*, oculoscapular canal continuous.

is also found in some species of the Eleotridinae. In the genus *Oxyeleotris*, *O. albooculata*, *O. aruensis*, and *O. urophthalmus* lack it whereas other species of the genus have the same sensory canals as *Bostrychus sinensis*. Such a difference in the sensory canals within a genus, including their complete loss, such as in the genus *Gobiomorphus*, is often found.

Although almost all the species of the Gobiinae have the oculoscapular canals separated into the anterior and posterior oculoscapular canals, some of them have a continuous oculoscapular canal, but lack the supratemporal bones and pores I and J as shown in Fig. 3. In the genera *Awaous* and *Bathygobius*, species with both a continuous oculoscapular canal (e.g., *A. sp.*, *B. cotticeps*, and *B. cyclopterus*) and separated oculoscapular canals (e.g., *A. ocellaris*, *B. cocosensis*, and *B. fuscus*) are found, and in the genus *Tridentiger*, species with

Table 1. The species which have the least loss of sensory canals in the gobiids.

Species	Pore D	Pore G	Additional pore
<i>Bostrychus sinensis</i>	single	present	absent
<i>B. strigogenys</i>	paired	present	absent
<i>B. zonatus</i>	paired	present	absent
<i>Oxyeleotris fimbriata</i>	single	present	absent
<i>O. herwerdenii</i>	single	present	absent
<i>O. heterodon</i>	single	present	absent
<i>O. lineolata</i>	single	present	present
<i>O. marmorata</i>	single	present	absent
<i>O. urophthalmoides</i>	single	present	absent
<i>Butis amboinensis</i>	paired	present	absent
<i>B. butis</i>	paired	present	absent
<i>B. melanostigma</i>	single	present	absent
<i>Prionobutis koilomatodon</i>	single	present	absent
<i>Incara multisquamatus</i>	single	absent	absent
<i>Ophiocara porocephala</i>	single	absent	absent

Table 2. Various degrees of loss of canals in the gobiids.

Species	Sensory canal pores present
Eleotridinae	
<i>Xenisthmus clarus</i>	A', B, C, D(S), E, F, H, I, J, K'; M', N, O, P, Q'
<i>Oxyeleotris urophthalmus</i>	A', B, C, D(S), E, F, G, H'; K', L'; M', N, O, P, Q'
<i>Hypseleotris cyprinoides</i>	C', D, E'; K', L'; M', N, O, P'
<i>Ophieleotris aporos</i>	N', O'
<i>Eleotris oxycephala</i>	all absent
Gobiinae	
<i>Tridentiger obscurus</i>	A', B, C, D(S), E, F, H'; K', L'; M', N, O'
<i>Glossogobius olivaceus</i>	B', C(S), D(S), E, F, G, H'; K', L'; M', N, O'
<i>Acanthogobius flavimanus</i>	B', D(S), F, H'; K', L'; M', O'
<i>Chaenogobius castaneus</i>	C', D, F'
<i>Stonogobiops xanthorhinica</i>	all absent

both nearly united oculoscapular canals (e.g., *T. barbatus* and *T. nudicervicus*) and completely separated oculoscapular canals (e.g., *T. obscurus* and *T. trigonocephalus*) are found. In species of the genus *Bathygobius* with separated oculoscapular canals, the posterior end of the anterior oculoscapular canal, and the anterior end of the posterior oculoscapular canal are very close to each other (Fig. 3 B).

Bones

The bones of the gobiids are also considerably degenerated when compared with generalized perciforms. Even the species which have the least degenerated bones in the gobiids lack the parietal, supramaxilla, predorsal bones, and all infraorbital bones except for one. There are also varying degrees of loss of bones within the gobiids.

Infraorbital bone. There is only one infraorbital bone or none in the gobiids (Fig. 4). It is horizontally placed, and has no vertical part as found in generalized perciforms. A small

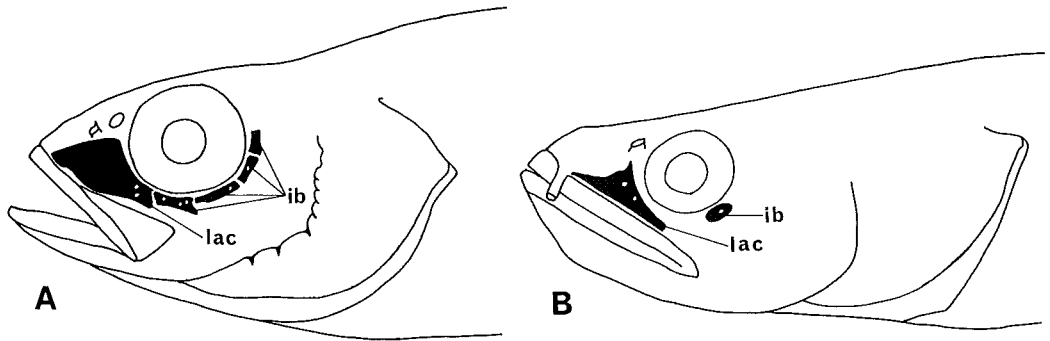


Fig. 4. The infraorbital bones of *Lateolabrax japonicus* and of *Bostrychus sinensis*. A, *Lateolabrax japonicus*; B, *Bostrychus sinensis*. ib, infraorbital bone; lac, lacrymal.

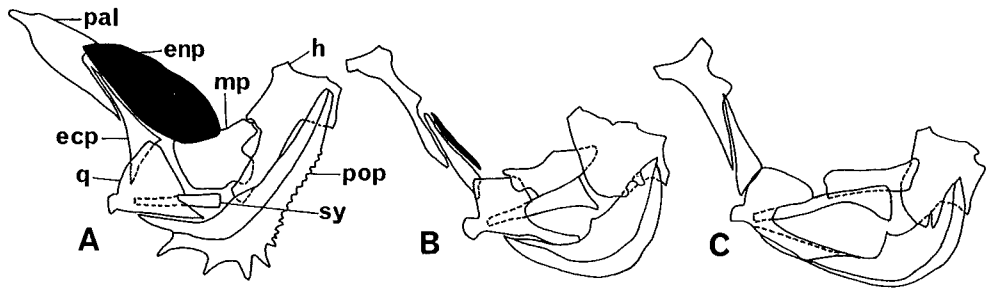


Fig. 5. The endopterygoid of *Lateolabrax japonicus* and of some gobiids. A, *Lateolabrax japonicus*; B, *Bostrychus sinensis*; C, *Acanthogobius flavimanus*. ecp, ectopterygoid; enp, endopterygoid (black portions); h, hyomandibular; mp, metapterygoid; pal, palatine; pop, preopercle; q, quadrate; sy, symplectie.

foramen for the nerve piercing the bone is sometimes found. Its presence is limited to *Bostrychus sinensis*, *B. strigogenys*, *Incara multisquamatus*, *Micropercops swinhonis*, *Oxyeleotris albooculata*, *O. herwerdenii*, *O. lineolata*, *O. marmorata*, and *O. urophthalmus* in the Eleotridinae. The examination of the infraorbital bone of many specimens of *Bostrychus sinensis* and *Oxyeleotris marmorata* reveals that there is individual variation in the shape and size, and some specimens even lack the infraorbital bone on one side. In the Gobiinae, the infraorbital bone is not found in any species.

Endopterygoid. The endopterygoid is present or absent in the gobiids. When the endopterygoid is present, its size is considerably more reduced than that of generalized perciforms (Fig. 5). Most species of the Eleotridinae have the endopterygoid, and it was found in all the species of the Eleotridinae with the infraorbital bone which were examined for its presence or absence. There is no individual variation in the presence or absence of the endopterygoid, but specific variation is found in the genera *Gobiomorphus* and *Hypseleotris*; e.g., in *G. australis*, *G. hubbsi*, *G. huttoni*, *H. aurea*, and *H. compressa* the endopterygoid is present; in *G. breviceps*, *G. cotidianus*, *H. cyprinoides*, *H. galii*, and *H. klunzingeri* it is absent. Other genera of the Eleotridinae without the endopterygoid are shown in Table 3. No species of the Gobiinae has the endopterygoid (Fig. 5 C).

Upper and lower postcleithra. In gobiids there are species with the upper and lower postcleithra, species with only the upper postcleithrum, species with only the lower postcleith-

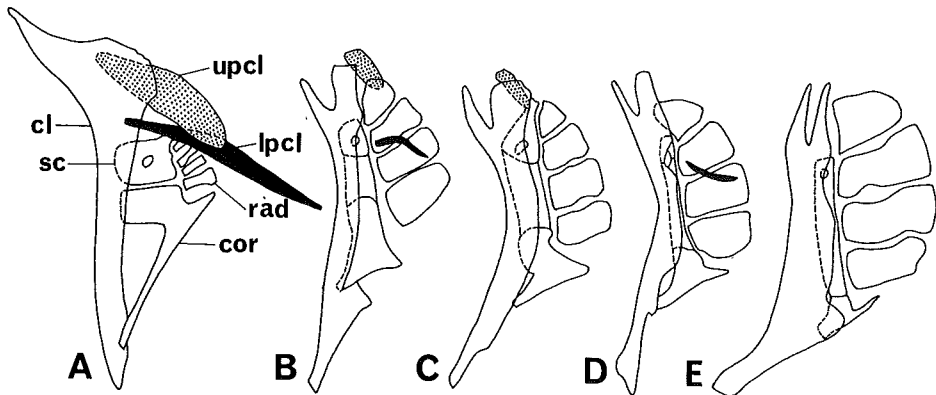


Fig. 6. The upper and lower postcleithra of *Lateolabrax japonicus* and of some gobiids. A, *Lateolabrax japonicus*; B, *Bostrychus sinensis*; C, *Odontobutis obscura obscura*; D, *Acanthogobius flavimanus*; E, *Sicyopterus japonicus*. cl, cleithrum; cor, coracoid; lpcl, lower postcleithrum (black portions); rad, radial; sc, scapula; upcl, upper postcleithrum (stippled portions).

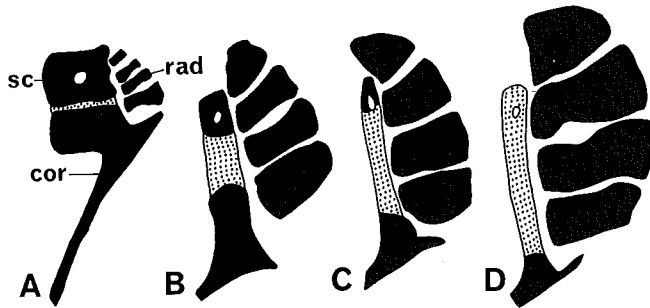


Fig. 7. The scapula of *Lateolabrax japonicus* and of some gobiids. A, *Lateolabrax japonicus*; B, *Bostrychus sinensis*; C, *Acanthogobius flavimanus*; D, *Sicyopterus japonicus*. Black portions, bones; stippled portions, cartilage; cor, coracoid; rad, radial; sc, scapula.

rum, and species without both postcleithra. The upper and lower postcleithra are connected by connective tissue in generalized perciforms, but those of gobiids are wide apart, as shown in Fig. 6. Most species of the Eleotridinae including all species with the endopterygoid have the upper postcleithrum, and most of them have also the lower postcleithrum. However, some of them have only the upper postcleithrum but lack the lower postcleithrum as shown in Table

Table 3. The infraorbital, endopterygoid, upper and lower postcleithra, and the ossified scapula in species of the Eleotridinae. +, ossified scapula incompletely surrounds the foramen; ++, ossified scapula completely surrounds the foramen; -, no ossified scapula.

species	Infraorbital	Endopterygoid	Upper postcleithrum	Lower postcleithrum	Ossified scapula
<i>Micropercops swinhonis</i>	present	present	present	absent	+
<i>Odontobutis obscura obscura</i>	absent	present	present	absent	++ or +
<i>Percottus glehmii</i>	absent	present	present	absent	+
<i>Xenisthmus clarus</i>	absent	absent	absent	absent	++
<i>Grahamichthys radiatus</i>	absent	absent	absent	absent	+
<i>Grahamichthys</i> sp.	absent	absent	absent	absent	-

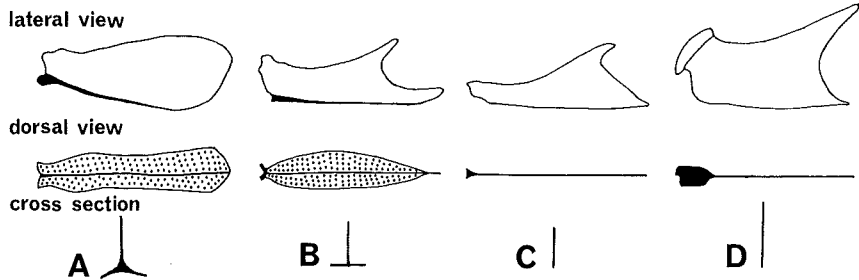


Fig. 8. The urohyal of *Lateolabrax japonicus* and of some gobiids.

A, *Lateolabrax japonicus*; B, *Bostrychus sinensis*; C, *Xenisthmus clarus*; D, *Acanthogobius flavimanus*. Stippled portions, laminae.

3. Among them is included *Micropercops swinhonis* which even has the infraorbital bone. A few species have neither the upper nor the lower postcleithrum (Table 3). Species which have the lower postcleithrum but lack the upper postcleithrum have not been found in the Eleotridinae. However, all species of the Gobiinae lack the upper postcleithrum, and they are divided into those with a lower postcleithrum and those without it. In some species of the Gobiinae there is individual variation in the presence or absence of the lower postcleithrum, e.g., *Pterogobius elapoides* and *Rhinogobius flumineus* (Prince Akihito, 1969).

Branchiostegal rays. Generalized perciforms have six to seven branchiostegal rays and gobiids have five to six. Species with six branchiostegal rays are included in the Eleotridinae and those with five branchiostegal rays in the Gobiinae, the species of which lack an anterior branchiostegal ray.

Scapula. The scapula is a bone which shows differences in ossification among various gobiids (Fig. 7). Compared with the scapula of generalized perciforms the ossified part of the scapula is reduced or absent in the gobiids. Most species of the Eleotridinae have an ossified scapula but *Grahamichthys* sp. has no ossified scapula. Many species of the Eleotridinae have the scapular foramen completely enclosed by the ossified scapula. This condition is also found in *Xenisthmus clarus*, which lacks various bones. On the other hand some species, including *Micropercops swinhonis* and the species of the genus *Butis*, whose loss of bones is limited to a very few, have the scapular foramen incompletely enclosed by the ossified scapula.

No species among the Gobiinae have the scapular foramen completely enclosed by the ossified scapula; most species have the scapular foramen incompletely enclosed by the ossified scapula (Fig. 7 C) or have no ossified scapula (Fig. 7 D). Some species have a much reduced ossified scapula.

Although there are cases where individual variation is found in such a species as *Odontobutis obscura obscura* of the Eleotridinae where the scapular foramen is completely or incompletely enclosed by the ossified scapula, or in such a species as *Mugilogobius abei* of the Gobiinae which has either a much reduced or no ossified scapula, the same type of scapula is usually found in all members within a genus (Prince Akihito, 1969).

Urohyal. Most species of the Eleotridinae have laminae on the lower side of the urohyal such as found in most generalized perciforms (Fig. 8), but a few species of the Eleotridinae and all of the Gobiinae lack these laminae. The species of the Eleotridinae without the laminae coincide with those without the upper and lower postcleithra.

Discussion

From the comparison of sensory canals of the gobiids with those of generalized perciforms, gobiids with the least loss of sensory canals are considered to be the most unspecialized. Among the gobiids with the least loss of sensory canals (Table 1), the type found in *Bostrychus sinensis* seems to retain a basic form of the gobiids. Because this type is closer to generalized perciforms in having a connecting canal between the right and left oculoscapular canals, and except for such species as *Oxyeleotris lineolata* with an additional pore, the sensory canals of most gobiids can be deduced from this type as the loss of a certain part of the canals or of a certain pore. However, from the fact that specific variation in the reduction of sensory canals is found within a genus, e.g., *Bostrychus* and *Oxyeleotris*, it is considered that the reduction of canals has often occurred independently during the course of evolution.

On the other hand the species of the Gobiinae with a continuous oculoscapular canal are considered to have a secondary reconnection of the anterior and posterior oculoscapular canals for the following reasons. Those species of the Gobiinae with a continuous oculoscapular canal lack supratemporal bones and pores I and J. In the case of the genus *Bathygobius*, the species with a continuous oculoscapular canal have more specialized characters than those with separated oculoscapular canals such as a row of sensory papillae on the cheek situated in a deeper groove than that of the species with separated oculoscapular canals; the two canals of some species of the genus are so close (Fig. 3 B) that the continuous canal found in other species of the genus is likely to have been formed by unification of the two canals. Thus, species with a continuous oculoscapular canal are considered to have evolved from species with separated oculoscapular canals within each genus. Accordingly although the reduction of the sensory canals has occurred independently in various gobiids, it is considered that all species of the Gobiinae have evolved from a gobiid which has separated oculoscapular canals and a reduced preopercular canal without the canal below pore O.

The degeneration trend of bones in the gobiids is also conspicuous when compared with the bones of generalized perciforms. With regard to the infraorbital bone, endopterygoid, upper postcleithrum, and one branchiostegal ray, their loss seems to be in the order shown in Table 4. Accordingly species with the infraorbital bone but without the endopterygoid have not been found, and species which lack one branchiostegal ray (Type E), namely those of the Gobiinae, have no infraorbital bone, endopterygoid, or upper postcleithrum. The loss of the laminae on the lower side of the urohyal seems to be accompanied by the loss of the upper postcleithrum.

Although the above mentioned bones of some species of the genera *Bostrychus* and

Table 4. Five types of gobiids classified on the basis of various degrees of loss of bones.

Examples: Type A, *Bostrychus sinensis*; Type B, *Eleotris oxycephala*; Type C, *Philypnodon grandiceps*; Type D, *Xenisthmus clarus*; Type E, *Acanthogobius flavimanus*. +, present; -, absent.

Bones	Eleotridinae				Gobiinae
	Type A	Type B	Type C	Type D	Type E
Infraorbital	+	-	-	-	-
Endopterygoid	+	+	-	-	-
Upper postcleithrum	+	+	+	-	-
Branchiostegals	6	6	6	6	5

Oxyeleotris were not examined except for the infraorbital bone, it is inferred that these bones should be present in these species from the observation of the bones in other species of these genera. Thus the species of the Eleotridinae with the infraorbital bone (Type A) are considered to be the most unspecialized, and the species of the Gobiinae (Type E) are very specialized. The other species of the Eleotridinae are between Types A and E from the degree of the specialization of bone. Although the process of the loss of these bones is in one direction, from the presence of individual variation in the infraorbital bone in *Bostrychus sinensis* and *Oxyeleotris marmorata* and specific variation in the endopterygoid within a genus, e.g., *Gobiomorphus* and *Hypseleotris*, it should be considered that the loss of these bones has also occurred in the same sequence but in different evolutionary lines.

The distribution of the loss of the lower postcleithrum and of the reduction of the ossification of the scapula in the gobiids does not coincide well with that of the infraorbital bone, endopterygoid, upper postcleithrum, and branchiostegal rays. For example, *Micropercops swinhonis* and the species of the genus *Butis* both have a larger number of bones than other species of the Eleotridinae, but their scapula foramen is not completely enclosed by the ossified scapula. On the other hand *Xenisthmus clarus*, which lacks even both upper and lower postcleithra, has the scapula foramen completely enclosed by the ossified scapula. However, in view of the general trend, the distribution of the loss of the lower postcleithrum and that of the reduction of the ossification of the scapula are not contradictory to the distribution of the loss of other bones.

Among the gobiids the species with the most unspecialized bones are those with the infraorbital bone which belong to the genera *Bostrychus*, *Incara*, and *Oxyeleotris*, except for *Micropercops swinhonis* which lacks the lower postcleithrum. It is an interesting coincidence that most of these unspecialized species have also the least loss of sensory canals. Among them *Bostrychus sinensis*, *Oxyeleotris herwerdenii*, and *Oxyeleotris marmorata* retain a basic form of gobiid sensory canals. Accordingly these species are considered to be the most unspecialized of the gobiids from the viewpoint of the sensory canals and bones.

From comparison of other characters of these species with generalized perciforms and other gobiids no definitely specialized characters are found in them except for the following.

The fact that the body of *B. sinensis* is mostly covered by cycloid scales except for the area behind the pectoral fins is considered to be more specialized than the condition of *O. herwerdenii* and *O. marmorata*, whose body is covered by ctenoid scales.

On the other hand the fact that *O. herwerdenii* and *O. marmorata* have no vomerine teeth is considered to be more specialized than the condition in *B. sinensis*, which has vomerine teeth, because generalized perciforms have this character. But although having the vomerine teeth seems a more unspecialized condition than lacking them, this conclusion is not necessarily true, because in some cases the vomerine teeth could have appeared secondarily. I found that, besides *Bostrychus*, the vomerine teeth are present only in a few other genera, *Gobiomorus* and *Percottus* in the Eleotridinae, and *Stonogobiops* in the Gobiinae. Since the genus *Stonogobiops* lacks all the bones previously mentioned as well as having reduced sensory canals or no canals, the genus is considered to be rather specialized even among the genera of the Gobiinae.

In conclusion, *B. sinensis*, *O. herwerdenii*, and *O. marmorata* seem to represent a basic form closest to the ancestral form of gobiids when compared with generalized perciforms.

A final remark is added about *Rhyacichthys aspro*, the sole species in the family Rhyacichthyidae in the suborder Gobioidi.

This species has sensory canals similar to those of generalized perciforms. However, it has a set of bones similar to that of *B. sinensis*, lacking several bones found in generalized perciforms. An unspecialized character of the bones of *R. aspro* is the number of epurals. It

has three epurals, which is the same number as in generalized perciforms, whereas the gobiids have one or two epurals. Three epurals are found as individual variation in a few species of gobiids, but are not found as a specific character in any gobiids*. But *R. aspro* has on the other hand specialized characters adapted to life in torrential streams, such as the strongly depressed head, the small ventrally directed mouth, the thickened pectoral fins, and widely separated thickened pelvic fins, in addition to loss of the lower postcleithrum.

R. aspro does not seem to be a form close to the ancestral gobiid form, because it has some specialized characters in addition to its unspecialized characters.

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* According to Wongrat (unpublished) *Micropercops swinhonis* has three epurals, but individuals with two epurals have also been found.